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La portada

LLémur rojo (*Varecia rubra*) tomando "tomar el sol" durante una fresca mañana, esta es una forma de calentar sus cuerpos. Los lémures rufos rojos comen frutas, hojas, flores y néctar. Esta especie se puede encontrar en las copas de los árboles hasta 25 metros sobre el suelo y es endémica del noreste de Madagascar en África (Fotografia de Sergio Ticul Alvarez Castañeda).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. "Ozomatli" es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. " Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo."

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DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 14, No. 3, Septiembre-diciembre del 2023, es una publicación cuatrimestral editada por la Asociación Mexicana de Mastozoología A. C. Hacienda Vista Hermosa 107, Colonia Villa Quietud, Coyoacan 04960. Distrito Federal, México. Telefono (612) 123-8486, www.mastozoologiamexicana.org, therya@cibnor.mx. Editor responsable: Dr. Sergio Ticul Álvarez Castañeda. Reservas de Derechos al Uso Exclusivo No. 04-2009-112812171700-102, ISSN: 2007-3364 ambos otorgados por el Instituto Nacional de Derechos de Autor. Responsable de la última actualización de este número, Unidad de informática de la Asociación Mexicana de Mastozoología A. C. Dr. Sergio Ticul Álvarez Castañeda. Instituto Politécnico Nacional 195. La Paz, Baja California Sur, C. P. 23096. Tel. (612) 123-8486, fecha de la última modificación 30 septiembre 2023.

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El objetivo y la intención de *THERYA* es ser una revista científica para la publicación de artículos sobre los mamíferos. Estudios de investigación original, editoriales y artículos de revisión son bienvenidas.

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Letter to the Editor:

The (integrative) taxonomy driving conservation of cryptic species: an example of Neotropical *Myotis*

Taxonomy is a discipline in biology responsible for describing, classifying, and naming organisms, as well as postulating hypotheses about the evolutionary relationships between taxa (Tancoigne *et al.* 2011). Taxonomic studies have profound implications in several areas of biology, such as ecology, evolution, genetics, epidemiology, and zoonotic surveillance, as well as directly influencing public policies focused on health and the environment (Cracraft 2002; Pearson *et al.* 2011; Cook *et al.* 2020). However, for decades, taxonomy has experienced a global crisis, which is largely related to the lack of large investments compared to other fields of biology (Buyck 1999; Godfray 2002; Drew 2011; Pearson *et al.* 2011).

The economic devaluation of taxonomy has created a cyclical problem, causing an abrupt reduction in the formation of new taxonomists over the past decades (Buyck 1999; Joppa *et al.* 2011; Drew 2011; Bacher 2012; Boubli *et al.* 2012). Consequently, (i) there are fewer citations from taxonomic studies, an index that is used to measure researcher productivity in many institutions; and (ii) self-citations are more frequent among taxonomy-specialized journals, which has resulted in a lower impact factor when compared to those in other areas (Zeppelini *et al.* 2020). This scenario can influence the choice of projects to be financed, feeding the cycle of disinterest and marginality of taxonomy in the biological sciences.

Knowing the real diversity of organisms on our planet is essential for the sustainable use of natural resources and the management and conservation of species (May 1988). Anthropogenic activities are transforming the Earth's surface, changing the composition of the atmosphere, and altering the climate, all of which are pointed out as important causes of biodiversity loss (Butchart *et al.* 2010). The decline in species richness has been documented for different taxa around the world (Pimm *et al.* 1995; Li *et al.* 2006; Spooner *et al.* 2018). The current species extinction rate is 100 to 1,000 times higher than the background extinction rate, with the highest species loss average in the last 65 million years, giving rise to the sixth mass extinction event on Earth (Pimm *et al.* 1995; Ceballos *et al.* 2015, 2017). It is estimated that a large part of these extinctions is represented by species still unknown to science since less than 25 % of the estimated biological diversity of eukaryotes has been formally described (Mora *et al.* 2011; Costello *et al.* 2013), putting taxonomic studies at the forefront of the biological sciences. In addition, taxonomic imprecision can generate bias in the management and conservation of Earth's biological heritage (Morrison *et al.* 2009; Gutiérrez and Helgen 2013).

Taxonomic studies often include hundreds or thousands of museum specimens and can, in addition to defining the real range of distribution, provide information on the natural and demographic history of species, which is essential for the management and conservation of biodiversity. The challenge is that many of the organisms that have yet to be described are within the gray zone, which is composed of phenotypically identical species, although they represent independent evolutionary lineages (Roux *et al.* 2016). A solid example of the importance of taxonomy for the conservation of cryptic taxa was revealed by the recent taxonomic revisions of the neotropical bats of the genus *Myotis*, which have revealed a high diversity of species, many endemic and with geographic distributions restricted to habitats severely impacted by modern human action (*e. g.*, Moratelli *et al.* 2011, 2013, 2016, 2017; Novaes *et al.* 2021a, b, c, 2022a, b).

Myotis is the most speciose bat genus, with more than 140 living species distributed in all ecoregions of the Earth, except for the polar icecaps (Moratelli *et al.* 2019a). In the Neotropics, there are *ca*. 35 species currently recognized, although this number is still under-sampled (Clare *et al.* 2011; Larsen *et al.* 2012; Novaes *et al.* 2022a, b, c). A comprehensive and exhaustive taxonomic review of *Myotis* has been conducted by our research team for over a decade, resulting in the description of new species and the recognition of cryptic complexes that have refined the taxonomic and geographic limits of species (see the list of references by R. Moratelli and R. L. M. Novaes in this letter). Our results support a conservation status revaluation for some species and may contribute to the creation of conservation plans for these taxa.

A striking example comes from Caribbean species. For more than four decades, *Myotis nesopolus* remained divided into two subspecies: *M. n. nesopolus*, occurring on the islands of Bonaire and Curaçao, in the Lesser Antilles; and *M. n. larensis*, occurring in semi-arid lowland habitats on mainland Venezuela (Genoways and Williams 1979; Moratelli *et al.* 2019a). However, recently we raised *M. larensis* to the species level using an integrative approach based on molecular and morphological data (Novaes *et al.* 2021a). Consequently, *M. nesopolus* is now an endemic species of two small Caribbean islands, and the restriction of the species to the islands of Curaçao and Bonaire raises a strong concern about its conservation. Solari (2016) indicates that these populations are under threat due to habitat loss caused by agriculture and urbanization that aim to meet greater tourist demand and human population growth. Therefore, we suggest a review of the conservation status of this species, currently classified as Least Concern in the IUCN Red List of Threatened Species (Solari 2016). Currently, *M. nesopolus* has a distribution range of 738 km^2, and the occupied area is certainly much smaller. Moreover, populations are fragmented, with only two known occurrence localities, and its habitat is experiencing continued decline due to human activities. Possibly, *M. nesopolus* is seriously threatened with extinction, and the conditions presented above allow us to classify the species in the IUCN category 'Endangered' by the criteria B1ab(iii), following IUCN (2016). The same rationale was applied for the other species of Caribbean *Myotis* (*M. dominicensis*, *M. martiniquensis*, and *M. nyctor*), currently classified as 'Vulnerable' due to endemism on small islands with progressive habitat loss (Larsen 2016a, b, c).

The conservation status of *M. attenboroughi* —an endemic species from Tobago that was recently described by our research group— has, however, not been defined yet (Moratelli *et al.* 2017). An integrative study based on molecular and morphological data resulted in the description of *M. attenboroughi* from individuals collected in 1981, which are the only known records for the species (Moratelli *et al.* 2017). Tobago is an island of 300 km^2 and experiences a marked change in its original vegetation cover (Maharaj *et al.* 2019). Therefore, comparing the information available on this species to the conservation status and potential threats identified for other Caribbean congeners, it is likely that *M. attenboroughi* also faces a serious risk of extinction (Moratelli *et al.* 2017).

Additional examples emerge from South American rainforests. An important focus of our studies was *M. nigricans*, a species historically considered widely distributed in the Neotropics, occurring from México southward to northern Argentina (LaVal 1973; Wilson 2008). However, our taxonomic assessments (some with integrative approach) revealed that *M. nigricans* is a species complex yet to be unveiled. Different populations previously included in *M. nigricans* have already been given new names and now represent full species (*i. e.*, Moratelli and Wilson 2011; Moratelli *et al.* 2011, 2013, 2016, 2017, 2019b; Novaes *et al.* 2022a). Far beyond taxonomy, this review made an unexpected discovery: many of these newly identified species may be at risk of extinction due to habitat loss and climate change. This appears to be the case for *M. dimimutus*, *M. izecksohni*, and *M. handleyi*, which were treated under *M. nigricans* until recently.

The tiny and delicate species *M. diminutus* was described in 2011 from a single specimen collected in 1979 in Los Ríos, a locality on the western slope of the Ecuadorian Andes (Moratelli and Wilson 2011). Later, a second specimen for the species, collected in 1959, was discovered in a biological collection, extending its distribution range to southern Colombia (Moratelli and Wilson 2014). Although we have examined over seven thousand specimens of neotropical *Myotis* deposited in over 40 biological collections worldwide, *M. diminutus* turned out to be an incredibly rare species, known from less than 10 specimens. This species appears to be associated with the lowlands in the western Andes, which are part of the Tumbes-Chocó-Magdalena biodiversity hotspot. The region includes moist and dry forests and other ecosystem formations, extending from the Panama Canal southward along the Pacific lowlands to northwestern Perú. The area houses high levels of species diversity and endemism and has experienced severe habitat loss in the last few decades (Myers *et al.* 2000; Ceballos and Ehrlich 2006). The Ecuadorian moist forests, where the holotype of *M. diminutus* was collected, currently include a disrupted series of small fragments under continuing threat (Moratelli and Wilson 2011). Given this loss of habitat and the absence of *M. diminutus* in collections from recent fieldwork in Ecuador (*e. g.*, the material in the Texas Tech University, Lubbock, Texas), the current conservation status of *M. diminutus* is uncertain. The species is known from a few individuals collected from the 1950s to the 1980s. Based on this meager documentation, it is likely that *M. diminutus* is facing problems maintaining its population viability in the long term, which deserves a reassessment of its conservation status at regional and global levels. No wonder Moratelli and Wilson (2014) recommend surveys in the Chocó ecoregion (where *M. diminutus* potentially still occurs) to try to confirm whether the species survives in those forest remnants.

Myotis izecksohni was described in 2011 based on specimens from the Brazilian Atlantic Forest as being endemic to this biome, where it appears to be strongly associated with highlands above 900 masl (Moratelli *et al.* 2011). The species occurs in dense rainforest habitats located on mountain tops in southeastern South America, where the landscape of the Atlantic Forest is highly fragmented due to a historical process of land occupation for agricultural activities and, more recently, due to the expansion of urbanization (Ribeiro *et al.* 2009). The Atlantic Forest is one of the most threatened biomes in the world and is currently reduced to less than 10 % of its original forest coverage (Ribeiro *et al.* 2009). At the northern portion of the South American continent is *M. handleyi*, described in 2013 from specimens that inhabit two cordilleras in northern Venezuela at altitudes between 1,000 and 2,200 masl (Moratelli *et al.* 2013). These mountains are formed by a complex landscape, which includes areas of deciduous dry forest in lower altitudes, evergreen rainforests in higher altitudes, and secondary areas with strong agricultural pressure and intense degradation of the original vegetation (Anderson and Gutiérrez 2009; Quiroga-Carmona and Molinari 2012).

Despite completely different evolutionary trajectories and biogeographical contexts, what can unite *M. izecksohni* and *M. handleyi* towards a single destination is climate change. It is widely recognized that biotic (*i. e.*, resource availability) and abiotic (*i. e.*, temperature and rainfall) changes along elevation gradients are among the main determinants of species occupation, richness, and abundance (McCain 2007; Byamungu *et al.* 2021). Both *M. izecksohni* and *M. handleyi* occur in mountainous habitats, and environmental changes may lead these species to shifts in their ranges; the shift to higher elevation habitats may represent the loss of a significant percentage of their current range or even regional extinction. Although no investigations have been carried out on the susceptibility of neotropical *Myotis* to climate change, it is not merely speculative to think that species associated with mountainous areas and high altitudes, especially endemic ones, could be at risk.

Species newly described from recently revealed cryptic complexes may also be under threat, as in *M. moratellii* —endemic to the same lowland area where *M. diminutus* occurs in Ecuador (Novaes *et al.* 2021b); in *Myotis pampa*— the only bat endemic to the subtropical grassland plains of the South American Pampa, with a very restricted occurrence area and strong anthropogenic pressure (Novaes *et al.* 2021c); and in *M. arescens*— a bat endemic to Chile and recently raised to species level, which occupies a narrow and highly impacted area of desertic shrubland and sclerophyllous forest (Novaes *et al.* 2021b). These species were only revealed from integrative taxonomic reviews that evaluated many morphological, genetic, and bioacoustic characters.

The message we want to highlight here is that studies that act on the frontiers of cryptic diversity have often revealed new species and indicated small distribution areas for several species, many of which come from environments already quite disturbed (*e. g.*, Moratelli and Wilson 2011, 2014; Novaes *et al.* 2021b). The case of neotropical *Myotis* is an emblematic and valuable example of this issue. Without this broad (integrative) taxonomic revision, all the newly described species of *Myotis* would still be considered part of a much less diverse evolutionary and ecological group and, therefore, of least concern from a conservation point of view. Thus, in the case of cryptic organisms, taxonomy becomes the initial step and, consequently, a very important tool for conservation.

The threat category of species is essential for directing biodiversity conservation efforts on local, regional, and global scales. However, the classification of taxa into any of the existing categories requires stable taxonomic knowledge and a considerable accumulation of information on species' population variation, natural history, distributional limits, habitat disturbances, etc. (*e. g.*, IUCN 2016). In the absence of ecological studies —which is a reality for most cryptic species— much of this information emerges from taxonomic reviews. Studies based on diverse datasets, such as DNA sequences and ecological niche modeling, have helped to understand the demographic trajectory of species in historical time, identifying factors such as the absence of gene flow, effective geographical barriers, and distributional limits based on the occupation capacity of specific habitats. Indeed, modern taxonomic studies have focused on delimiting species as products of a unique evolutionary trajectory, analyzing large sets of morphological, genetic, ecological, bioacoustic, and behavioral data that help tell the life story of taxa. These datasets can and should be considered during risk assessments of threatened species.

Taxonomy, especially when using integrative approaches, can be decisive in pointing out priority localities for research and conservation actions due to the presence of endemic species and high diversity. Also, the enormous systematic knowledge that has been generated lays the groundwork for studies with biogeographic and demographic approaches, which are essential to assess environmental threats to species and support action plans for conservation (Costello *et al.* 2015).

Considering this, the strengthening of taxonomy in the face of the current biodiversity crisis is imperative. In this way, a stimulus for the training of new taxonomists who maintain an integrated view of other branches of biology is also essential. Therefore, we point out here the need to create specific funding for taxonomic research, increasing the knowledge on the biological diversity on Earth and, consequently, determining the real conservation status of species in a changing world.

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Spatial and temporal coexistence of medium-sized felines and their potential preys in Sierra Madre del Sur of Guerrero, México

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Two species of similar size and trophic niche could not coexist in the same space and time unless the resources are diverse, abundant, and can be shared. In the Sierra Madre del Sur, Guerrero, Mexico, three felines of similar size coexist, *Herpailurus yagouaroundi*, *Leopardus pardalis,* and *Leopardus wiedii*. The objective of this research was to identify the spatiotemporal patterns that allow the coexistence of three felines and their potential preys, as well as to evaluate how the presence of humans and livestock influence their use of space and time. We hypothesized that the three felines coexist due to a differential use of time and space. Therefore, low or moderate overlap is expected, as well as a positive relationship with prey richness but negative regarding the presence of humans and livestock. Between 2009 and 2019, information was obtained on how the three feline species and their potential prey use time and space in eight landscapes with wide environmental variation using camera trapping. With a total sampling effort of 27,014 days/trap in 1,170 km^2, 362 independent records of felids and 2,287 of 12 potential preys were obtained. Overlap in daily activity patterns (Δ) was estimated, and spatial co-occurrence was calculated using epsilon ($\mathcal{E}$) values. Our results show that jaguarundi displayed a diurnal activity pattern and had an overlap of $\Delta = 0.22$ with ocelot and $\Delta = 0.26$ with margay; ocelot and margay were nocturnal with an activity overlap of $\Delta = 0.87$. The spatial co-occurrence between the three felid species was positive: $\mathcal{E} = 2.61$ between ocelot and margay, $\mathcal{E} = 3.22$ between ocelot and jaguarundi; and $\mathcal{E} = 6$ between jaguarundi and margay. The temporal overlap and spatial co-occurrence among felines showed a similar use of resources, and their distribution coincide with the one of some of their potential preys, may be related to predation strategies. Temporal overlap and spatial co-occurrence alone do not limit the coexistence of species; but the environmental differences of the landscapes do influence the variation and temporal dynamics of the felines studied in the Sierra Madre del Sur de Guerrero.

Dos especies de tamaño y nicho trófico similar no podrían coexistir en un mismo espacio y tiempo, a menos que los recursos sean diversos, abundantes y puedan ser repartidos. En la Sierra Madre del Sur (SMS) del estado de Guerrero, México, cohabitan tres felinos de talla similar: *Herpailurus yagouaroundi*, *Leopardus pardalis* y *Leopardus wiedii*. Por lo que, el objetivo de esta investigación fue identificar los patrones espacio-temporales que permiten la coexistencia de los tres felinos y sus presas potenciales, así como evaluar el efecto de la presencia humana y de ganado sobre el uso que las especies hacen del tiempo y el espacio. Se planteó la hipótesis de que los tres felinos coexisten debido a un uso diferente del tiempo y del espacio; por lo que se esperan traslapes bajos o moderados, así como una relación positiva con la riqueza de presas, pero negativa respecto a la presencia de humanos y de ganado. Entre los años 2009 y 2019, en ocho paisajes con una amplia variabilidad ambiental y mediante fototrampeo, se obtuvo información sobre como las tres especies de felinos y sus presas potenciales usan el tiempo y el espacio. Con un esfuerzo total de muestreo de 27,014 días/trampa en 1,170 km^2, se obtuvieron 362 registros independientes de los felinos y 2,287 de 12 presas potenciales. Se estimó el traslape en los patrones de actividad diaria (Δ), y se calculó la co-ocurrencia espacial mediante el valor de épsilon ($\mathcal{E}$). Nuestros resultados muestran que, el patrón de actividad diaria del jaguarundi fue diurno y tuvo un traslape de $\Delta = 0.22$ con el ocelote y $\Delta = 0.26$ con el margay, el ocelote y el margay fueron nocturnos y presentaron un traslape de actividad de $\Delta = 0.87$. La co-ocurrencia espacial entre las tres especies de felinos fue positiva: entre el ocelote y margay de $\mathcal{E} = 2.61$, entre el ocelote y jaguarundi de $\mathcal{E} = 3.22$; y entre el jaguarundi y el margay fue de $\mathcal{E} = 6$. El traslape temporal y la co-ocurrencia espacial, entre estos felinos mostró un uso similar de los recursos, que también coinciden con algunas de sus presas potenciales, lo que podría estar relacionado con las estrategias de depredación. El traslape temporal y la co-ocurrencia espacial por sí solas no limitan la coexistencia de las especies; pero las diferencias ambientales de los paisajes si influyen en la variación temporal de los felinos en la Sierra Madre del Sur de Guerrero.

Keywords: Activity pattern*; Herpailurus yagouaroundi; Leopardus pardalis*; *Leopardus wiedii*; potential prey; spatial co-occurrence; time.

Introduction

Understanding species coexistence and biodiversity maintenance has long been a central subject for ecologists, so the theory of community assembling based on the ecological niche concept has dominated community ecology for almost a century. However, understanding the mechanisms of species coexistence remains hard to elucidate (Niu *et al.* 2009). One of the most widely cited principles is competitive exclusion (two or more species cannot have exactly the same niche in a habitat and achieve long-term coexistence), which shapes community dynamics (Gause 1934; Albrecht and Gotelli 2001; Valeix *et al.* 2007). Therefore, if the resources available for species (food, space, shelter, and others) in a given ecosystem are limited, one species is ultimately displaced from the community, or this triggers changes in its morphology and behavior, thereby modifying its essential resource requirements (Hutchinson 1959; MacArthur and Levins 1967; Di Bitetti *et al.* 2010). When resources and habitat availability are limited, potentially competing species can coexist through niche differentiation (Schoener 1974; Gordon 2000; Nunez 2011), body sizes, or traits (Rosenzweig 1966; Hunter and Caro 2008). For example, they can change the time of daily activity, select a different area, modify their morphology to use different strata of the habitat, or feed on different prey species, thereby decreasing competition intensity. This has been explained for several groups of carnivores, such as mustelids (Rosenzweig 1966), canids, mephitids, procyonids, and ursids (Hunter and Caro 2008), as well as felids (Di Bitetti *et al.* 2010; Romero-Muñoz *et al.* 2010; Hernández-Saintmartín *et al.* 2013; Ávila-Nájera *et al.* 2016; Porfirio *et al.* 2017; Santos *et al.* 2019).

The temporal and spatial axes of the fundamental niche, which include the abiotic and biotic elements used by a species that does not face competition, have been used to explain the coexistence of species through their differential use of these elements as a segregation strategy to evade competitors or predators. This strategy can strongly influence the structure of feline populations, affecting their distribution, relative abundance, and activity patterns (Carothers and Jaksic 1984; Di Bitetti *et al.* 2010). Similar-sized sympatric felines sharing similar ecological requirements and life histories frequently exploit the same resources (Foster *et al.* 2013), which should lead to competitive exclusion if it were not for the spatial or temporal partition of the ecological niche (Valeix *et al.* 2007). Therefore, interspecific competition can induce niche segregation to avoid interference and improve hunting efficiency through optimal foraging (Cozzi *et al.* 2012).

Human disturbance of natural areas decreases biodiversity and generates indirect and cascading negative effects, such as the alteration of species behavior and interspecific interactions. These can limit the use of space and time, thus affecting the activity patterns of species, niche partitioning, and community structure (Frey *et al.* 2017). Information on these aspects can only be obtained by using non-invasive monitoring technologies and techniques such as camera traps and photo trapping, whose implementation in large areas in the mid and long term is essential in generating this important knowledge.

Three species of medium-sized felines are distributed in the Sierra Madre del Sur (SMS) of Guerrero: jaguarundi (*H. yagouaroundi*), ocelot (*L. pardalis*), and margay or tigrillo (*L. wiedii;* Ruiz-Gutiérrez *et al.* 2020). Many aspects of the natural history of these felids and the factors allowing their coexistence in this area are unknown. Therefore, the present work analyzes information gathered over 10 years in the SMS of Guerrero to establish the temporal and spatial use patterns of these three species as a coexistence mechanism.

Our initial hypothesis was that if the three medium-sized felines coexist through the differentiated use of time and space in the SMS of Guerrero, a low or moderate overlap would be expected in these two ecological niche axes. In addition, we also expected a coincidence between the use of time and space concerning the presence of potential prey and a discrepancy relative to the presence of humans and livestock. Finally, activity patterns were expected to be consistent for all three species across the study area.

Therefore, this work aimed to identify the spatio-temporal patterns of the three felines and their potential prey and the influence of the presence of humans and livestock on the use of collection stations during sampling through information recorded with camera traps.

Materials and methods

Study Area. The study consisted of nine systematic sampling campaigns using camera traps in eight landscapes of the Sierra Madre del Sur (SMS) ecoregion of the state of Guerrero (INEGI-CONABIO-INE 2008). The landscapes considered cover an area of 1,170 km^2 and are located within ejidos and rural communities in the SMS foothills and highlands. They display wide environmental heterogeneity, which includes eight vegetation types: Tropical Deciduous Forest (TDF), Tropical Subdeciduous Forest (TSF), Pine Forests (PF), Oak Forest (OF), Pine-Oak Forest (POF), Oak-Pine Forest (OPF), Mountain Cloud Forest (MCF), Savanna (SAV), in addition to areas with secondary vegetation, grasslands, and crops (Ruiz-Gutiérrez *et al.* 2020). These landscapes stretch across an altitudinal range from 350 masl to more than 2,800 masl (Table 1). They are located in the municipalities of Ajuchitlán del Progreso, Chilpancingo de los Bravo, Coyuca de Benítez, Petatlán, Técpan de Galeana, Tecoanapa, Tlacoachistlahuaca, and Xochistlahuaca (Figure 1).

Field Work. Sampling took place from April 2009 to June 2019 in the eight landscapes. In each, sampling was carried out with a duration between two and six months, covering areas of different sizes (between 81 km^2 and 270 km^2); these comprised 9 to 21 quadrants measuring 9 km^2 each (Table 1). This work was part of the National Census of the jaguar and its preys (Chavez *et al.* 2007).

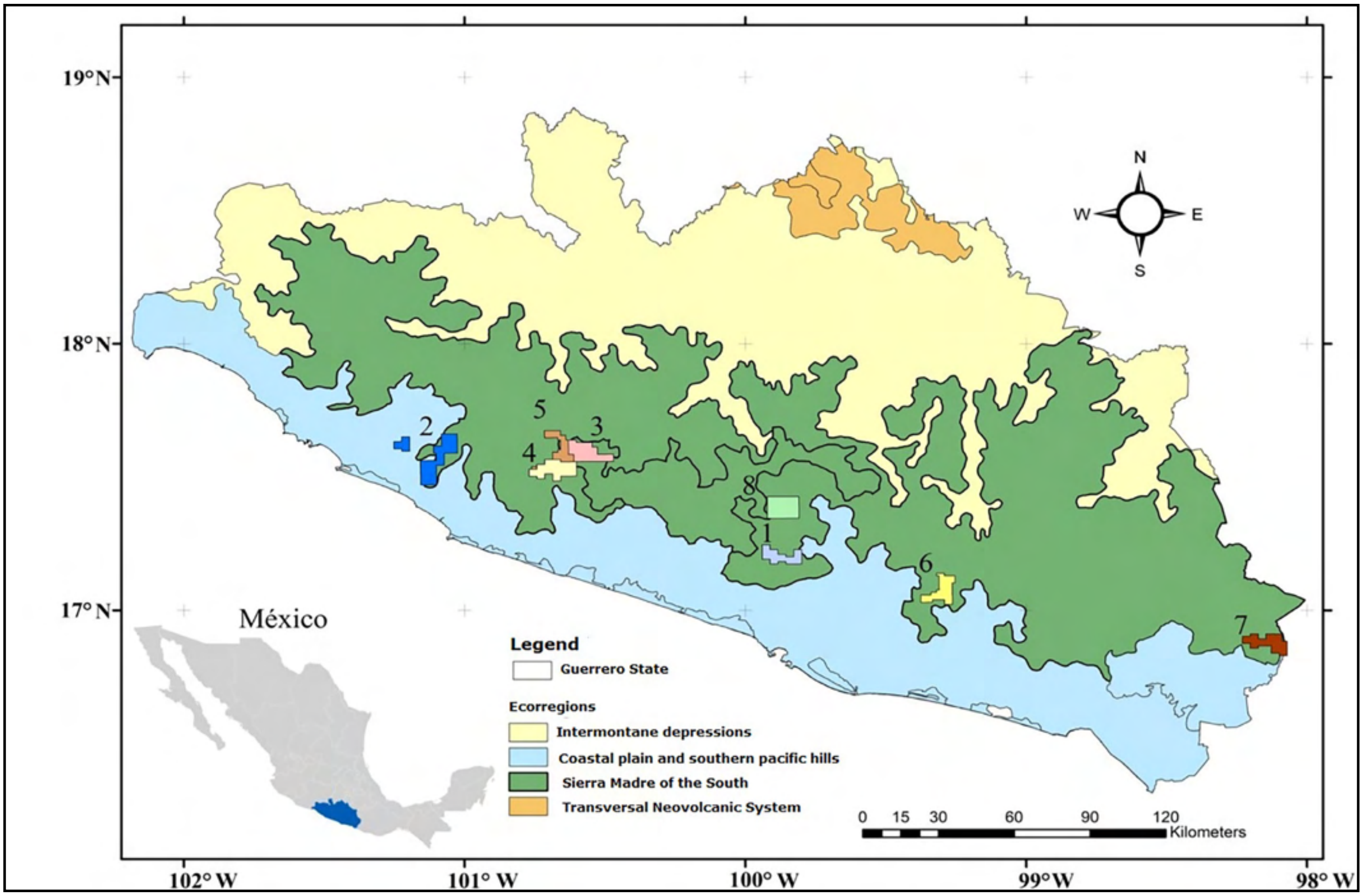

Figure 1. Location of the study area. The figure shows the eight landscapes where sampling was conducted and the ecoregions in the state of Guerrero, Mexico.

In each quadrant, we installed two to three photo trapping stations, each including one and sometimes two camera traps (double stations) separated by 1 to 3 linear kilometers between them. To capture the photographs, we used mainly Cuddeback Digital® camera traps (Xpert, Attack, F2 IR, C1 X-Change Color, and E3 IR), supplemented with Scoutguard® (Sg560) and LTL Acorn® 6210MC. The number of camera traps used for landscape sampling varied between 20 and 80, using a total of 382 cameras in 363 sampling stations; the sampling period fluctuated between 30 and 165 consecutive days. The photo trapping stations were installed on footpaths, roads, nature trails, and water bodies, considering sites with traces (Chavez *et al.* 2013). Cameras were affixed to tree trunks at a height between 30 cm and 50 cm above the ground, at an angle that allowed capturing the flanks of the individuals; these cameras were set with the date and time, to capture one event per minute over 24 hours (Chavez *et al.* 2013; Ruiz-Gutiérrez *et al.* 2020).

Daily Activity Patterns and Overlap Coefficient. The factors analyzed to understand the coexistence of species included daily activity patterns, their overlap, spatial co-occurrence of felines, and the influence exerted by the presence of potential prey, humans, and livestock in the use of the habitat by felines.

Daily activity patterns were analyzed using independent records for each feline species and their potential prey. Only those species with at least 11 independent records were considered (Monroy-Vilchis *et al.* 2011). Photographic records were considered independent when they met any of the following characteristics: 1) consecutive photographs of different individuals of the same species, 2) photographs of the same species with a separation of one hour when the identification of each individual was impossible, and 3) each individual in a photographed group (Ávila-Nájera *et al.* 2016; Contreras-Díaz *et al.* 2021).

The analysis considered independent records of jaguarundi, ocelot, and margay, while potential prey included 12 recorded species that can be potentially preyed on by these felines due to their size and habits. These species are American hog-nosed skunk (*Conepatus leuconotus*), nine-banded armadillo (*Dasypus novemcinctus*), opossum (*Didelphis virginiana*), weasel (*Mustela frenata*), coati (*Nasua narica*), raccoon (*Procyon lotor*), gray squirrel (*Sciurus aureogaster*), porcupine (*Coendou mexicanus*), rabbit (*Sylvilagus cunicularius*), gray fox (*Urocyon cinereoargenteus*), long-tailed wood partridge (*Dendrortyx macroura*) and crested guan (*Penelope purpurascens*; Silva-Pereira *et al.* 2011; Cinta-Magallón *et al.* 2012; Hidalgo-Mihart *et al.* 2020; Pérez-Arteaga *et al.* 2020). The species of mammals (mid-sized and large) and birds were identified by scientific name based on the Mammal Diversity Data Base (2022) and the Peterson and Chalif field guide (1989) field guide, respectively.

The photographs of each species were grouped according to the time of capture into nighttime (20:01 hrs to 6:00 hrs), twilight (6:01 hrs to 8:00 hrs and 18:01 hrs to 20:00 hrs), daytime (8:01 hrs to 18:00 hours; Ávila-Nájera *et al.* 2019). Subsequently, species were sorted according to the observed activity pattern. Daily activity patterns were plotted with the Clock.24 function of the Plotrix package in R version 3.5.1 (Lemon 2006).

The overlap of daily activity patterns between the three felines and their potential prey was assessed through the overlap coefficient (d o Δ), d = , where , are the two functions of activity density over time that are compared; the coefficient can take values between 0 (no overlap) and 1 (total overlap; Ridout and Linkie 2009). Additionally, 95 % confidence intervals for the overlap coefficient were calculated from 1000 repetitions by resampling (*Bootstrap*; Efron and Tibshirani 1993). The statistical and graphical analyses were performed with the *overlay* scrip (Ridout and Linkie 2009) in R version 3.5.1 (R Core Team 2020). It is assumed that activity data are generated by a circular probability distribution. Therefore, activity patterns are contrasted against Δ values. In this sense, Δ values lower than or equal to the 50 percentile of our sample were considered "low-overlap values". Activity patterns ≥ percentile 51 and ≤ percentile 75 were considered "moderate-overlap values", and values equal to or larger than percentile 76 were defined as "high-overlap values" (Monterroso *et al.* 2014).

To analyze whether the time of capture of each of the three species changes in each landscape or across the vegetation types of the Guerrero SMS, a contingency table was constructed with the independent collection records. To determine whether daily activity patterns are random (Zar 2010), a homogeneity test was performed in R version 3.5.1. Specifically, we evaluated a) whether the daily time of capture of the three species remains constant across all the sampled landscapes; b) whether the daily time of capture remains constant when contrasted by vegetation types.

To know whether environments with human activities influence the strategies of temporal and spatial use of the habitat by feline species (Frey *et al.* 2017), we evaluated whether the presence of humans and livestock in photo trapping stations affects the activity patterns of the three felines in the study area. To this end, we categorized the registration data (presence-absence of humans and presence-absence of livestock in the photo trapping stations), and then the patterns were evaluated with the *overlap* package. In addition, to calculate whether there are significant differences in the variation of the hours of activity of the felines in the SMS considering the presence of humans and livestock, a nonparametric Mann-Whitney U-test was performed using the program Past V.4.05. (Zar 2010; Hammer and Harper 2006).

To evaluate the co-occurrence of species, two collection points within the same cell in a two-dimensional grid are considered inputs. To this end, it is necessary to locate the objects in space and measure the distance between those objects (Stephens *et al.* 2017). This work considered the number of photo trapping stations in which each species was recorded within each 9 km^2 quadrant and used the equation by Stephens *et al.* (2019) to estimate the degree of spatial co-occurrence, epsilon (ε).

Where: X and Y are the species, whose co-occurrence will be evaluated, N is the number of records for each species in a particular site or collection station, and ε corresponds to the degree of spatial co-occurrence between species X and Y.

Epsilon (ε) values of zero indicate no interaction between the species; if $\varepsilon \neq 0$, an interaction is inferred, which can be either positive or negative. If $\varepsilon > 0$, species co-occur more frequently than expected in the absence of interaction; conversely, when $\varepsilon < 0$, these two species co-occur less frequently than expected. ε values lower than -1.96 are interpreted as a repulsive interaction, corresponding to a pair of species that do not co-occur; conversely, positive ε values above 1.96 correspond to a pair of species that do interact, that is, an attractive interaction (Stephens *et al.* 2017).

Table 1. Location information of the landscapes in the municipalities that make up the SMS of Guerrero. It indicates the years and months in which the fieldwork was carried out, the number of stations installed with their respective sampling effort by landscape, the territorial extension sampled, and some landscape characteristics such as altitudinal range and vegetation types. #S, Number of Camera trap stations; SE, sampling effort; BTC, Tropical Deciduous Forest; BTS, Tropical Subdeciduous Forest; BP, Pine Forest; BQ, Oak Forest; BQP, Pine-Oak Forest; BMM, Mountain Cloud Forest; SAB, Savanna.

Landscape number	Municipality name	Sampling year	Sampling months	EF/EM	Altitudinal range (m asl)	Sampling area (km^2)	Vegetation types
1	Coyuca-Chilpancingo	2009	April–May	65/2370	900–1900	117	TDF, POF, PF, OPF
2	Petatlán	2011	April–May	67/3486	408–1479	198	TDF, TSF, OF, OPF, POF, MCF
3	Tecpan, Cordón Grande	2013	January–April	32/2438	1299–2810	108	TSF, OPF, POF, MCF
4	Tecpan, Humedades	2014	March–June	27/1380	514–1417	126	TDF, TSF, OF, PF, POF, MCF
5	Técpan, Regional	2015	November–May	53/6314	648–2317	270	TDF, TSF, OF, PF, POF, MCF
	Tecpan, Regional	2019	March–June	20/2040	648–2317	270	TDF, TSF, OF, PF, POF, MCF
6	Tecoanapa	2016–2017	November–January	38/1700	358–1103	81	TDF, TSF, OF, POF, OPF, SAV
7	Tlacoachistlahuaca–Xochistlahuaca	2017	April–June	25/2618	522–1498	117	TDF, TSF, OF, OPF, POF
8	Chilpancingo, Jaleaca	2017–2018	November–March	36/4668	649–1500	117	TDF, OF, OPF, POF

Results

A total of 413 photographic records of the three feline species were obtained, of which 365 were considered independent; for potential prey, 2,287 independent records were captured (Table 2).

Our results suggest that *H. yagouaroundi* has a daytime activity pattern, with 80 % (*n* = 47) of the total records in this category and a peak of activity occurring between 08:01 hrs and 09:00 hrs. The two *Leopardus* species are considered mainly nocturnal: the ocelot had 79 % (*n* = 157) of its records in nighttime hours, with greater activity between 19: 00 hrs and 23:00 hrs, while the margay had 80 % (*n* = 161) of its records at night (Figure 2).

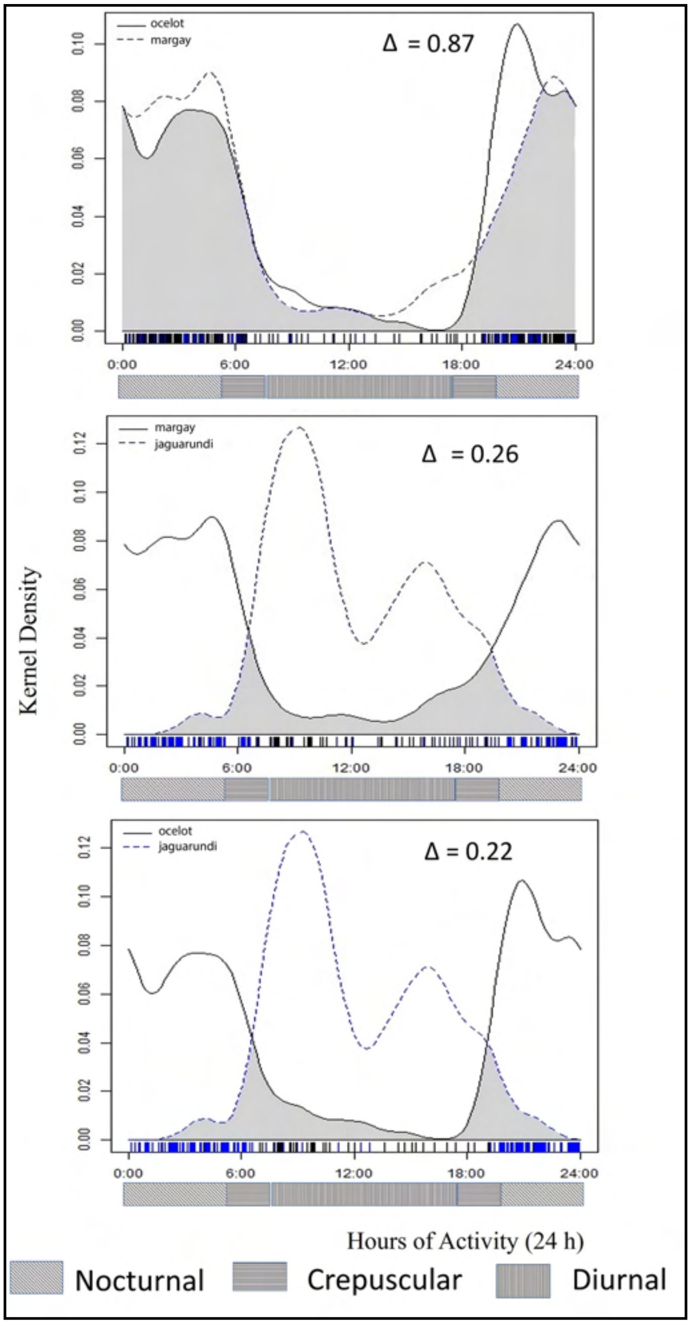

Figure 2. Patterns and overlap of daily activity of medium-sized wild felines in Sierra Madre del Sur of Guerrero, Mexico. The shaded area corresponds to Delta (Δ) values for the overlap between pairs of species.

Table 2. Results of daily activity patterns and number of records of medium-sized felines and their potential prey in Sierra Madre del Sur of Guerrero, Mexico. Nighttime (20:01 hrs–6:00 hrs); twilight (6:01 hrs–8:00 hrs and 18:01 hrs–20:00 hrs); daytime (8:01 hrs–18:00 hrs); ND, not determined (without the minimum of 11 records).

Order/Family/Species	**Number of independent records**	**Activity patterns**
	Mammals	
Carnivora		
Felidae		
Leopardus pardalis	157	Nocturnal
Leopardus wiedii	161	Nocturnal
Herpailurus yagouaroundi	47	Diurnal
Canidae		
Urocyon cinereoargenteus	545	Nocturnal
Procyonidae		
Nasua narica	414	Diurnal
Procyon lotor	40	Nocturnal
Mustelidae		
Mustela frenata	8	ND
Conepatus leuconotus	68	Nocturnal
Didelphimorphia		
Didelphidae		
Didelphis virginiana	495	Nocturnal
Rodentia		
Sciuridae		
Sciurus aureogaster	204	Diurnal
Erethizontidae		
Coendou mexicanus	11	Nocturnal
Cingulata		
Dasypodidae		
Dasypus novemcinctus	187	Nocturnal
Lagomorpha		
Leporidae		
Sylvilagus cunicularius	240	Nocturnal
	Aves	
Galliformes		
Odontophoridae		
Dendrortyx macroura	63	Diurnal
Cracidae		
Penelope purpurascens	12	Diurnal

When human or livestock presence was recorded at the sampling stations, the daily activity patterns of the three feline species showed slight differences according to the Mann-Whitney *U*-test (*e. g.*, *Z* = 0.25/0.35, for jaguarundi); however, these differences are not statistically significant (*P* = 0.79), so the overall activity patterns in the SMS do not vary for this species. The same was observed in the other two species evaluated (Figure 3).

When considering the overlap (Δ) of daily activity patterns in the three species of felines, we observed an overlap of Δ = 0.87 (87 %) between margay and ocelot, with differences in the peaks of activity of each species. The overlap was Δ = 0.26 (26 %) between jaguarundi and margay and Δ= 0.22 (22 %) between jaguarundi and ocelot (Figure 2).

Considering our hypothesis that the activity patterns of the three feline species are constant throughout the study area, our results showed that the frequencies of the time of daily activity of jaguarundi by landscape were constant throughout the study area. By contrast, those of ocelot and margay showed variations in the different landscapes sampled ($P < 0.05$). Considering the vegetation types sampled in the SMS, the period of activity of each of the three species also showed considerable variation, reaching statistical significance ($P < 0.05$).

Regarding potential prey, 2,287 records were captured of 10 species of mid-sized mammals and two bird species, considered here as potential prey for the three feline species. The highest temporal overlap values between predators and their potential prey in this study were as follows. Between ocelot and its potential prey: tlacuache (Δ = 0.83), rabbit (Δ = 0.82), armadillo (Δ = 0.82), porcupine (Δ = 0.80). Between margay and its potential prey: hog-nosed skunk (Δ = 0.90), opossum (Δ = 0.85), gray fox (Δ = 0.84), rabbit (Δ = 0.82), armadillo (Δ = 0.82). And between jaguarundi and its potential prey: long-tailed wood partridge (Δ = 0.79), gray squirrel (Δ = 0.77), coati (Δ = 0.70; Table 3).

Spatial co-occurrence values among the three feline species were significant positive epsilon (ε) values ranging between 2.61 and 6, indicating that these species share the space significantly. With the rest of the mammals (potential

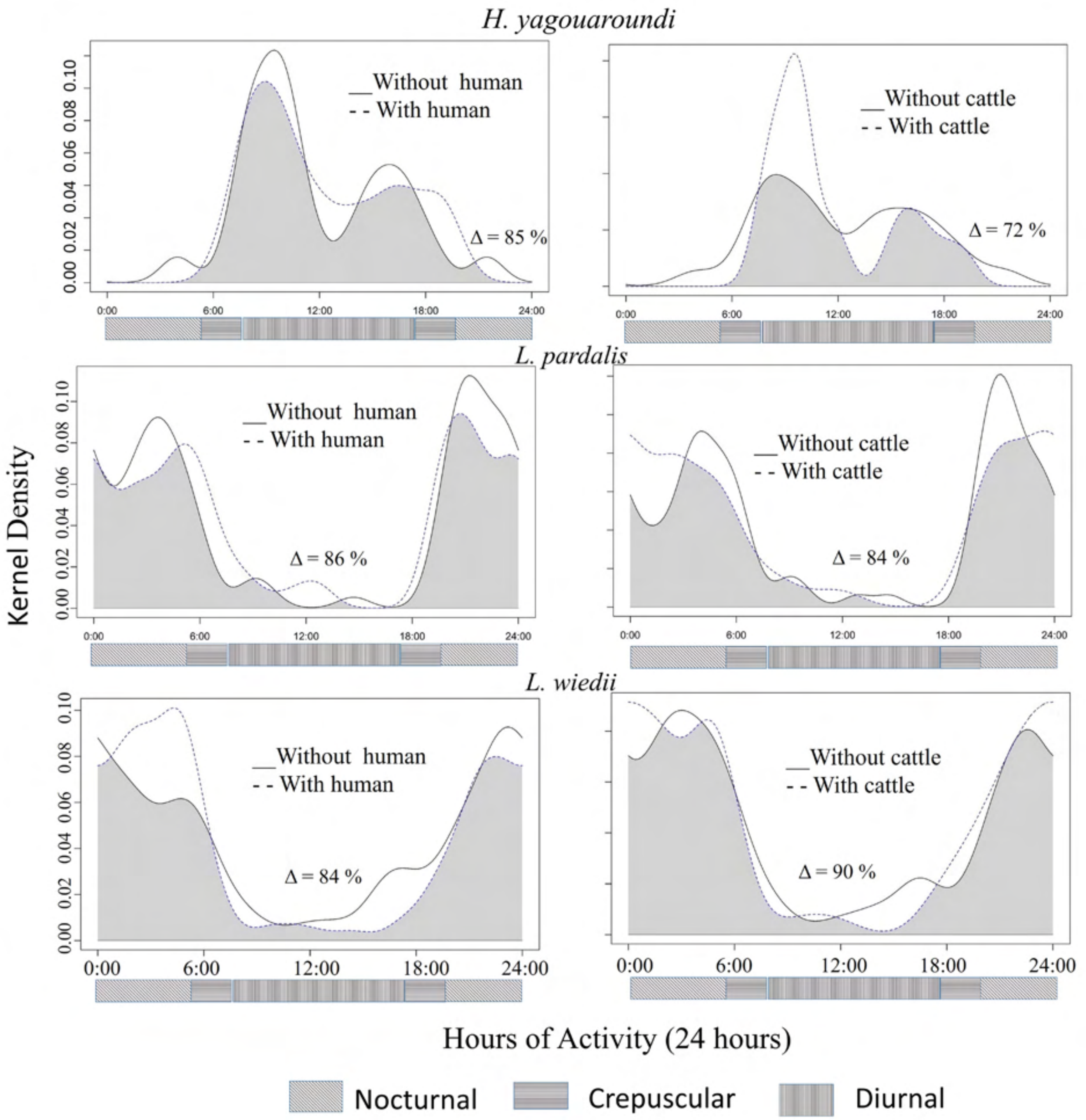

Figure 3. Comparison of daily activity patterns, with emphasis on the overlapping time of activity among the three medium-sized wild feline species, considering the presence of human communities (left) and cattle (right). The shaded area corresponds to Delta (Δ) values for the overlap between pairs of species.

prey), the values are mostly significant and positive, except for some pairs of species with low values (<1.96) and even negative values, such as the case between *H. yagouaroundi* and *P. lotor* or between *L. pardalis* and *Sylvilagus cunicularius*, which showed no spatial co-occurrence (Table 3).

Discussion

The differential use of time (temporal segregation) is one of the factors explaining why species of similar size and feeding patterns can coexist in the same space (Schoener 1974; Kronfeld-Schor and Dayan 2003; Jaksic and Marone 2007). Despite this, the temporal partitioning of the niche is not considered the primary mechanism used by competitors to reduce competition and coexist (Herrera *et al.* 2018), and it is common for animals to be segregated across the trophic or spatial axes of the ecological niche (Schoener 1974). This study documented a diurnal activity pattern of jaguarundi, with a low temporal overlap with ocelot and margay (Giordano 2015). These data support the findings of other studies suggesting that jaguarundi reduces competition by interference with ocelot and margay by selecting opposite periods of activity (Carrera-Trevino *et al.* 2018; Santos *et al.* 2019). We observed that both ocelot and margay are nocturnal and have a wide overlap in their activity patterns. This finding differs slightly from the observations of Santos *et al.* (2019) for Central and South America, who recorded an average overlap of 69 %.

In Sierra Madre del Sur of Guerrero, margay had more records than ocelot, similar to the findings reported elsewhere (*e. g.*, Oliveira *et al.* 2010; Pérez-Irineo and Santos-Moreno 2016). However, for some authors (*e. g.*, Carrera-Treviño *et al.* 2018), ocelot does not appear to negatively influence margay; consequently, there is a wide temporal and spatial overlap between both species. This evidence requires a more in-depth analysis, carrying out specific projects to test whether there are negative spatiotemporal interactions between both species.

The estimated daily activity patterns show that ocelots and margays were active between 17:00 hrs and 06:00 hrs (exclusively at night), similar to other studies (Carrera-Treviño *et al.* 2018; Di Bitetti *et al.* 2010). However, some authors have reported occasional daytime activity (Aliaga-Rossel *et al.* 2006; Di Bitetti *et al.* 2010; Briones *et al.* 2016; Pérez-Irineo and Santos-Moreno 2016; Santos *et al.* 2019). This indicates slight variations in the activity patterns of the species in the different regions it inhabits but that its daily activity is mainly nocturnal. Jaguarundi maintained a consistent daily activity pattern in all landscapes, consistent with our initial hypothesis; however, the pattern changes when vegetation types are considered. Separately, the daily activity patterns of ocelot and margay showed differences considering both factors. As for the records for each of the three species, the presence of livestock generated a difference only in the daily activity pattern of jaguarundi; however, this was not significant.

Table 3. Overlap coefficient (Δ) and co-occurrence values ($\mathcal{E}$) of the three medium-sized felines and their potential prey in Guerrero, Mexico. Epsilon ($\mathcal{E}$) values lower than -1.96 or higher than 1.96 are significant (marked in bold). Negative values (repulsive interaction) correspond to species with which they do not co-occur; positive values above 1.96 correspond to species that co-occur (attractive interaction).

Taxon	***H. yagouaroundi***	***L. pardalis***	***L. wiedii***
	Δ $\mathcal{E}$	**Δ $\mathcal{E}$**	**Δ $\mathcal{E}$**
Mammals			
Carnivora			
Felidae			
Herpailurus yagouaroundi		0.22/ **3.22**	0.26 / **6.00**
Leopardus pardalis			0.88 / **2.61**
Canidae			
Urocyon cinereoargenteus	0.21 / 1.84	0.84 / **3.62**	0.84 / 0.49
Procyonidae			
Nasua narica	0.70 / 0.22	0.44 / 1.53	0.47 / **2.69**
Procyon lotor	0.32 / -0.03	0.78 / 1.42	0.82 / -0.08
Mustelidae			
Mustela frenata	0.13 / **3.51**	0.10 / **3.70**	0.13 / 1.03
Conepatus leuconotus	0.23 / **3.21**	0.86 / **2.09**	0.91 / **4.62**
Didelphimorphia			
Didelphidae			
Didelphis virginiana	0.15 / **2.54**	0.83 / 1.55	0.85 / **4.75**
Rodentia			
Sciuridae			
Sciurus aureogaster	0.77 / **4.65**	0.18/ **2.44**	0.22 / **4.19**
Erethizontidae			
Sphiggurus mexicanus	0.25 / 1.26	0.80 / 0.66	0.81 / 1.89
Cingulata			
Dasypodidae			
Dasypus novemcinctus	0.16 / 1.30	0.82 / 0.53	0.84 / 1.09
Lagomorpha			
Leporidae			
Sylvilagus cunicularius	0.28 / **3.89**	0.82 / -0.72	0.83 / **3.66**
Aves			
Galliformes			
Odontophoridae			
Dendrortyx macroura	0.79 / **6.69**	0.15 / **2.18**	0.19 / **3.45**
Cracidae			
Penelope purpurascens	0.52 / 0.53	0.20 / 0.46	0.23 / 0.78

The presence of potential prey shows a low and moderate overlap of their activity patterns with those of felines (between 25 % and 58 %). Therefore, a broader set of factors likely determines the temporary use of habitat. For example, jaguarundi shared a high temporal overlap (>70 %) with only three of the 12 potential prey (*Dendrortyx macroura, Sciurus aureogaster*, and *Sylvilagus cunicularius*) recorded here; Nonetheless, it is important to consider that this species also feeds on other groups of animals, such as invertebrates, birds, and reptiles (Tófoli *et al.* 2009; Giordano 2015), which are of diurnal habits. Ocelot and margay share a high temporal overlap with seven of their potential prey whose activity is nocturnal. This could influence the daily activity patterns of both species; however, prey abundance may also influence feline patterns, as suggested by Botts *et al.* (2020), An evaluation of the relationship between prey richness, foraging habits, richness of eating habits, and avoidance mechanisms among predators is necessary to identify the factors that influence the daily activity patterns of felines.

Margay showed a high overlap of its daily activity pattern with ocelot, possibly to minimize competition and avoid conflict. This feline uses the arboreal stratum differentially and frequently, preferring sites with low ocelot presence (Di Bitetti *et al.* 2010). This is partially consistent with our data, where margay was the only feline species captured in 63 stations. However, the two species converged in 22 stations, which may indicate that even when the two species were captured at the same time and station, the time elapsed between one record and the next may imply that the two species did not run into one another.

On the other hand, jaguarundi, ocelot, and margay displayed different daily activity patterns, which may allow a high spatial co-occurrence since it substantially decreases the probability of an agonistic encounter between them. However, the latter is hard to demonstrate, although potential intra-guild predation exists (De Oliveira and Pereira 2014).

With respect to prey, eight species co-occurred with felines significantly and more frequently than expected (Table 3). The presence of potential prey species shows a moderate influence on the spatial use of the habitat by felines because only between 41 % and 50 % of these preys coincide with spatial co-occurrence. In contrast, Santos *et al.* (2019) argue that prey availability importantly influences the use of space by these felines, even to a greater degree than environmental variables or interactions between species.

Low ecological niche overlap in some axes indicates coexistence between species (Hardin 1960; Carrera-Treviño *et al.* 2018), as observed along the temporal axis between margay and jaguarundi. However, this work documented that species with high temporal overlap, such as ocelot and margay, can coexist in the same area due to subtle differences in the foraging behavior and daily activity patterns. Therefore, this temporal segregation mechanism may effectively reduce competition between both species (Carothers and Jaksic 1984; Di Bitetti *et al.* 2010). Other mechanisms may also participate in this respect, such as the differentiated use of the habitat and the microhabitat (Hunter and Caro 2008), trophic differentiation, and prey availability, diversity, and abundance (Di Bitetti *et al.* 2010; Botts *et al.* 2020).

The daily activity and habitat use patterns of medium-sized felines result from species adaptation to biotic and abiotic interactions. However, anthropogenic factors such as habitat loss and illegal hunting of these predators and their potential prey may exert an additional influence on them. The results of this study show two coexistence mechanisms. The first implies a marked segregation in the temporal axis of the ecological niche by jaguarundi, whose daily activity pattern is diurnal. In the second, despite a considerable temporal and spatial overlap between ocelot and margay, the coexistence between these species is possible due to the segregation of the ecological niche in one of these two axes.

Our finding of moderate spatial and temporal coincidence with their prey suggests that there are strategies among felines that were not measured in the present study. Therefore, we should evaluate which prey are actually consumed and whether their consumption is different or similar among species (the diet axis of the niche).

Although evaluating the interactions between species with similar biological and ecological traits is an emerging and highly complex topic to analyze in a wide geographic space, as in the present study, it may be the starting point for future studies that address the interactions between pairs of species in further detail. However, future evaluations should cover the three main axes (time, space, and diet) of the ecological niche at different scales and resolutions to improve our understanding of the mechanisms favoring coexistence in these species.

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Influence of forest type on the diversity, abundance, and naïve occupancy of the mammal assemblage in the southeastern Brazilian Atlantic Forest

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The Brazilian Atlantic Forest has the highest rate of native vegetation destruction, which is one of the principal drivers of mammal extinctions. Therefore, reducing information gaps regarding diversity patterns, abundance, and habitat use is crucial to understand mammal persistence in fragmented landscapes. Our objective was to establish the γ diversity and to assess the extent to which the α, and β diversity, the relative abundance, and naïve occupation of medium and large-sized mammal communities differ between seasonal and ombrophilous forests. Between January 2019 and March 2020, we placed 22 camera traps in the Atlantic Forest of Minas Gerais. We calculate Hill's numbers using iNEXT.4steps package, the β-diversity with the Betapart package, as well as the relative abundance index (RAI), and naïve occupancy (PAO). We used Kruskal-Wallis and Mann-Whitney statistical tests to compare the RAIs between different species and forest types. Finally, we calculated the correlation between the RAIs and PAOs. We found 32 species, principally from the orders Carnivora and Artiodactyla. The alpha diversity and evenness profiles were not different between the two forest types (seasonal $q0 = 0.91$, $q1 = 0.99$, $q2 = 1$, $J = 0.83$; ombrophilous $q0 = 0.96$, $q1 = 0.99$, $q2 = 1$, $J = 0.85$). The beta diversity was low ($\beta JAC = 0.37$) which was mostly associated with species turnover ($\beta JTU = 0.34$), while nestedness was almost non-existent ($\beta JNE = 0.02$). The RAIs varied among mammalian species ($H = 115.24$, $P = 0.000$), with the highest values for *Didelphis aurita* ($RAI = 4.55 \pm 7.66$) and *Cuniculus paca* ($RAI = 2.35 \pm 3.73$) and the minor values for *Speothos venaticus* ($RAI = 0.04 \pm 0.24$) and *Galictis cuja* ($RAI = 0.06 \pm 1.19$). The RAIs of species was not significantly different between forests ($U = 453.5$; $Z = 0.37$; $P = 0.70$), and only *Leopardus wiedii* showed significant differences between forests ($U = 84.5$; $P = 0.01$). Most of the mammalian species had restricted occupancy to a few localities (< 50 %). The species *Eira barbara* and *Didelphis aurita* had the highest PAOs in both forests (> 50 %), and the species *Tayassu pecari*, *Tamandua tetradactyla*, and *Speothos venaticus*, the lowest values (5 %). We found a correlation of 75 % between the average RAI and naïve occupancy. The γ diversity was representative and consistent with the species found in the Atlantic Forest, and the relative abundance and naïve occupancy reflected the rarity of most species in the area. Additionally, the only difference between the two forests corresponds to species turnover. Therefore, we must conserve native remnants of both forests to ensure the existence of native mammals, mainly the most threatened species, to prevent more dramatic scenarios of local extinction in Minas Gerais.

La Mata Atlántica Brasileña presenta la mayor tasa de destrucción de vegetación nativa, causa principal de la extinción de mamíferos. Por lo tanto, reducir las lagunas de información relacionadas con los patrones de diversidad α, β y γ, abundancia, ocupación y uso de hábitat es una prioridad, para comprender la persistencia de mamíferos en paisajes fragmentados. Nuestro objetivo fue establecer la diversidad γ, y evaluar en qué medida la diversidad α y β, la abundancia relativa y la ocupación naïve de las comunidades de mamíferos medianos y grandes, contrastan entre bosques estacionales y ombrófilos. Entre enero (2019) y marzo (2020), colocamos 22 cámaras trampa en el Bosque Atlántico de Minas Gerais. Calculamos los números de Hill utilizando el paquete iNEXT.4steps, la β-diversidad con el paquete Betapart, el índice de abundancia relativa (RAI) y la ocupación naïve (PAO). Utilizamos pruebas de Kruskal-Wallis y Mann-Whitney para comparar los RAI entre especies y bosques. Finalmente, calculamos la correlación entre los RAIs y PAOs. Registramos 32 especies, principalmente de los órdenes Carnivora y Artiodactyla. La diversidad alfa y los perfiles de uniformidad no difirieron entre bosques (estacional $q0 = 0.91$, $q1 = 0.99$, $q2 = 1$, $J = 0.83$; ombrófilo $q0 = 0.96$, $q1 = 0.99$, $q2 = 1$, $J = 0.85$). La beta-diversidad fue baja ($\beta JAC = 0.37$), correspondiente al recambio de especies ($\beta JTU = 0.34$), y a una anidación casi inexistente ($\beta JNE = 0.02$). Los RAIs difirieron entre especies ($H = 115.24$, $P = 0.000$), los valores más altos fueron para *Didelphis aurita* ($RAI = 4.55 \pm 7.66$) y *Cuniculus paca* ($RAI = 2.35 \pm 3.73$), y los valores más bajos para *Speothos venaticus* ($RAI = 0.04 \pm 0.24$) y *Galictis cuja* ($RAI = 0.06 \pm 1.19$). Los RAIs no difirieron entre bosques ($U = 453.5$; $Z = 0{,}37$; $P = 0.70$), y exclusivamente *Leopardus wiedii* mostró diferencias significativas entre bosques ($U = 84.5$; $P = 0.01$). La mayoría de las especies presentaron una ocupación restringida (< 50 %). *Eira barbara* y *Didelphis aurita* presentaron los valores más altos en ambos bosques (> 50 %), mientras que *Tayassu pecari*, *Tamandua tetradactyla* y *Speothos venaticus*, los valores más bajos (5 %). Observamos una correlación del 75 % entre los RAIs y PAOs. La diversidad γ fue representativa de la riqueza de especies reportada para la Mata Atlántica. Los RAIs y PAOs reflejaron la rareza de la mayoría de las especies. Adicionalmente, la única diferencia entre los dos bosques correspondió a la rotación de especies. Por lo tanto, debemos conservar los remanentes nativos de ambos bosques para asegurar la existencia de los mamíferos nativos, principalmente las especies más amenazadas, para evitar escenarios más dramáticos de extinción local en la Mata Atlántica de Minas Gerais.

Keywords: Biodiversity; Brazil; conservation; habitat use; mammals; relative abundance index.

Introduction

The Atlantic Forest is widely recognized as a biodiversity hotspot (Myers *et al.* 2000), yet it is also one of the most severely defaunated subregions on the planet, primarily due to anthropogenic drivers (Bogoni *et al.* 2020; Galetti *et al.* 2021). It harbors one of the world's most depleted mammal faunas, with an average historical loss of 62 % (Bogoni *et al.* 2020), primarily resulting from habitat loss, landscape fragmentation (Ribeiro *et al.* 2009; Haddad *et al.* 2015; Bogoni *et al.* 2018; Püttker *et al.* 2020), agricultural expansion, wildlife trafficking, urbanization, industrial development (Campanili and Schäffer 2010) and lack of protected areas (Bogoni *et al.* 2020).

Brazil is home to 770 mammal species, of which 384 are found in the Atlantic Forest (Abreu *et al.* 2021). Among these, 262 are terrestrial, and 109 are endemic to the region (Figueiredo *et al.* 2021). The state of Minas Gerais contains roughly 70 % of all mammal species found in the Brazilian Atlantic Forest, including nearly 60 endemic species (Campanili and Schäffer 2010). Unfortunately, Minas Gerais also harbors 45 species threatened with extinction, according to the List of Endangered Fauna Species in the State of Minas Gerais (COPAM 2010).

Mammals in the region are highly sensitive to changes in landscape structure (Regolin *et al.* 2020), floristic composition (Galetti *et al.* 2009), alterations in species abundance (Fahrig *et al.* 2019), changes in community composition (Beca *et al.* 2017), and the size of assemblages (Bogoni *et al.* 2020a). This vulnerability has resulted in the local extinctions of several mammal species (Bogoni *et al.* 2020), as well as alterations in ecological processes (Oliveira *et al.* 2020) and ecosystem services (Bogoni *et al.* 2020). The degree of threat faced by mammal species in Minas Gerais justifies the urgent need for conservation action in the region.

Insufficient data on population sizes, distribution, and occurrence of many threatened mammal species in Minas Gerais included in the Brazilian Red List pose challenges to understanding their conservation status (Corrêa *et al.* 2021). Particularly for rare species, data gaps occur mainly in the interior of forests, highlighting the need for increasing sampling efforts in the Atlantic Forest to identify priority areas for conservation (Corrêa *et al.* 2021; Figuereido *et al.* 2021). Among various monitoring methods, camera trapping has proven highly effective for medium to large mammals in neotropical forests (Srbek-Araujo and Chiarello 2005; Rovero and Spitale 2016), providing standardized data at regional or global scales (Wearn *et al.* 2019). This method can be especially useful for obtaining information about uncommon, rare, or cryptic species, supporting decision-making for biodiversity conservation in hotspots such as the Atlantic Forest (Trolliet *et al.* 2014).

Species richness, abundance, and distribution patterns are influenced by a variety of environmental and landscape factors, which can vary depending on the spatial scale (Bogoni *et al.* 2017). While forest type may have a greater impact on species response at smaller scales, larger-scale patterns remain poorly understood (Bogoni *et al.* 2016). Therefore, it is crucial to gather additional data (De Barros *et al.* 2021) on species abundance (Galetti *et al.* 2009; Bogoni *et al.* 2020), diversity, habitat use, species occurrence (Beselga *et al.* 2010; Vilas *et al.* 2022), and assemblage organization to better comprehend the ecological requirements of mammals across various habitat types (Regolin *et al.* 2020; De Barros *et al.* 2021; Vilas *et al.* 2022).

It is imperative to understand how native vegetation contributes to the persistence of many species in fragmented agricultural landscapes (Ikin *et al.* 2014). This includes identifying the α and β-diversity components to gain insight into the processes that drive differences in species assemblages (Regolin *et al.* 2020). Such knowledge can serve as a baseline for making comparisons between current, past, and future species richness, and for inferences about species distributions and differences across locations (Cooke *et al.* 2019; Steinbeiser *et al.* 2019). Additionally, it can contribute to the management of natural areas (Corrêa *et al.* 2021) and land-use decisions (Wearn *et al.* 2017), to expand and strengthen public policies and good agricultural practices. This, in turn, can support the implementation of Brazil's Vegetation Protection Law aimed at restoring native vegetation in the Atlantic Forest (Brancalion *et al.* 2016).

Our study aimed at estimating gamma diversity and comparing alpha and beta diversity, relative abundance, and naïve occupation of medium and large-sized mammals between seasonal and ombrophilous forests. Our specific objectives were: (a) analyzing the mammalian gamma diversity, abundance, and naïve occupation in the Atlantic Forest; (b) comparing mammal alpha diversity, abundance, and naïve occupation between seasonal and ombrophilous forests; and (c) assessing beta-diversity, species turnover and species nesting between the forests. We hypothesized that forest type would affect mammalian assemblages, resulting in significant differences between α-diversity, abundance, and occupancy, mainly due to differences in species' habitat use. Furthermore, we expected a high beta-diversity (>70 %) explained by the nestedness of species between forests.

Materials and methods

Mammal sampling. This study was conducted in 22 fragments located in the southeastern Brazilian Atlantic Forest, spanning 15 municipalities in Minas Gerais and one in Rio de Janeiro (-46° 0′ W to -43° 0′ W, -23° 0′ S to -21° 0′ S; Figure 1; Supplementary material 1), covering an area of approximately 22,049 km^2. Fragment selection was based on satellite images from Google Earth Pro software and updated maps of remaining forest fragments provided by the SOS Mata Atlântica Institute (2013/2014). The selection criteria included the presence of both seasonal and ombrophilous forest, with a minimum distance of 2.85 km between fragments.

To survey medium- and large-sized mammals (≥1 kg), we utilized one camera trap per sampling point (Bushnell® HD Bushnell Outdoor Products, California, USA) in each of the 22 fragments. The camera trap in each fragment operated continuously for an average of 130 days between January 2019 and March 2020, capturing images 24 hours per day. To ensure independence between pictures and avoid pseudo-replication, we implemented a 24-hour interval between pictures of the same species (Porfirio *et al.* 2014).

The study area consisted of a highly fragmented landscape surrounded by agricultural matrices and villages. The regional relief is rugged and occurs at elevations ranging from 887 to 2,087 masl. The lower elevations are predominantly characterized by a humid temperate climate with dry winters and hot summers (Cwa type), while the mountainous areas have dry winters and rainy and moderately hot summers (Cwb type), according to the classification by the Instituto Brasileiro de Geografia e Estatística (IBGE 2012).

We organize the data using the Wild.ID Program 0.9.31 (Conservation International 2018). We identified the species at the lowest taxonomic level possible, grouping the records of *Mazama americana* and *Mazama gouazoubira*, as *Mazama* sp., due to the difficulty of differentiating between these two species.

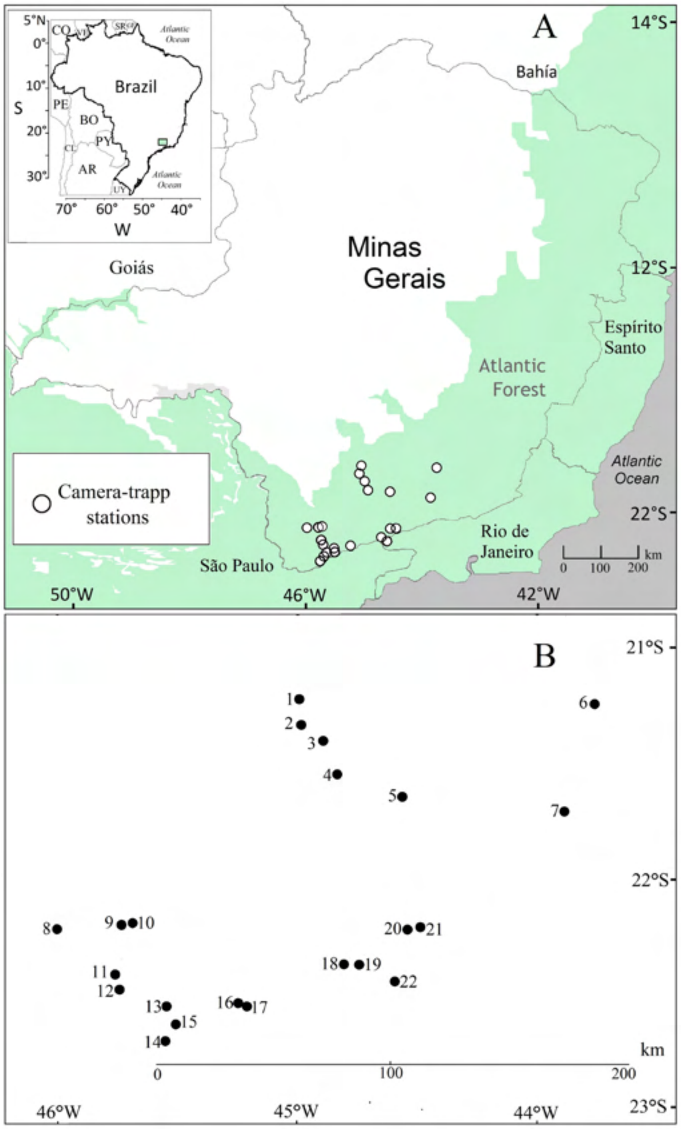

Figure 1. Study area showing the location of the fragments sampled with the camera traps in the southeastern Brazilian Atlantic Forest of Minas Gerais.

Gamma, alpha, and beta diversity. We assessed the gamma diversity (Whitaker 1972) of the southeastern Brazilian Atlantic Forest using the TEAM library program 1.7.R for Windows (Rovero and Spitale 2016). To evaluate the sampling effectiveness and compare it with the richness of native species in other Atlantic Forest studies, we excluded domestic species. Accumulation curves were generated with the Vegan package (Oksanen *et al.* 2013) and used the non-parametric Jackknife 1 estimator from the Biodiversity R package (Kindt and Coe 2005), which is known for its precision in reducing bias of estimated values (Burnham and Overton 1979).

To compare the alpha diversity of seasonal and ombrophilous forests, we used the R package iNEXT.4steps online for rarefaction and extrapolation of species diversity with Hill numbers based on abundance data (Chao *et al.* 2020). We performed fifty bootstraps to calculate 95 % confidence intervals. Hill numbers included species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$; Chao *et al.* 2014; Hsieh *et al.* 2016). We followed a four-step procedure to assess each forest: (a) sample completeness profile, (b) size-based rarefaction/extrapolation, (c) asymptotic and empirical diversity profiles, (d) non-asymptotic coverage-based rarefaction and extrapolation analysis, and (e) evenness profile among species abundances (Pielou J), derived from the slopes of the diversity profile (Chao *et al.* 2020).

To compare species composition between seasonal and ombrophilous forests, we used the Partitioning Beta Diversity into Turnover and Nestedness Components package (betapart package; Baselga and Orme 2012; Baselga *et al.* 2021) in R v4.1.0 (R Core Team 2021). We computed the beta.JTU value of turnover, measured as the turnover fraction of Simpson's dissimilarity, the beta.JNE of the nesting component, measured as the resulting fraction of Simpson's dissimilarity nesting, and the beta.JAC value of overall beta diversity. We computed using a resampling procedure, taking 100 random samples. We performed this analysis by a) grouping native and non-native species and b) considering only native species.

Species abundance. We calculated the relative abundance index (RAI) for each species as follows: RAI $ij = \mathrm{N}j/\mathrm{days}\ j * 100$ nights traps, where "N*j*" is the number of independent records of the species, "*i*" is each species, and "*j*" is each landscape (Mandujano and Pérez 2019), throughout the study area and at each forest. We performed all analyses with the RAI.1 package (Mandujano and Pérez 2019). Finally, we used the Kruskal-Wallis and Mann-Whitney statistical tests to compare the RAIs between species and forests. To determine the magnitude of the differences obtained with the Kruskal Wallis test, we computed the epsilon squared (Tomczak and Tomczak 2014). In all the comparative analyses carried out, we used a significance level of $p < 0.05$.

Species distribution in the study area. We calculated the naïve occupancy, also known as the Percent of Area Occupied (PAO; MacKenzie and Kendall 2002; sensu Kéry and Royle 2015), throughout the study area and at each type of forest. It was calculated as the number of camera trap sites occupied by each species divided by the total number of sites surveyed. The maximum occupancy value is 1, which indicates that a species occupies 100 % of the sites surveyed. Subsequently, to determine the influence of spatial distribution on species abundance, we calculated the correlation between the PAO and the RAI for each species (Mandujano and Pérez 2019). We performed all analyses using the R program 4.2.1 (R Core Team 2021).

Results

Estimation of mammal gamma, alpha and beta diversity. Based on 2,856 camera traps per day, we recorded 589 independent camera trap events of mammalian species in the entire region. The mammal richness in the study area was 32 species (Figures 2-3), distributed among 26 genera, 9 orders, and 17 families (Table 1). Native mammal species richness was 26, distributed among 22 genera, 8 orders, and 15 families (Table 1). The accumulation curve almost reached the asymptote, and according to the expected richness (Jackknife 1 = 29 ± 2 species) of mammalian species, the sampling effort was deemed sufficient. Therefore, we obtained a representative percentage (90 %) of the native species in the area.

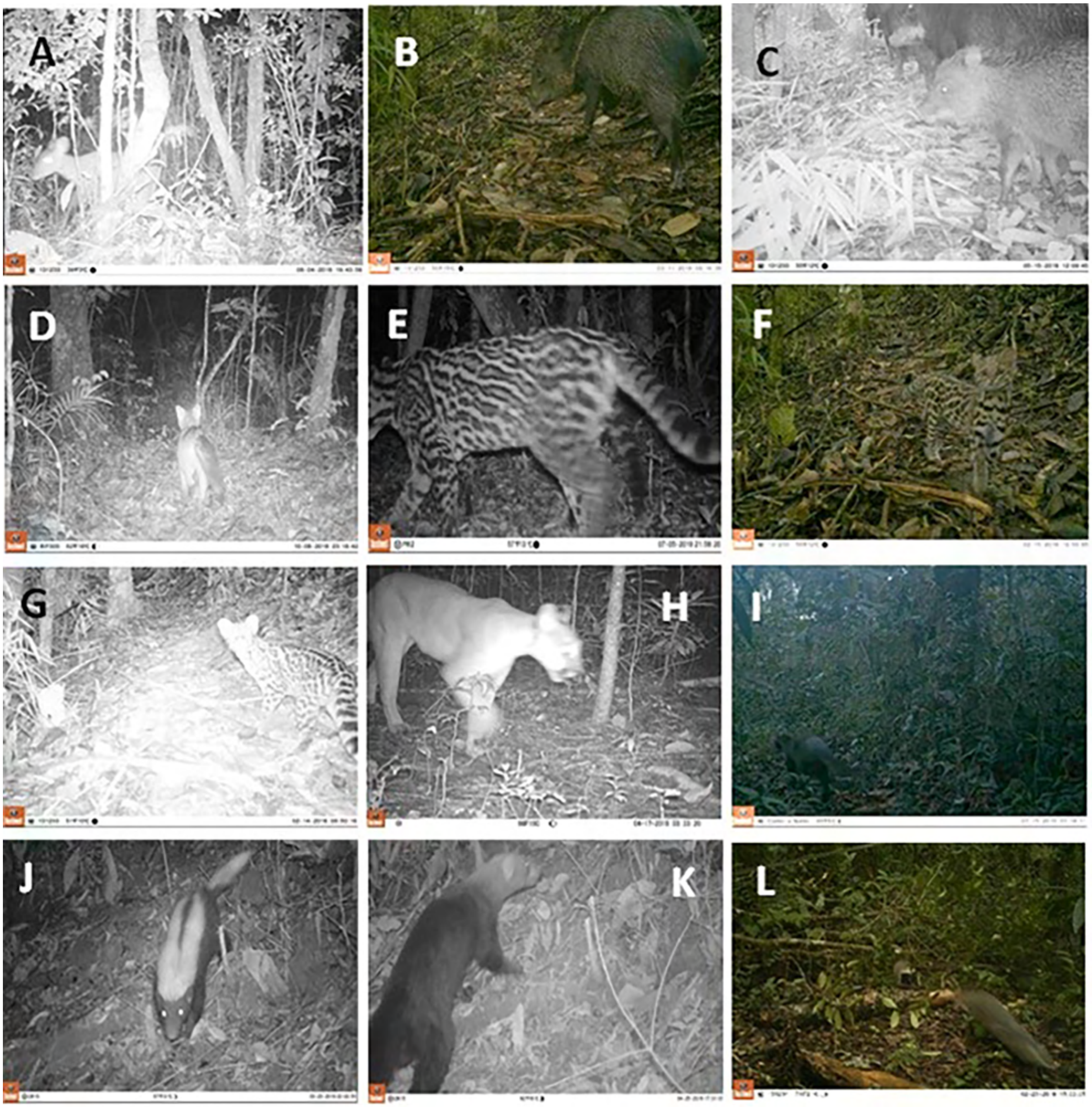

Figure 2. Mammal species recorded in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) *Mazama* sp. B) *Tajacu pecari*. C) *Tayassu pecari*. D) *Cerdocyon thous*. E) *Leopardus pardalis*. F) *Leopardus guttulus*. G) *Leopardus wiedii*. H) *Puma concolor*. I) *Herpailurus yagouaroundi*. J) *Conepatus semistriatus*. K) *Eira barbara*. L) *Galictis cuja*.

The orders Carnivora and Artiodactyla were the most represented, with five and four families, respectively. The order Rodentia was represented by two families, while Cingulata, Didelphimorphia, Lagomorpha, Perissodactyla, Pilosa, and Primates were each represented by one family. Most of the recorded species were native to the Atlantic Forest (81 %), while 16 % were domestic and 3 % exotic (Table 1). Additionally, we recorded one new species in southeastern Minas Gerais, the bush dog *Speothos venaticus* (Soto-Werschitz *et al.* 2023).

There are some differences in the classification of threatened species at the global (International Union for the Conservation of Nature IUCN 2021), national (Instituto Chico Mendes de Conservação da Biodiversidade ICMBio 2018), and state levels (COPAM 2010). Among the species observed on the List of Endangered Species of Fauna in Minas Gerais state, the species *Leopardus pardalis* and *L. guttulus, Pecari tajacu, Puma concolor*, and *Tamandua tetradactyla* are classified as vulnerable; *L. wiedii* is classified as threatened and *Sapajus nigritus, Speothos venaticus*, and *Tayassu pecari* are classified as critically endangered (COPAM 2010; Table 1). The other species recorded in the study area are classified as Least Concern (IUCN 2021; ICMBio 2018) or are not included in the state list (COPAM 2010).

We collected a representative number of species in seasonal and ombrophilous forests (24 and 25 respectively), resulting in a sample completeness profile (seasonal $q0$ = 0.91, $q1$ = 0.99, $q2$ = 1; ombrophilous forest $q0$ = 0.96, $q1$ = 0.99, $q2$ = 1; Figures 4a, b, c; Supplementary material 2). Size-based rarefaction and extrapolation analysis and the asymptotic empirical diversity profiles suggest that our asymptotic diversity estimates for these forests are reliable to infer true diversities ($q = 1$ and $q = 2$; Figures 4b, c; Supplementary material 2). We calculated diversity and evenness measures up to a standardized coverage value of 99.8 % (*Cmax*). The alpha diversity ($q = 0$, $q = 1$, $q = 2$, and evenness

Table 1. Mammalian species richness, conservation status categories, and definition as non-native, native, or exotic species in the southeastern Brazilian Atlantic Forest of Minas Gerais (IUCN 2021; ICMBIO 2018; COPAM 2010).

Order	Family	Species	IUCN	ICMBIO	COPAM	Sp type
Artiodactyla	Bovidae	*Bos taurus*	NA	NA	NA	N-N
	Cervidae	*Mazama americana*	DD	DD	NA	N
		Mazama gouazoubira	LC	LC	NA	N
	Suidae	*Sus scrofa*	LC	NA	NA	E
	Tayassuidae	*Pecari tajacu*	LC	LC	VU	N
		Tayassu pecari	VU	VU	CR	N
Carnivora	Canidae	*Canis lupus familiaris*	NA	NA	NA	N-N
		Cerdocyon thous	LC	LC	NA	N
		Speothos venaticus	NT	VU	CR	N
	Felidae	*Felis silvestris*	NA	NA	NA	N-N
		Herpailurus yagouaroundi	LC	VU	NA	N
		Leopardus guttulus	VU	VU	VU	N
		Leopardus pardalis	LC	LC	VU	N
		Leopardus wiedii	NT	VU	EN	N
		Puma concolor	LC	VU	VU	N
	Mephitidae	*Conepatus semistriatus*	LC	LC	NA	N
	Mustelidae	*Eira barbara*	LC	LC	NA	N
		Galictis cuja	LC	LC	NA	N
	Procyonidae	*Nasua nasua*	LC	LC	NA	N
Cingulata	Dasypodidae	*Cabassous unicinctus*	LC	LC	NA	N
		Dasypus novemcinctus	LC	LC	NA	N
		Dasypus septemcinctus	LC	LC	NA	N
		Euphractus sexcinctus	LC	LC	NA	N
Didelphimorphia	Didelphidae	*Didelphis albiventris*	LC	LC	NA	N
		Didelphis aurita	LC	LC	NA	N
Lagomorphia	Leporidae	*Sylvilagus brasiliensis*	EN	LC	NA	N
Perissodactyla	Equidae	*Equus asinus*	NA	NA	NA	N-N
		Equus caballus	NA	NA	NA	N-N
Pilosa	Myrmecophagidae	*Tamandua tetradactyla*	LC	LC	VU	N
Primates	Cebidae	*Sapajus nigritus*	NT	NT	EN	N
Rodentia	Cuniculidae	*Cuniculus paca*	LC	LC	NA	N
	Sciuridae	*Sciurus aestuans*	LC	LC	NA	N

Not apply (NA), Insufficient Data-Know (DD), least concern (LC), vulnerable (VU), near threatened (NT), Endangered (EN) and critically endangered (CR). Non-native species (N-N). Native species (N). Exotic (E).

Figure 3. Mammal species recorded in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) *Nasua nasua*. B) *Dasypus novemcinctus*. C) *Cabassous unicinctus*. D) *Euphractus sexcinctus*. E) *Dasypus septemcinctus*. F) *Didelphis aurita*. G) *Sylvilagus brasiliensis*. H) *Tamandua tetradactyla*. I) *Sapajus nigritus*. J) *Cuniculus paca*. K) *Sciurus aestuans*. L) *Sus scrofa*. M) *Canis lupus familiaris*. N) *Felis silvestris*.

profiles among species abundances) were similar between the two forests (Figures 4a, b, c, d, and e; Supplementary material 2). We observed that the profile curve decreased sharply in both vegetations, and the values of Pielou J index indicated an equal evenness among species abundances in each forest (seasonal $J = 0.83$; ombrophilous $J = 0.85$; Figure 4-e; Supplementary material 2).

We found that the overall beta diversity between sites was $\beta JAC = 0.37$, with a turnover of $\beta JTU = 0.34$ and species nestedness of $\beta JNE = 0.02$ (Figure 5a). When considering only the native species, the total beta diversity between sites was $\beta JAC = 0.28$, with a turnover of $\beta JTU = 0.25$ and species nestedness of $\beta JNE = 0.03$ (Figure 5b). In each forest, we observed a small number of species exclusive to it. Specifically, we found six species unique to the seasonal forest (*Dasypus septemcinctus*, *Didelphis albiventris*, *Speothos venaticus*, *Tamandua tetradactyla*, *Equus ferus*, and *Felis silvestris*), and seven species were unique to the ombrophilous forest (*Euphractus sexcinctus*, *Galictis cuja*, *Herpailurus yagouaroundi*, *Leopardus wiedii*, *Tayassu pecari*, *Bos taurus*, and *Equus africanus*). However, the overall beta diversity is primarily driven by turnover, while nestedness is almost absent.

Relative abundance. The Relative Abundance Indices (RAIs) between species were significantly different ($H = 115.24$, $d.f. = 30$, $P = 0.000$), but the effect size was not strong (Epsilon-squared $\varepsilon^2 = 0.16$). Four species, *Didelphis aurita* (*RAI* = 4.55 ± 7.66), *Cuniculus paca* (*RAI* = 2.35 ± 3.73), *Pecari tajacu* (*RAI* = 1.65 ± 7.1), *Eira barbara* (*RAI* = 1.65 ± 6.03), had the highest RAIs, (Figure 6a; Supplementary material 3). In contrast, the species with the lowest abundance indices were *Speothos venaticus* (*RAI* = 0.04 ± 0.24) and *Galictis cuja* (*RAI* = 0.06 ± 1.19; Figure 6a; Supplementary material 3). Among the non-native species, *Canis lupus familiaris* (*RAI* = 1.08 ± 2.55) had the highest relative abundance, while the *Sus scrofa* (RAI = 0.15 ± 0.56), and *Equus ferus* (*RAI* = 0.04 ± 0.18), *Equus africanus* (*RAI* = 0.04 ± 0.62), and *Bos taurus* (*RAI* = 0.06 ± 0.27), the lowest values (Figure 6a; Supplementary material 3).

The relative abundance of species did not show significant differences between the two forests ($U = 453.5$; $Z = 0.37$; $P = 0.70$). However, the species *Leopardus wiedii* showed significant differences in relative abundance between forests ($U = 84.5$; $P = 0.01$; Figure 6b). In the seasonal forest, the species *Didelphis aurita* (*RAI* = 4.70 ± 8.28), *Puma concolor* (*RAI* = 2.40 ± 7.55), and *Sylvilagus brasiliensis* (*RAI* = 2.38 ± 8.91) showed the highest abundance indices. On the other hand, *Speothos venaticus* (RAI = 0.08 ± 0.03) and *Sus scrofa* (RAI = 0.08 ± 0.22) had the lowest abundance indices (Figure 6b; Supplementary material 3). In the ombrophilous forest, the species *Didelphis aurita* (RAI = 4.28 ± 6.97), *Cuniculus paca* (*RAI* = 3.26 ± 5.3), and *Leopardus guttulus* (*RAI* = 2.23 ± 2.16)

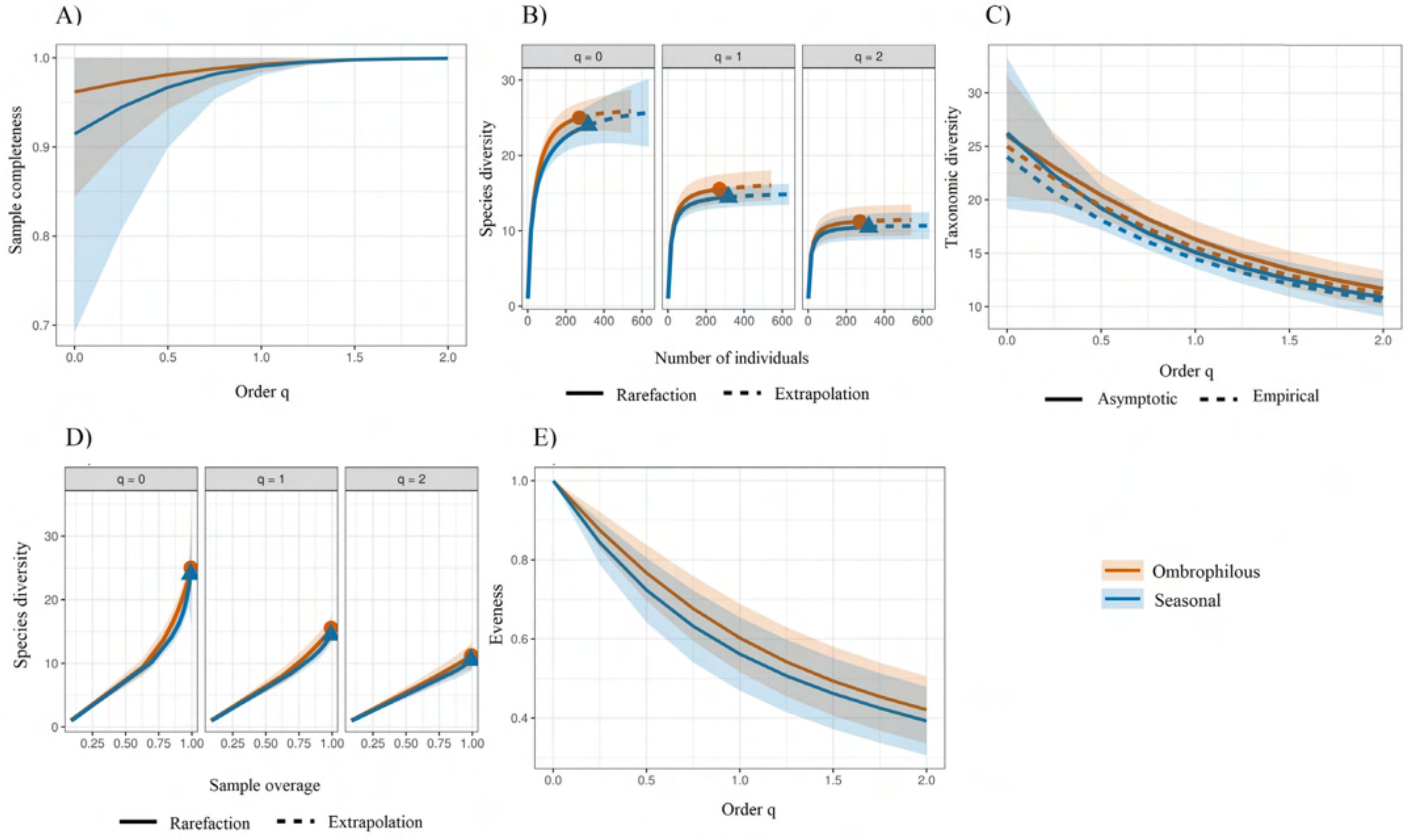

Figure 4. Diversity of mammal species assemblages in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) Sample completeness profiles. B) Size-based rarefaction/extrapolation. C) Asymptotic and empirical diversity profiles. D) Non asymptotic coverage-based rarefaction and extrapolation analysis. E) Evenness among species abundances based on the normalized slope of Hill numbers. Size-based rarefaction is represented by solid curves, while extrapolation is represented by dashed curves.

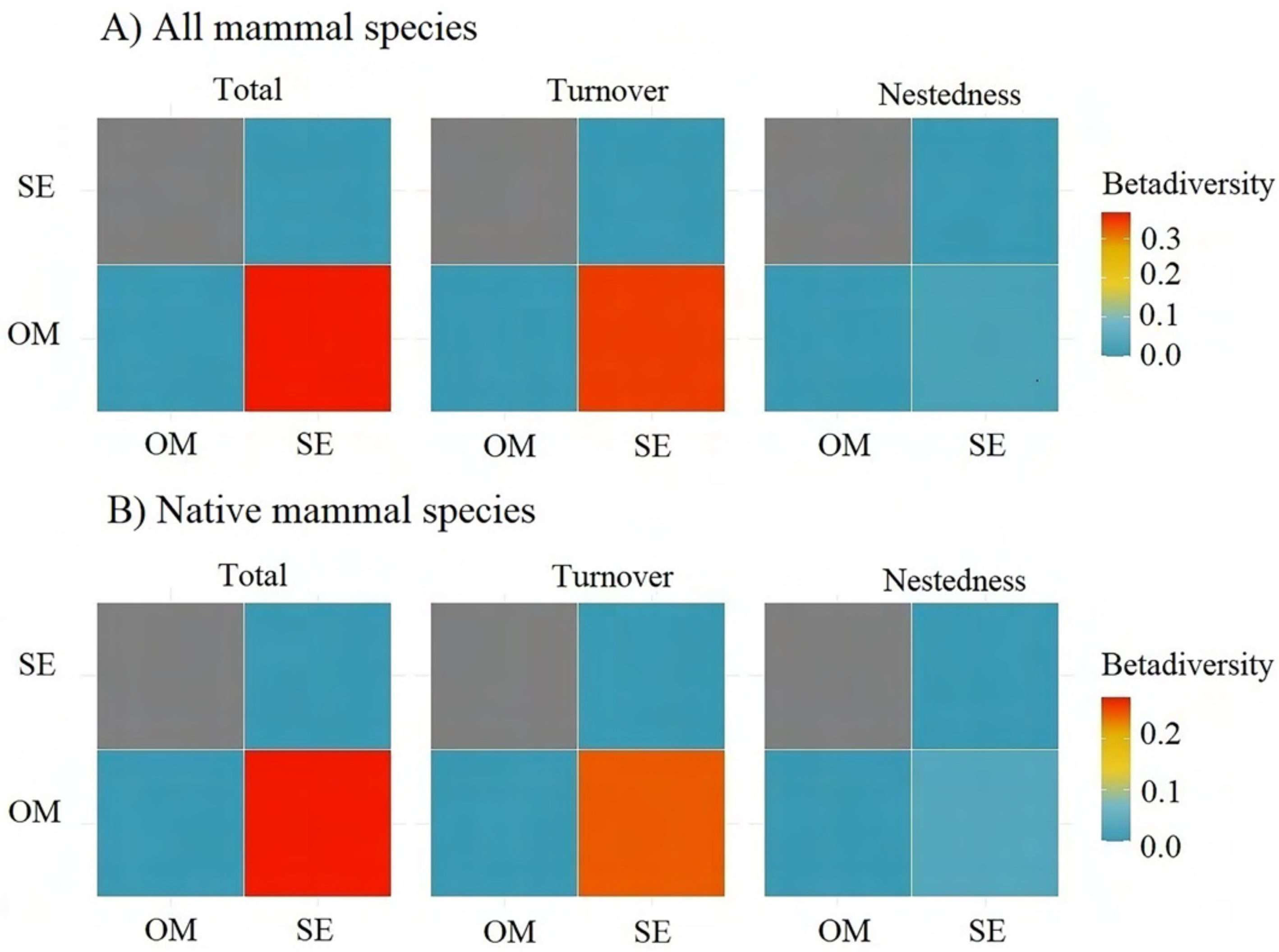

Figure 5. Beta-diversity components of mammal species between ombrophilous (OM) and seasonal (SE) forests in the southeastern Brazilian Atlantic Forest of Minas Gerais.

showed the highest abundance indices. Finally, the species *Cabassous unicinctus* (*RAI* = 0.08 ± 0.22) and *Sapajus nigritus* (*RAI* = 0.08 ± 0.22) showed the lowest indices of abundance (Figure 6-b; Supplementary material 3).

Distribution of species. The *naïve* occupancy of mammal species in the study area did not reach totality (naïve < 1; detection rate, min = 0, max = 0.68). Most of the mammalian species had restricted occupancy to a few localities and values lower than 50 % (Supplementary Material 3). The highest values were for the species *Eira barbara* (68 %), *Didelphis aurita* (55 %), *Cuniculus paca* (45 %), *Pecari tajacu* and *Puma concolor* (41 %), *Leopardus guttulus* and *Leopardus pardalis* (36 %). Instead, the species *Tayassu pecari*, *Tamandua tetradactyla*, and *Speothos venaticus* presented the lowest values (5 %). Regarding the non-native species, *Canis lupus familiaris* had the highest naïve occupancy values (32 %), whereas *Sus scrofa* (9 %), *Bos taurus*, *Equus ferus*, *Equus africanus*, and *Felis silvestris* had the lowest values (5 %; Supplementary Material 3).

In the seasonal forest, the naïve occupancy of the 24 mammal species ranged from 7 % to 57 %. The species with the highest values of naïve occupancy were *Eira barbara* (57 %), *Didelphis aurita* (50 %), *Puma concolor*, and *Cuniculus paca* (43 %; Supplementary Material 3). In contrast, in the ombrophilous forest, the naïve occupancy of the 25 mammal species ranged from 12 % to 88 %. The species with the highest values were *Eira barbara* (88 %), *Didelphis aurita*, *Pecari tajacu*, and *Leopardus guttulus* (62 %; Supplementary Material 3). Finally, we found a correlation of 75 % between the average RAI and naïve occupancy ($r^2 = 0.75$). The species *Didelphis aurita*, *Cuniculus paca*, *Pecari tajacu* and *Eira barbara* showed the high occupancy and RAIs (Figure 7; Supplementary Material 3).

Discussion

The gamma diversity was 32 mammalian species, which accounts for approximately 12 % of the terrestrial non-flying mammal species recorded in the Brazilian Atlantic Forest (Figueiredo *et al.* 2021). The richness of species found in our study area was similar to the reported in other localities within the Atlantic Forest, which varies from 17 to 39 species (Bogoni *et al.* 2016, 2017, 2018; Souza *et al.* 2019; Ríos *et al.* 2021). Therefore, our results suggest that the study area is preserving a representative fraction of the original rich-

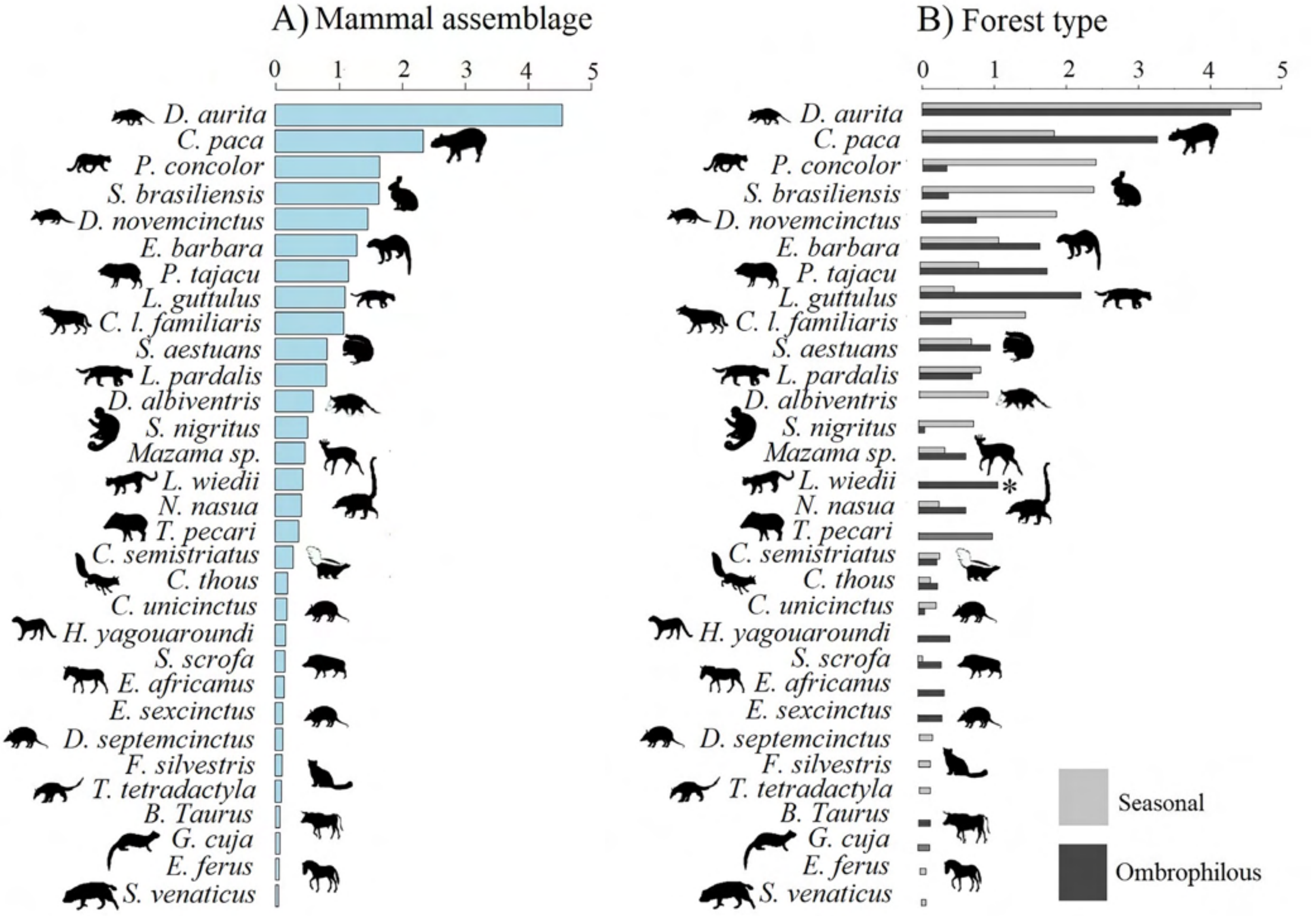

Figure 6. Differences in Relative Abundance Index (average RAIs) between mammals based on camera trap photographs in the southeastern Brazilian Atlantic Forest of Minas Gerais. *Leopardus wiedii* (*U* = 84.5; *P* = 0.011*).

ness of medium to large-sized in the Atlantic Forest. Furthermore, our study demonstrates that camera trapping is a suitable method to record rare, uncommon, and cryptic species (Figueiredo *et al.* 2021; Trolliet *et al.* 2014; Wearn *et al.* 2019), such as *Speothos venaticus*.

The order Carnivora exhibited the highest species richness, which is consistent with previous studies in the Atlantic Forest (Santos *et al.* 2016; Bogoni *et al.* 2018; Souza *et al.* 2019). Mesocarnivores accounted for the majority of the diversity (87 %), supporting the findings of Bogoni *et al.* (2018, 2020), Regolin et al. (2017), and the mesopredator release hypotheses (Crooks and Soulé 1999), which explains how the extirpation of apex predators benefits medium-sized carnivores. The detection of the puma, the only large mammal species in the area, is particularly noteworthy in the Atlantic Forest of Minas Gerais due to its crucial role in ecosystem structure, services, and functioning (Botelho *et al.* 2018).

Contrary to our expectations, we found no evidence for differences in alpha diversity or evenness profiles between the two forests, and the β-diversity values (<37 %), corresponded almost entirely to species turnover. Therefore, the expected degree of species homogenization in the Atlantic Forest in Minas Gerais, was not found in the sampling area. The observed β-diversity could be due not only to differences between vegetation types but also likely to a mixture of factors such as body size (Bogoni *et al.* 2017), activity areas (Botelho *et al*. 2018), and habitat loss and fragmentation (Püttker *et al.* 2020).

Of the registered mammals, 35 % corresponded to species on the List of Endangered Species of Fauna in Minas Gerais, which explains their restricted distribution (naïve <0.5), and the low relative abundances (RAI <1). Our results confirm that variation in species abundance and occupancy of mammals in the Atlantic Forest (Souza *et al.* 2019), but in our case the species with the highest RAI were *Didelphis aurita* and *Cuniculus paca*. Additionally, our results confirm the high levels of defaunation present in the Atlantic Forest (Bogoni *et al.* 2016, 2018; Ríos *et al.* 2021), corresponding to 46 % (Galetti *et al.* 2021).

The only mammal species with the highest abundance indices and naïve occupancy in the seasonal and ombrophilous forest was *Didelphis aurita*. This didelphid exhibits strong plasticity in habitat, resource use, and higher matrix tolerance (Bogoni *et al.* 2016), which probably explains its presence in landscapes with agricultural matrices such as those in this study. Furthermore, we must consider that species with small home ranges have a higher probability of detection (Santos *et al.* 2021). Therefore, it is likely that we overestimated their abundance by photographing the same individuals several times at some localities, because the cameras were placed in areas that covered their home range.

Surprisingly, the relative abundance and occupancy values of non-native species were not high in the sampled areas. The specie *Canis lupus familiaris* had a moderate abundance and a restricted distribution (*RAI* = 1.8; 32 % naïve occupancy), while *Sus scrofa* had one of the lowest values (*RAI* = 0.15; 9 % naïve occupancy). It is possible that they have not yet extended their population to the areas we sampled, or that we underestimated their abundance. Therefore, we should not ignore their presence as these species can cause increased disturbances to native fauna, predation, competition for resources, and transmission of diseases (Quintela *et al.* 2020). The wild boar continues to expand their distribution in the forest remnants (Galetti *et al.* 2021; Rosa *et al.* 2016). Therefore, we need planning management strategies to control their presence (De Assis Morais *et al.* 2020; Rosa *et al.* 2016).

Our study highlights the rarity of most species in the Atlantic Forest and provides valuable insights into the habitat use of mammals. Notably, while both forests exhibit similar species richness, their compositions differ. Therefore, we emphasize the importance of conserving all remaining native forest remnants, to favor particularly rare and threatened species (35 %) that are susceptible to local extinctions in the Minas Gerais Atlantic Forest (Ferreira *et al.* 2020).

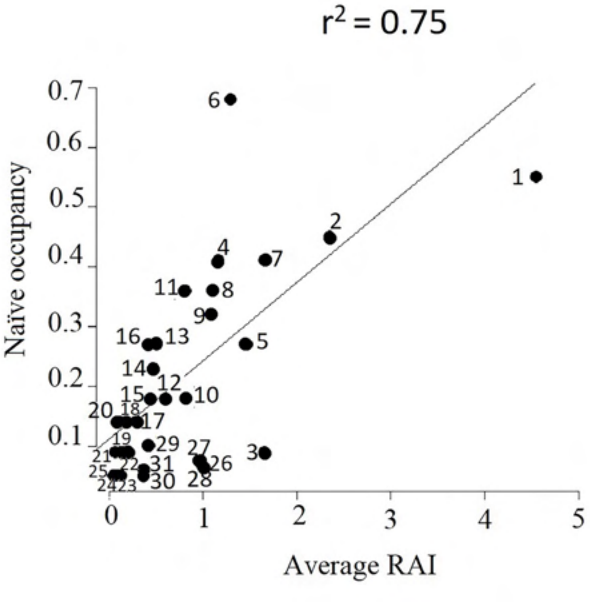

Figure 7. Correlation between the Relative Abundance Index (average RAI) and the naïve occupancy (PA0) for the community of mammals in the southeastern Brazilian Atlantic Forest of Minas Gerais. 1. *D. aurita*. 2. *C. paca*. 3. *P. concolor*. 4. *S. brasiliensis*. 5. *D. novemcinctus*. 6. *E. Barbara*. 7. *P. tajacu*. 8. *L. guttulus*. 9. *C. l. familiaris*. 10. *S. aestuans*. 11. *L. pardalis*. 12. *D. albiventris*. 13. *S. nigritus*. 14. *Mazama* sp. 15. *L. wiedii*. 16. *N. nasua*. 17. *T. pecari*. 18. *C. semistriatus*. 19. *C. thous*. 20. *C. unicinctus*. 21. *H. yagouaroundi*. 22. *S. scrofa*. 23. *E. africanus*. 24. *E. sexcinctus*. 25. *D. septemcinctus*. 26. *F. silvestris*. 27. *T. tetradactyla*. 28. *B. Taurus*. 29. *G. cuja*. 30. *E. ferus*. 31. *S. venaticus*.

In conclusion, in order to prevent further extinctions and mitigate the risk of dramatic scenarios, it is crucial to understand the alpha and beta diversity of forest fragments in different landscapes (Bogoni *et al.* 2016). We need to prioritize restoration programs and establish functional connectivity between fragments to ensure species dispersal between the two forests and across landscapes (Beselga 2010; Bogoni *et al.* 2018).

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New potential distribution and overlap areas of woolly opossum, genus *Caluromys* (Didelphimorphia: Didelphidae), in Colombia

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The woolly opossums of the genus *Caluromys*, despite their wide distribution range, are poorly known species. In Colombia, the presence of *C. derbianus* and *C. lanatus* is recognized, and the presence of *C. philander* has been proposed. This study sought to update the distribution and know overlapping areas of the species of the genus *Caluromys* in Colombia. We modeled the current and potential distribution of *C. derbianus* and *C. lanatus,* and discussed the potential presence of *C. philander*. We extend the distribution range for *C. derbianus* and *C. lanatus* by obtaining new records mainly in the Colombian Caribbean region. For *C. derbianus*, we found that the estimated model area was 177,337 km^2, with the most suitable areas in the Caribbean region in the department of Córdoba and the coast of the department of Sucre, in the north and south of the Pacific region, and in the Andean region on the western mountain range, associated with forest cover. For *C. lanatus*, the estimated model area was 940,007 km^2 with the greatest habitat suitability in the forest cover of the Sierra Nevada de Santa Marta, the central mountain range, the Magdalena River valleys and the Andean-Orinosence piedmont. The areas of occupancy (AOO) and extent of occurrence (EOO) in Colombia are 268 km^2 and 182,741 km^2 for *C. derbianus*, 652 km^2 and 1,036,486 km^2 for *C. lanatus*, with an overlap area of 37,889 km^2. Although we found high uncertainty in the records for *C. philander* in Colombia, we consider that the species probably has representation in the eastern Amazon and Orinoquia regions. This information could be useful to provide new perspectives for the study of the ecological interactions of these Neotropical marsupials, as well as for assessing threats to woolly opossums in Colombia.

Las zarigüeyas lanudas del género *Caluromys* a pesar de su amplio rango de distribución son especies poco conocidas. En Colombia se reconoce la presencia de *Caluromys derbianus* y *C. lanatus*, y se ha propuesto la presencia de *C. philander*. Este trabajo buscó actualizar la distribución y conocer áreas de sobrelapamiento de las especies del género *Caluromys* para Colombia. Modelamos la distribución actual y potencial de *C. derbianus* y *C. lanatus*, y discutimos la presencia potencial de *C. philander*. Ampliamos el intervalo de distribución para *C. derbianus* y *C. lanatus* a partir de la obtención de nuevas localidades de registros principalmente para la región Caribe colombiano. Encontramos para *C. derbianus* un área estimada por el modelo de 177,337 km^2, con áreas más idóneas sobre la región Caribe en el departamento de Córdoba y la costa del departamento de Sucre, al norte y sur de la región Pacífica y en la región Andina sobre la Cordillera Occidental, asociadas a coberturas boscosas. Para *C. lanatus* el área estimada por el modelo fue 940,007 km^2 con mayor idoneidad de hábitat sobre las coberturas boscosas en la Sierra Nevada de Santa Marta, la Cordillera Central, los valles del río Magdalena y el piedemonte Andino-Orinosence. Las áreas de ocupación (AOO) y extensión de ocurrencia (EOO) en Colombia es 268 km^2 y 182,741 km^2 para *C. derbianus*, 652 km^2 y 1,036,486 km^2 para *C. lanatus*, con un área de sobrelapamiento de 37,889 km^2. Aunque encontramos alta incertidumbre en los registros para *C. philander* en Colombia, consideramos que es probable que la especie tenga representación al oriente de las regiones de la Amazonia y Orinoquia. Esta información podría ser útil para brindar nuevas perspectivas para el estudio de las interacciones ecológicas de estos marsupiales Neotropicales, así como poder evaluar amenazas y cambios potenciales en los patrones de distribución para Colombia.

Keywords: Areas of occupancy (AOO); *Caluromys philander*; Colombian Caribbean; extent of occurrence (EOO); range expansion.

Introduction

In Colombia, the order Didelphimorphia is represented by 39 marsupials species grouped in one family and 13 genera that represent 7.2 % of the mammals present in the national territory (Ramírez-Chaves *et al.* 2021). The genus *Caluromys* known as woolly opossum is a lineage of the family Didelphidae characteristic of the New World (Voss and Jansa 2009). This genus is composed of three species, *C. derbianus*, *C. lanatus*, and *C. philander*. They are distributed from the state of Veracruz in México southward in association with forests in Central and South America, including Trinidad and Tobago, to eastern Bolivia, Paraguay, and northeastern Argentina, with an elevational range up to 2,500 m approximately (Gardner 2008; Voss and Jansa 2009). The woolly opossum is arboreal marsupials (rarely descend to the ground), nocturnal, solitary, considered opportunists that consume a wide variety of fleshy fruits, insects, small vertebrates, and flower parts, including nectar, these species inhabit primary and disturbed tropical rainforests (Gardner 2008; Astúa 2015).

In Colombia, there are confirmed records of the species *C. derbianus* and *C. lanatus* (Solari *et al.* 2013), and the presence of *C. philander* has been proposed (Alberico *et al.* 2000). *C. derbianus* has been reported for the Pacific region and on the western cordillera in the Andean region, between 0 and 2,600 masl (Solari *et al.* 2013), and more recently for the Caribbean region (Chacón-Pacheco *et al.* 2022a, b). While *C. lanatus* for the Amazon, Andean, and Caribbean regions, up to 2,000 m (Solari *et al.* 2013), and some occasional records for the Orinoquia region (Fonseca and Astúa 2015). Despite this, for the species of the genus for the country there are gaps in information, the main antecedents date from condensed reports in general lists of mammals (Ramírez-Chaves and Noguera-Urbano 2010; Ramírez-Chaves and Pérez 2010; Rojas-Diaz *et al.* 2012; Solari *et al.* 2013; Chacón-Pacheco *et al.* 2022a, b), and even more unknown about its possible sympatry in areas where there is potential overlapping.

Due to aspects related to their habits and the lack of knowledge that human communities have about their importance for ecosystems, opossums are stigmatized and little appreciated (Flórez-Oliveros and Vivas-Serna 2020). Ecosystems in Colombia are favorable scenarios for interactions between organisms in the Neotropics, which are only possible if there is a certain overlap in their geographic distributions. This is little studied in marsupials, which makes it difficult to understand several ecological dynamics related to the energy flow in ecosystems (Kuhnen *et al.* 2017). The use of environmental and biotic variables and their correlations with species occurrence points can contribute to know overlapping areas of potential species distribution (Rödder and Engler 2011). The aim of this study is present new information on the current and potential distribution and overlap areas of the species of the genus *Caluromys* in Colombia. We update their distribution, indicate areas with possible sympathy in the country and present new information that contributes to determine the conservation status of the species of the genus in Colombia. We also discuss the presence of *C. philander* in the country based on the records revision.

Materials and methods

To know the current and potential distribution and overlap areas of *Caluromys* species in Colombia, was used the Ecological Niche Modeling (ENM) approach using the Maximum Entropy Algorithm Maxent 3.4.3 (Phillips *et al.* 2006) and estimated the area of occurrence extension (EOO) and area of occupancy (AOO) in Colombia. Occurrences (Figure 1) were obtained from: 1) specimens captured or observed in the field during the years 2011 to 2019. 2) Biological col-

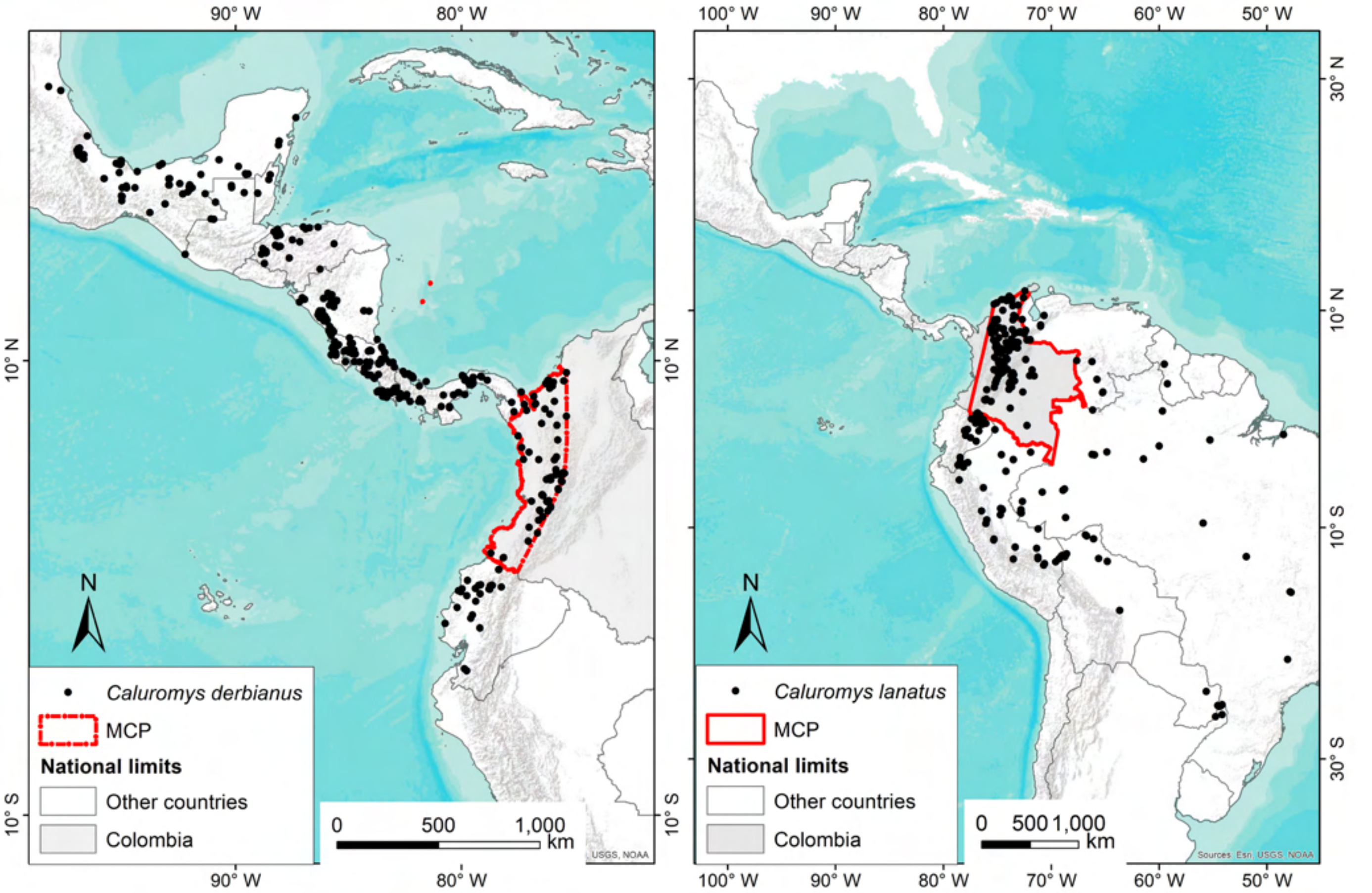

Figure 1. Occurrence records of the woolly opossums *Caluromys derbianus* (left) and *C. lanatus* (right). The minimum convex polygon (MCP) used to calculate the extent of occurrence (EOO) and area of occupancy (AOO) of the species in Colombia.

lections, national and departmental mammal lists were reviewed. 3) Literature databases such as Google Scholar, Scopus, and ScienceDirect were consulted using keywords, ("*Caluromys*" OR "*Caluromys derbianus*" OR "*Caluromys lanatus*" OR "*Caluromys philander*") AND "Colombia". 4) Also were obtained records shared by other researchers and citizen science (iNaturalist; https://www.inaturalist.org/). And, 5) in addition, complementary records for the species *C. derbianus* and *C. lanatus* for Colombia and records for another countries where these species are distributed were obtained from the biodiversity platforms, Species Link (https://specieslink.net/) and the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.bxauh6, https://doi.org/10.15468/dl.3wpryf, https://doi.org/10.15468/dl.caktxu). The search for records of the species *C. philander* was restricted to Colombia, due to the uncertainty of the presence of the species in the country (see records https://github.com/jchacon-bio/Ocurrences_Caluromys). Individuals recorded in fieldwork and from citizen science were identified based on external characteristics such as woolly fur; long, prehensile tail, lacking long, dense fur for 1/3 or more of distal length; large, naked ears; dark, conspicuous medial facial stripe (Gardner 2008).

To understand the potential distribution of woolly opossums, *C. derbianus* and *C. lanatus*, were used bioclimatic variables from WorldClim 2.0 (Fick and Hijmans 2017) for recent climates (~2000 years) at 2.5 minutes (~4.5 km) resolution. Were excluded variables with combined precipitation and temperature information (bio8: Mean temperature of the wettest quarter; bio9. Mean temperature of the driest quarter; bio18: Precipitation of the warmest quarter; bio19: Precipitation of the coldest quarter) because they show spatial anomalies in the form of discontinuities between adjacent pixels (Booth 2022). The models were calibrated in a hypothetical area where the species has been able to explore and potentially colonize using the minimum convex polygon with a buffer of 1 km from the centroid calculated from all occurrences. Was used the random kfolds method, 10,000 background points. Were used different responses (Linear, Quadratic, Linear-Quadratic, Hinge, Linear-Quadratic-Hinge), and different regularization multipliers [RM] (0.1 to 4, growing to 0.5), and three sets of environmental variables (six PC; Muscarella *et al.* 2014; Radosavljevic and Anderson 2014).

Within the known distribution range for *C. derbianus* and *C. lanatus*, 598 occurrence records were obtained (80 records from citizen science in Colombia). For *C. derbianus* 348 (67 in Colombia) and 250 for *C. lanatus* (145 in Colombia) after spatial filtering (~4.5 km^2). Were generated 32 candidate models for each species (*C. derbianus* and *C. lanatus*) that were evaluated by partitioning the records using the random kfold method, into 50 % training data and 50 % test data. A three-step framework was used to evaluate and choose an automated model in the R environment (R Core Team 2022) and the Wallace v2.0 package that allow the work with multiple species in the same session (Kass *et al.* 2023). At first, in order to evaluate models performance, was estimated the partial area under the curve (AUC) of the receiver operating characteristic (pROC; Peterson *et al.* 2008). Second, was calculated the statistical significance of the models with omission rates (5 %; Peterson *et al.* 2011; Muscarella *et al.* 2014), and, finally, were selected models with low complexity and good fit to the underlying data, was used the corrected Akaike information criterion (AICc; Burnham *et al.* 2011; Muscarella *et al.* 2014). From the final model for each species, we selected the logistic output of each model and converted the suitability map into a binary map using the 10P (tenth percentile) cutoff threshold value. This approach was selected because it assumes that 10 % of the records do not occur in representative regions of the general habitat of the species and should therefore be omitted (Babich-Morrow 2019).

The resulting models were trimmed following the national limits of Colombia and the terrestrial ecoregions (Olson *et al.* 2001) where there was no evidence for each of the species were extracted. For *C. derbianus* were extracted the terrestrial ecoregions, Eastern Cordillera real montane forests, Cordillera Oriental montane forests, Magdalena Valley dry forests, Magdalena Valley montane forests and Napo moist forests. While for *C. lanatus* ecoregions were excluded Northern Andean paramo, Cauca Valley dry forests, Cauca Valley montane forests, Western Ecuador moist forests, Northwestern Andean montane forests and Chocó-Darién moist forests.

Later, the overlapping area of the species was estimated as the intersection of the distribution ranges of the two species. For the estimation of the extent of occurrence (EOO) in Colombia we used a minimum convex polygon joining the extreme records of the species. The area of occupancy (AOO) was calculated by adding the area of the grid where the species is known (we used grid of 2 km^2 as recommended in IUCN 2012) within Colombia using the GeoCat tool (Bachman *et al.* 2011).

Results

For Colombia, we obtained 222 occurrence records for the genus *Caluromys*, 67 for *C. derbianus*, 145 for *C. lanatus*, three for *C. philander*, and seven undetermined records (Figure 1).

We confirm the presence of *C. derbianus* for the Andean and Pacific regions and extend its distribution to the Caribbean region in the departments of Córdoba and Sucre (Figure 2). While for *C. lanatus* its distribution range extends to the Colombian Caribbean in all the continental departments of the region (Atlántico, Bolívar, Cesar, Córdoba, La Guajira, Magdalena, and Sucre), and we confirm its presence in the Andean region in the departments of Antioquia, Boyacá, Caldas, Cauca, Cundinamarca, Huila, Norte de Santander, Santander, Tolima, and Valle del Cauca (Figure 2). We also confirm its distribution in the Orinoquia region in the department of Meta, and for Amazon region, in the departments of Amazonas, Caquetá, Guaviare, and

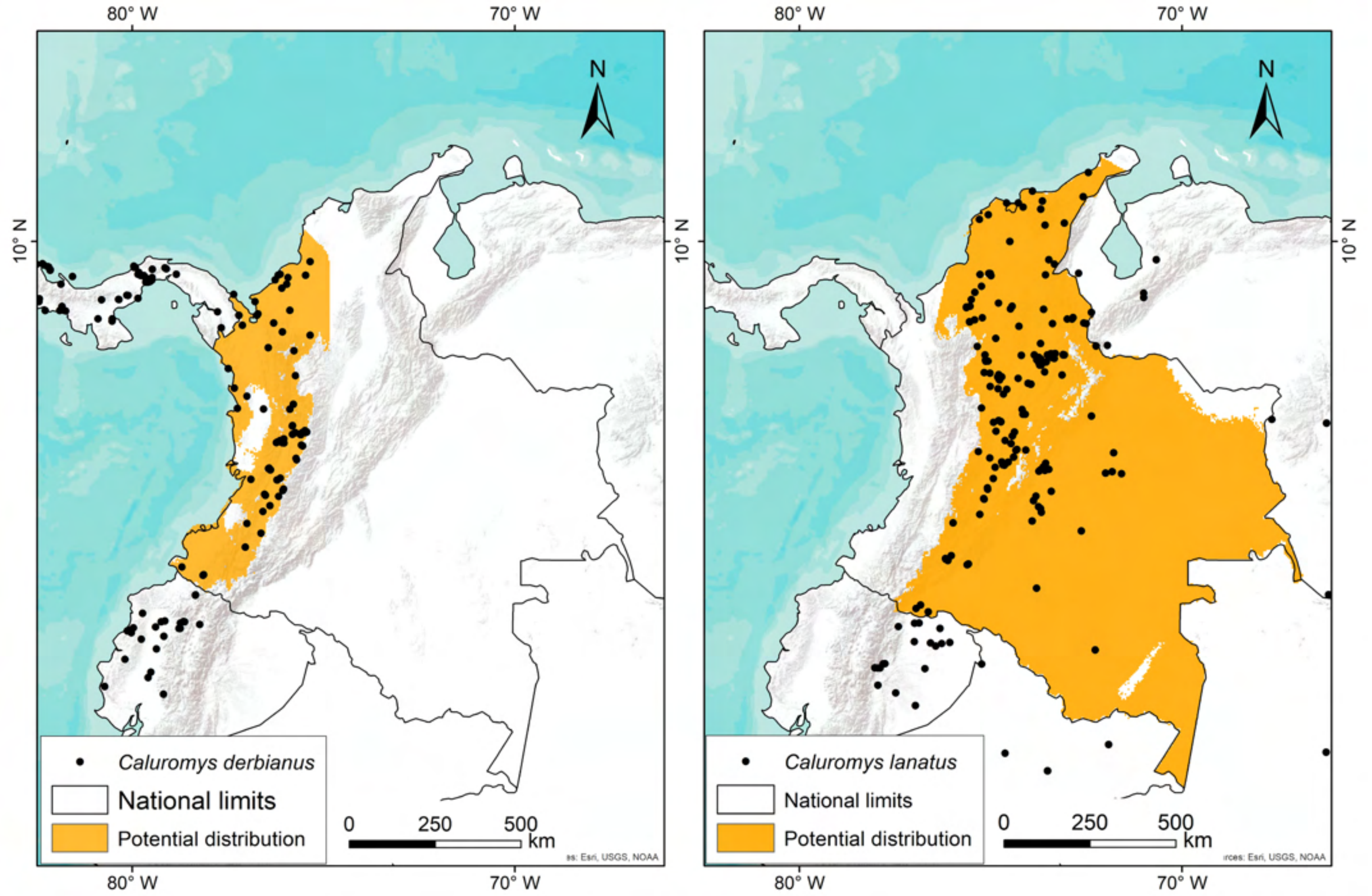

Figure 2. Potential distribution for *Caluromys derbianus* (left) and *C. lanatus* (right) in Colombia based on the Maximum Entropy (Maxent) algorithm model. The binary map (orange) was created using the threshold cut-off of the tenth percentile.

Putumayo. We found overlapping of species, *C. derbianus* and *C. lanatus*, in the Andean and Caribbean region, for the departments Antioquia, Bolívar, Córdoba and Sucre, with an area 37,889.48 km^2 (Figure 3).

For *C. derbianus* the model predicted that the most suitable areas for the species were the department of Córdoba, the coastal region of the department of Sucre, the north and south of the Pacific region, and the Western Cordillera, associated with forest cover (Figure 4). The EOO was 182,741.51 km^2 and AOO was 268 km^2 (Figure 1). The estimated area with the model was 177,337.01 km^2 (Linear + Quadratic 0.50; AUC test = 0.70; AUC train = 0.73; 10 percentile = 0.10). On the other hand, the regions with the most suitable habitat for *C. lanatus* are shown over forest cover in the Sierra Nevada de Santa Marta, the Cordillera Central, the Magdalena River valleys and the Andean-Orinosence foothills (Figure 4). The EOO was 1,036,485.97 km^2 and AOO was 652.00 km^2 (Figure 1). The estimated area with the model was 940,007.40 km^2 (linear 0.5; AUC test = 0.77; AUC trainning = 0.78; 10 percentile = 0.12).

For *C. philander* we discarded a record for the Corregimiento de Arusí in Nuquí municipality, Chocó department, that probably refers to *C. derbianus* given the observed distribution. For the Meta department, a report was recovered as part of a study of *Leptospira* reservoirs (Aycardi *et al.* 1980), however, there is no specimen or material to verify its determination. In eastern Colombia there are two records, one associated with a specimen deposited in the Museum of the Rancho Grande Biological Station, Venezuela (EBRG 2166; 01°51'N, 67°03'W), and another recorded in machine observation by the Fundación Puerto Rastrojo-Colombia (FPR-Colombia 63750; 1°55'N, 67°04'W), both georeferenced for Guainía department, but which refer to collections made at Caño Ardabo in San Carlos de Río Negro, Amazonas state, Venezuela (Figure 3).

Discussion

The results obtained extend the distribution of the species *C. derbianus* and *C. lanatus* to northern Colombia and despite uncertainty about the occurrence records of *C. philander* in the country we consider that the species probably has representation in the eastern Amazon and Orinoquia regions in the departments of Guainía, Guaviare and Vichada, where it is likely to show sympatry with *C. lanatus*. We found overlap areas for *C. derbianus* and *C. lanatus* for the departments of Antioquia, Bolívar, Córdoba and Sucre (Solari and Lew 2015; Costa *et al.* 2021), where may exist coexistence interactions given the functional roles of these two species, know for their habits omnivorous (Astúa 2015). However, it is necessary know how these species utilize their environment and resources.

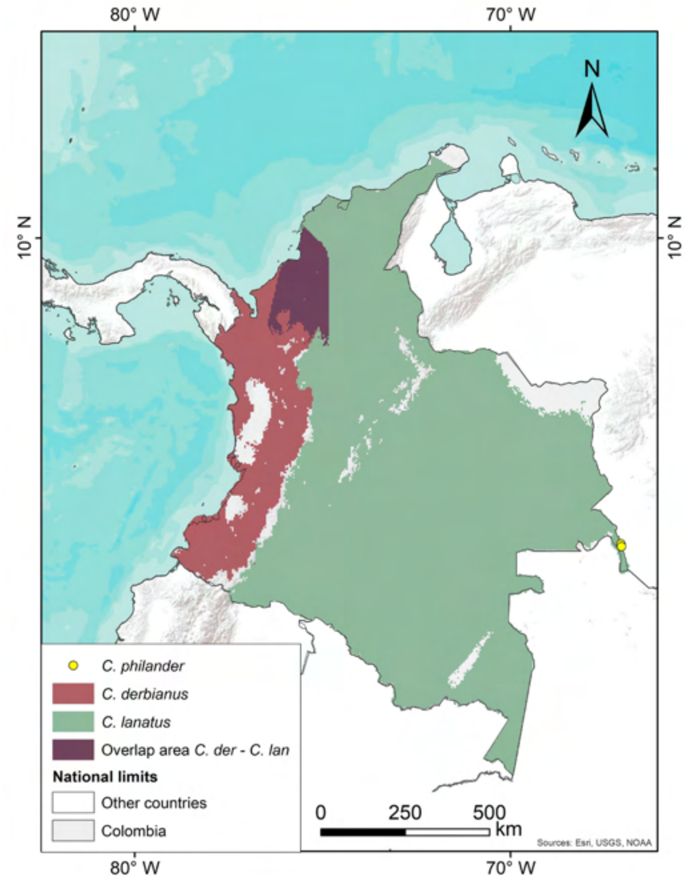

Figure 3. Predicted current area of distributions and overlap (purple) of *C. derbianus* (red) and *C. lanatus* (green) in Colombia (gray) under current climatic condition. Yellow circles represent the records of *C. philander* georeferenced for Guainía department, but which refer to collections made at Caño Ardabo in San Carlos de Río Negro, Amazonas state, Venezuela (EBRG 2166; 01°51'N, 67°03'W and FPR-Colombia 63750; 1°55'N, 67°04'W).

In Colombia, there is few information on the ecosystems occupied by species of the genus *Caluromys*. According to the recovered records and the model projection, we recognize the presence of the species in various ecosystems and vegetation cover, mainly associated with primary and secondary forests and cultivated areas with greater cover such as banana (*Musa* spp), in humid and dry tropical forests for *C. derbianus* and for *C. lanatus* additionally in sub-Andean forests and gallery forests towards the Orinoquía. In addition, in urban areas, as electrocution records in the Caldas, Quindío and Valle del Cauca departments (Sánchez and Alvear 2003; Saavedra-Rodríguez *et al.* 2013; Bastidas-Domínguez *et al.* 2021). Congruent with the models presented for México by Ortiz-Acosta (2022), showing *C. derbianus* is associated with dry and moist forests, for the regions of Chiapas and the Yucatán Peninsula. Likewise, this is consistent for *C. lanatus* that is considered one of the tropical marsupial species most associated with moist and dense forests (Cáceres *et al.* 2022).

The fact these species are found in diverse environments with varying degrees of anthropic disturbance reflects its relatively good tolerance to habitat transformation (Astúa 2015; Solari and Lew 2015; Brito *et al.* 2021; Costa *et al.* 2021). Also, for being generalist species, omnivorous that consume a high variety of resources from fruits, insects, nectar, invertebrates, small vertebrates to carrion (Astúa 2015), they are able to occur in areas where humans may consider them an annoyance. Although these species have rarely been associated with conflict with humans, with few hunting reports to avoid damage to crops and poultry (Marineros *et al.* 2016).

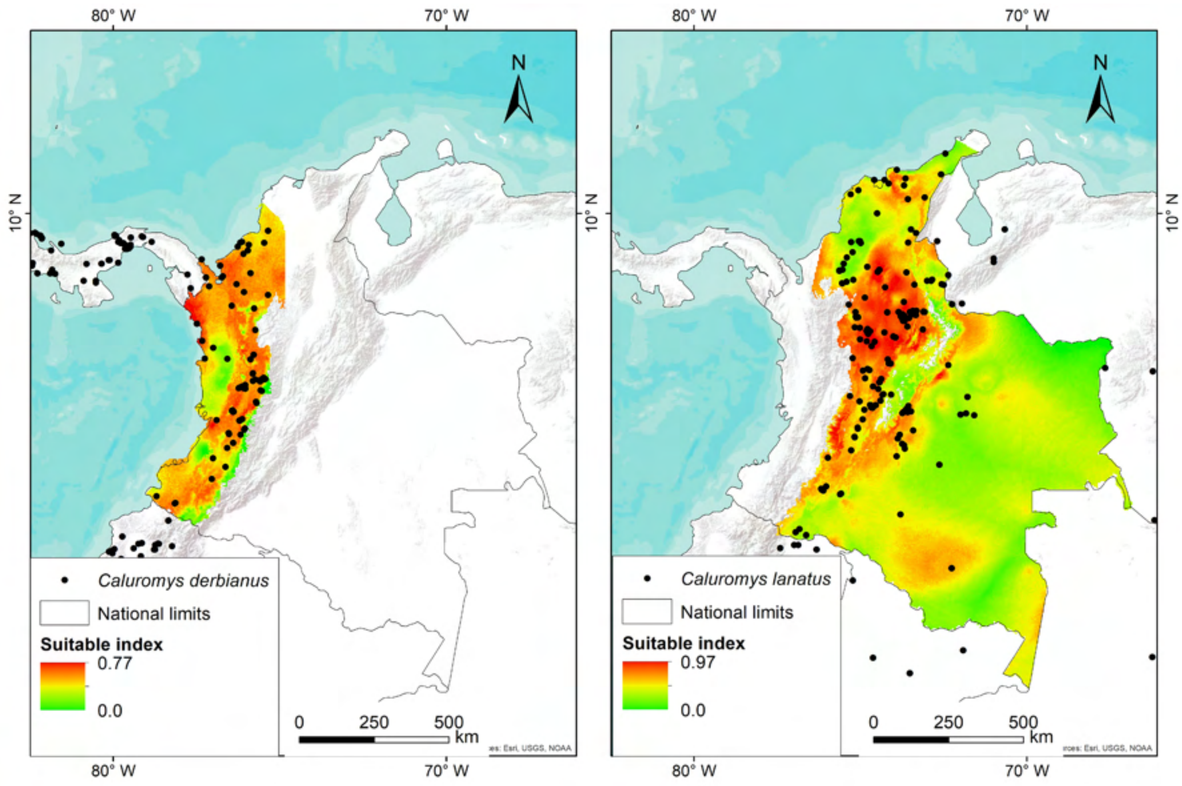

Figure 4. Suitability areas in climatic environment in Colombia of *Caluromys derbianus* (left) y *C. lanatus* (right).

Among the field records, we found the corpses of four specimens (one female and her three young) that were stoned to death associated with banana crops.

Due to the considerable knowledge gap on the species of the genus, our results serve as a basis for further analysis that involves aspects of their ecology and conservation status. The distribution range reports provided in this study constitute a basis for obtaining novel information on local populations of the genus in the country, considering the high deforestation rates in the Caribbean and Andean regions (Correa-Ayram *et al.* 2020), where population monitoring and confirmation of species sympatry through field studies is recommended, contributing to defining conservation and management areas common for these species. Thus, it is necessary new perspectives on the ecology studies of these two Neotropical marsupials, such as the association of different but complementary methods (*i. e.,* diet overlap and temporal segregation) that allow a more complete understanding of resource partitioning and species coexistence (Kuhnen *et al.* 2017).

Furthermore, although these species are recognized as tolerant to ecosystem changes and models indicate a continuous distribution, new efforts should be considered to resolve aspects of their taxonomy, especially for *C. lanatus*, which in Colombia could be another taxonomic entity different from those distributed in southern South America, according to reported variations in color and cranial morphology (López-Fuster *et al.* 2008; Fonseca and Astúa 2015). Likewise, it is important to study aspects of their life history in the different areas of the country where the woolly opossums occur, according to their habitat requirements, ecological characteristics and their interactions with human communities.

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Population parameters of the Phillips kangaroo rat (*Dipodomys phillipsii*)

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Populations respond dynamically to biotic and abiotic changes in their habitat. The identification and description of such demographic oscillation can inform conservation plans that support threatened species. Human activities have reduced and fragmented the already restricted habitat of the Phillips's kangaroo rat (*Dipodomys phillipsii*), threatening its existence. The objective of this study was to describe and analyze *D. phillipsii*'s annual population cycle and structure in the context of its increasing vulnerability to extinction. The capture-recapture technique was performed monthly from 2012 to 2016. Total individual counts, age, reproductive condition, weight, and sex of *D. phillipsii* were determined and recorded. Daily temperature and precipitation data of the study area were analyzed with population parameters and frequency data. *D. phillipsii* populations responded to changes in temperature and precipitation. The highest population densities were recorded in the spring and summer and were correlated with the highest values of the environmental variables studied. Sex ratio was nearly equal during samplings, with non-pregnant females and males with abdominal testes as the most frequently presented secondary sexual characteristics. Most captured individuals were adults. Individual body weights were highly variable, which can be attributed to reproduction and fluctuations in resource availability. *D. phillipsii* populations severely decreased in the last year of the study, with low juvenile and pregnant or lactating female frequency counts. Anthropogenic pressures on *D. phillipsii* habitat persist, indicating that the proliferation of this species is at risk. Information from this study could be used to address the pressing need for the management and conservation of *D. phillipsii.*

Las poblaciones responden de manera dinámica a los cambios bióticos y abióticos de su hábitat. El conocimiento de estas oscilaciones es prioritario en especies con problemas de conservación o con interés en su manejo. La rata canguro de Phillips (*Dipodomys phillipsii*) se considera amenazada debido a la reducción y fragmentación de su restringido hábitat. Dada su vulnerabilidad, se tuvo como objetivo analizar su ciclo anual y estructura poblacional. Con la finalidad de obtener los parámetros poblacionales (edad, condición reproductiva y proporción de sexos) de la especie, se utilizó la técnica de captura-recaptura durante los años 2012 al 2016. Además, los datos de temperatura y precipitación de la zona y de los años de estudio fueron analizados junto con las frecuencias de las ratas canguro. *D. phillipsii* respondió a los cambios en la temperatura y precipitación. Sus densidades más altas se registraron en la primavera y verano. Además, coincidieron con los mayores valores de las variables ambientales estudiadas. La proporción de sexos fue casi equitativa durante los muestreos. Las hembras no preñadas y los machos con testículos abdominales fueron registrados con mayor frecuencia. Los adultos fueron los más abundantes. El peso de los organismos fue variable, probablemente causado por la reproducción y por su respuesta a los cambios de los recursos ambientales. Los resultados indican que, en los últimos años de estudio, las densidades poblacionales de la especie han disminuido severamente. Además los registros de juveniles, así como de hembras con condiciones de preñez o lactancia fueron bajos. Aunado a esto, las presiones antrópicas son persistentes, por lo que, la existencia de la especie está en riesgo. La información de este estudio podría ser utilizada para su lograr su inminente manejo y conservación.

Keywords: Density; desert rodents; Heteromydae; México; reproductive characteristics; temperature.

Introduction

In habitats with high climatic variability, organisms temporally select for seasonably favorable conditions to complete certain aspects of developmental stages and reproduction. When conditions are unfavorable, organisms evade such conditions through various strategies (Walsberg 2000; Visser and Both 2005; Ward 2016). For example, in heteromyids rodents such as kangaroo rats (*Dipodomys spp.*), adaptive body temperature and metabolic changes occur as a response to unfavorable feeding and environmental temperature conditions (French 1993; Gummer 2005). Kangaroo rats also rely on a system of underground burrows, which with their regulated temperature and humidity, serve as a respite from intense solar radiation and food storage (Walsberg 2000).

Climatic variables can influence the growth of populations and modify the structure of heteromyid communities (Brown and Ernest 2002; Lima *et al.* 2008; Hernández et al 2005, 2011); temperature changes can stimulate the beginning or end of reproduction and hibernation (Lane *et al.* 2012), while precipitation is often correlated to food resource availability (Hoditschek and Best 1983; Ernest *et al.* 2000; Thibault *et al.* 2010). This is particularly relevant in desert systems (Lane *et al.* 2012) since precipitation is responsible for plant shoot emergence and seed production, the primary food sources of heteromyids (Reichman and Van

De Graaff 1975; Beatley 1976; Zeng and Brown 1987; Walsberg 2000; Hernández et al 2005, 2011; Thibault *et al.* 2010). As such, these environmental variables generally demark rodent reproductive periods (Beatley 1976; Walsberg 2000; Brown and Ernest 2002; Lane *et al.* 2012). Interruptions to precipitation cycles and prolonged periods of extreme heat can result in reproduction and survival rate decreases, causing population instability (Visser and Both 2005; Miller-Rushing *et al.* 2010; Lane *et al.* 2012). Demographic and reproductive data based on annual frequency records (Caughley 2000; Miller-Rushing *et al.* 2010) can identify vulnerable conditions and times of year for a threatened species (Daskalova *et al.* 2020; Price and Kelly 1994; Morrison *et al.* 1996; Purvis *et al.* 2000), making such records a valuable tool for effective conservation and management.

Kangaroo rats (*Dipodomys spp.*) provide multiple benefits to North American arid ecosystems (Daskalova *et al.* 2020). Known as ecosystem engineers, kangaroo rats modify vegetative species composition and soil micro topology with the construction of underground burrows. They also consume and store forb and grass seeds, increasing plant dispersal (Longland and Dimitri 2021). Since their feeding habits favor the establishment and permanence of native species, kangaroo rats are keystone species for arid and semi-arid deserts (Hafner 2016; Longland and Dimitri 2021). As keystone species, kangaroo rat populations can serve as indicators of overall ecosystem health (Fernández *et al.* 2014). Additionally, they represent an important protein source for reptiles, birds, and other desert mammals (Hafner 2016; Longland and Dimitri 2021). The Phillips kangaroo rat (*Dipodomys phillipsii*) is endemic to arid or semi-arid regions of the Northern Valley of México, Southern Puebla, and Northern Oaxaca, dominated by sandy soils and xerophytic and grassland vegetation (Jones and Genoways 1975; Hafner 2016). Despite its ecological relevance, little is known about the natural history, ecology, distribution, and demography of this rodent (Hafner 2016; Flores-Zamarripa and Fernández 2018; Montero-Bagatella y Cervantes 2022). Only 40 % of the Phillips kangaroo rat's original habitat remains due to the expansion of human land use (Sánchez-Cordero *et al.* 2005) for agricultural practices and livestock (Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018). Despite its classification as "Threatened" by the Official Mexican Standard (SEMARNAT 2019), the International Union for Conservation of Nature classifies *D. phillipsii* as a species "of least concern" (Álvarez-Castañeda *et al.* 2016). Anthropic pressures continue to affect arid and semi-arid habitats (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014; Jiménez-García *et al.* 2014; Durán-Antonio and González-Romero 2018; Flores-Zamarripa and Fernández 2018), which, coupled with an already restricted range, makes this species especially vulnerable to extinction (Purvis *et al.* 2000; Sykes et al. 202019; Longland and Dimitri 2021). In the face of such anthropic pressures, long-term demographic characteristics (*i. e.*, body mass, population size structure, reproductive viability) and environmental habitat (*i. e.*, biotic and abiotic) monitoring should be prioritized in order to effectively conserve a species (Price and Kelly 1994; Durán-Antonio and González-Romero 2018; Daskalova *et al.* 2020; Braun *et al.* 2021). This research describes and analyzes the annual demographic cycle of *D. phillipsii* and examines its relationship between climatic conditions and *D. phillipsii* population dynamics. This much-needed information can and should be used to support their conservation.

Material and methods

The presented study was conducted in the Perote Valley in the municipality of Perote, Veracruz, México. This valley, located between the Sierra Norte de Puebla and the Cofre de Perote mountain ranges (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014) has high rates of endemism for flora and fauna. Altitude ranges between 2,300 and 2,700 masl. The climate is the most humid of the semiarid climates with a mean annual temperature of 14 ºC and a mean annual rainfall of 500 mm, making for a semi-arid ecosystem (Gerez-Fernández 1985). Vegetation includes pine-oak forest, tascate forest, scrubland, natural and induced grassland, and halophytic vegetation (Montero-Bagatella *et al.* 2017). The area is facing severe conservation problems due to intensive agricultural practices and livestock, that have fragmented and decreased the limited available habitat in the region (Gerez-Fernández 1985; Montero-Bagatella *et al.* 2017).

Population structure and annual cycle. To capture the kangaroo rats, three sites with the succession of native pastures (*Jarava. ichu* and *Bouteloua scorpioides)*, some succulents and shrub were sampled. Sites 1 and 2 were enclosed with barbed wire and electric fencing to prevent grazing and intrusion by domestic fauna (Montero-Bagatella *et al.* 2017; Figure1). Each worksite consisted of two plots (1 ha) separated from each other by 100 m. In each plot, 36 Sherman traps (30 x 10 x 8 cm) were placed in a grid (6 x 6 traps) and separated from each other by 20 m. Traps were baited with peanut butter and oat flakes and activated from 17:00 to 8:00 hrs. From 2012 - 2016, rodents were surveyed monthly using the capture, mark, and recapture technique for two consecutive nights (Durán-Antonio and González-Romero 2018; Caughley 2000). Captured individuals were marked in the ventral region with a permanent marker. Sex, age, and secondary sexual characteristics (*i. e.,* scroted testicles in adult males and signs of pregnancy / lactation in adult females; Price and Kelly 1994; Kaufman and Kaufman 2015; Durán-Antonio and González-Romero 2018) were recorded for each specimen captured. Size, weight, coat coloration, and reproductive condition were used to estimate age (*i. e.*, juvenile or adult; Price and Kelly 1994). After data recording, organisms were released *in situ* (Sikes and Gannon 2011; Durán-Antonio and González-Romero 2018). In 2015, heavy rains interrupted sampling continuity, resulting in an incomplete data set for this year. In addition, as the sampling was carried out at the same time as the research of the Perote ground squirrels' activity

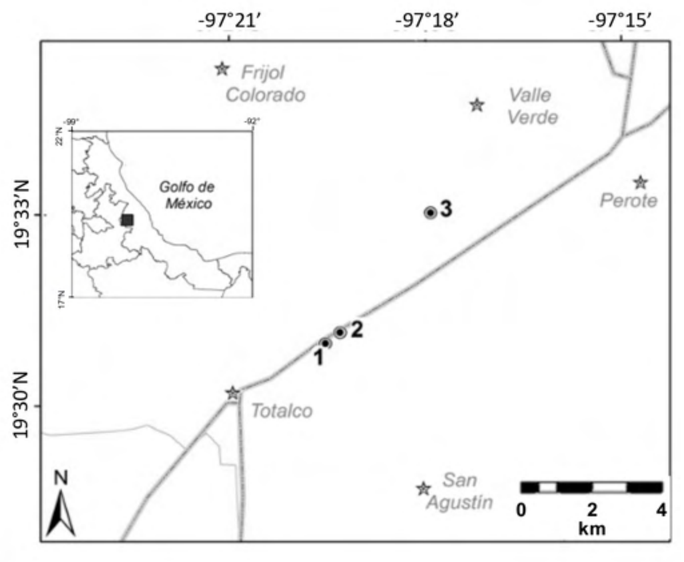

Figure 1. Map of study sites. Areas 1 and 2 had fencing and surveillance. Stars = villages. Black points = study sites. Grey and black lines = roads.

cycle (Montero-Bagatella *et al.* 2017), February and November were not sampled.

Temperature and precipitation data for the study area were provided by the Comisión Nacional del Agua (CONAGUA; https://smn.conagua.gob.mx/). For each study site, live individual totals, sex ratio, age, and reproductive condition of individuals were recorded (Caughley 2000). In order to examine annual reproductive cycles, the years of study and demographic variables were grouped by annual seasons (*i. e.*, spring, summer, winter, and fall). Temperature, precipitation, and reproductive status were analyzed by one-way analysis of variance (ANOVA) and a *t* - test. Body weights were compared using one-way ANOVAs. In order to detect differences between ages and sexes, Tukey's *post hoc* tests were performed. Spearman correlations were made between the precipitation of the same year and previous year and the number of *D. phillipsii* individuals, as well as the number of *D. phillipsii* individuals and temperature (Ernest *et al.* 2000). Analyses were performed using Minitab 21.1.1.0 software.

Results

The total sampling effort was 4, 536 trap / nights (Table 1). Figure 2 shows total live individual counts, monthly precipitation, and average monthly temperature from 2011 to 2016. The highest abundance values mostly coincide with the peaks in temperature and precipitation. The highest temperatures were registered in April and May (spring). In October (fall), temperatures began to drop. The warmest year was 2011, and the coldest 2013. The average temperature of the study area was 24.9 °C. Temperature values for annual seasons differed significantly (F = 3.11, *d. f.* = 3, *P* = 0.05), with the post hoc test showing differences between fall and spring (*P* = 0.033). Significant differences existed between average temperatures and study years (F = 5.95, *d. f.* = 5, *P* = < 0.001); Tukey's test indicated differences between 2011 and 2013 (*P* = < 0.001), as well as between 2013 and 2014 (*P* = 0.001). Precipitation was statistically different between seasons (F = 11.16, *d. f.* = 3, *P* = < 0.001), with the *post hoc* test indicating differences between winter and summer, and winter and spring (*P* = 0.001 for both). Statistical differences were found between fall and spring (*P* = 0.012), as well as between fall and summer (*P* = 0.011). 65 % of all annual precipitations occurred during spring and summer months, with little precipitation in winter months. The rainiest year studied, exceeding 170 mm. was 2013. There was no correlation between temperature and the number of captures of *D. phillipsii* (*r* = 0.12, *P* = 0.58), the previous year's precipitation and the number of captures (*r* = 0.20, *P* = 0.38) and same-year precipitation and the number of captures (*r* = 0.12, *P* = 0.58).

Table 1. Total captures of the Phillips´ kangaroo rat (*Dipodomys phillipsii*) recorded by year, sex, and age category, from Perote, Veracruz.

	Females		Males	
Years	**Juveniles**	**Adults**	**Juveniles**	**Adults**
2012	12	191	15	211
2013	5	40	0	31
2014	3	178	6	185
2015	3	61	4	47
2016	2	10	0	19

The highest number of live captures for *D. phillipsii* occurred in August 2012 with 130 individuals, contrasting with the lowest number of capture individuals (2 individual) in July 2015. There was a continuous decrease in captures from 2013 to 2016. Most captured individuals were adults, with juvenile capture numbers peaking in the month of May (Figure 3). Sex ratios for both adults and juveniles were maintained steadily at 1:1 with no significant differences for neither adults (F = 0.01, *d. f.* = 1, *P*=0.93) nor juveniles (F = 0.32, *d. f.* = 1, *P* = 0.58). Overall numbers of adults and juveniles were just at the margin of statistical differences (F = 3.93, *d. f.* = 1, *P* = 0.063). There were however, significant differences between numbers of adult vs. juvenile for both males (F = 9.0, *d. f.* = 1, *P* = 0.010) and females (F = 8.8, *d. f.* = 1, *P* = 0.010).

Non-pregnant females and males with abdominal testicles were the most abundant (Figure 4), and pregnant or lactating females were the least abundant. Statistical differences existed between frequencies of pregnant or lactating vs. non-pregnant females (F = 3.93, *d. f.* = 2, *P* = 0.010). Males with abdominal testicles were present throughout all the samplings, their abundance increasing in May. Scroted males were present during all samplings, reaching maximum numbers in the spring. The number of males with abdominal vs. scrotal testicles was close to being statistically significant (*t* = 1.98, *d. f.* = 13, *P* = 0.069). Adults body weights varied evenly throughout the seasons (Figure 5); female body weights were highest in the summer, exceeding the weights of the males. The weights of the juveniles did not vary by season, and there were no differences between male and female juvenile weights (F = 0.01, *d. f.* = 1, *P* = 0.93).

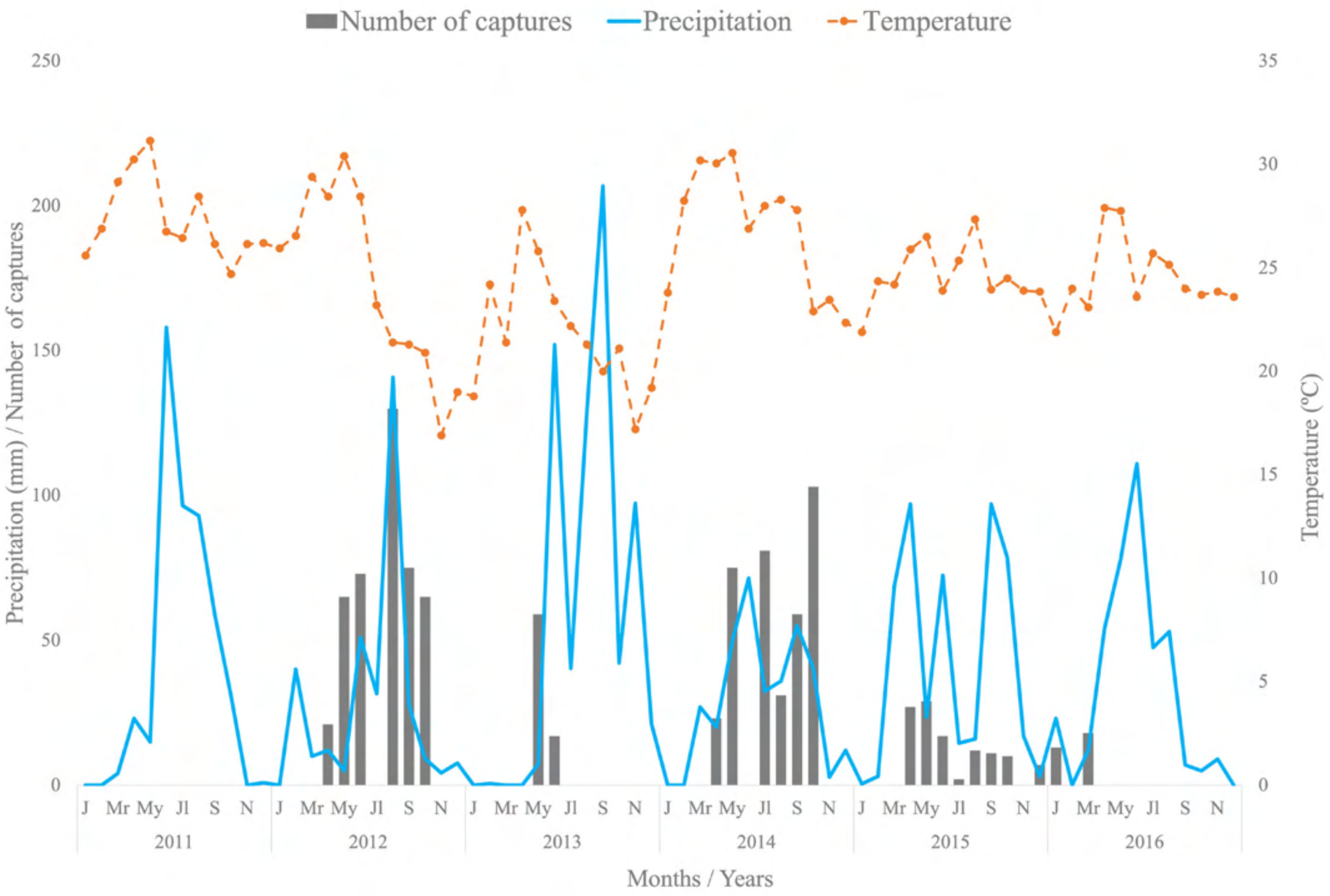

Figure 2. Average rainfall and temperatures of Perote, Veracruz and Phillips' kangaroo rats (*Dipodomys phillipsi*) monthly frequencies.

Discussion

This study captures the population oscillations of *D. phillipsii* in response to temperature and precipitation changes, as has been described for other species of its genus (Bradley and Mauer 1971; Hoditschek and Best 1983; Morrison *et al.* 1996; Brock and Kelt 2004; Kelt 2011; Kaufman and Kaufman 2015). The maximum captures coincided with peaks in precipitation and temperature as reported for *D. merriami* and *D. stephensi* (Price and Kelly 1994; Koontz *et al.* 2001). Heavy rains interrupted sampling continuity, resulting in a lack of information that could have influenced the correlations values. Studies such as Ernest *et al.* (2000) and Hernández *et al.* (2005, 2011) have demonstrated a positive correlation between the number of rodent captures and precipitation; nonetheless, their study sites were in arid ecosystems with marked seasonality of droughts. In contrast with the Chihuahuan desert, where 60 % of annual precipitation occurs in the summer (Brown and Ernest 2002), the Perote Valley´s precipitation maximums occurred equally in both spring and summer. Hence the distinct rainy seasons and the amount of precipitation received may make it more difficult to discern statistical patterns of response (Hernández et al 2005). Authors such as Reichman and Van De Graaff (1975), Ernest *et al.* (2000), as well as Kaufman and Kaufman (2015) report a synched phenology for vegetative growth and the reproductive seasons *Dipodomys* genus species after rainfall, thus complementary studies as cover vegetation could be used as indicator of the species' response to rainfall (Hernández et al 2005).

In this study, reproductive activity lasted from January to October. Neither pregnancy nor lactation was common among captured individuals, as females with such conditions typically remain in their burrows caring for their young (Eisenberg 1993). Studies by Bradley and Mauer (1971), as well as Hoditschek and Best (1983) indicate that male *D. merriami*, *D. ordii*, and *D. stephensi* have longer reproductive periods than females, thus the species can have more than one litter per year (Bradley and Mauer 1971; Hoditschek and Best 1983; Price and Kelly 1994).

Gestation periods can influence extinction risk (Purvis *et al.* 2000); in animals with long gestation stages that produce few offspring this risk increases. While juvenile counts in this study were low, as reported by Durán-Antonio and González-Romero (2018), gestation periods for *D. phillipsii* are short and populations can grow relatively fast (Eisenberg 1993; Hafner 2016). Predation and burrowing life can result in low trapping success (Hafner 2016) which in this case could have accounted for the low capture numbers (Zeng and Brown 1987). Males, which tend towards dispersal are more likely to be captured than females, which tend toward philopatry (Hafner 2016). Additionally, males' home ranges may overlap with multiple females (Zeng and Brown 1987; Kaufman and Kaufman 2015; Hafner 2016). While overall numbers for males were slightly higher, a 1:1 sex ratio was maintained, as indicated by Durán-Antonio and González-Romero (2018). Continuous capture data, even the regular catches of juveniles, indicated that this species is active throughout the entire year, a behavior that has also been reported for *D. nitratoides*, *D. merriami, D. ordii*, *D. stephensi*, and *D. simulans* (Bradley and Mauer 1971; Jones and Genoways 1975; Hoditschek and Best 1983; Morrison *et al.* 1996; Brock and Kelt 2004; Kelt 2011; Kaufman and Kaufman 2015). *D. ordii* and *D. merriami* can go into torpor during extreme climatic and dietary conditions (French 1993; Gummer 2005), but torpor in *D. phillipsii* is yet to be confirmed; Jones and Genoways (1975) reported activity in this species during low-temperature conditions, yet no observations of feeding activity during heavy rains.

In this study *D. phillipsii* population densities varied by both month and year; in 2016, the population drastically declined, an occurrence also observed by Durán-Antonio and González-Romero (2018). Such population declines are present in other *Dipodomys* genus species; *D. spectabilis* populations fluctuated in response to human activities and alterations to plant species compositions (Valone *et al.* 1995); *D. nitratoides*, *D. elator* and *D. gravites* are at risk of extinction due to the continual degradation of their rare and restricted habitat (Hafner 2016; Patton *et al.* 2019; Braun *et al.* 2021). Indirect effects of human disturbances to these vulnerable populations include increased predation (Wilkening *et al.* 2019) and zoonotic diseases (Valone *et al.* 1995; Brown and Ernest 2002), with endemic species being the most vulnerable to such threats (Sykes et al. 202019; Purvis *et al.* 2000). It is likely that the restricted distribution of Phillips´s kangaroo rat populations are already responding to both direct and indirect effects of human activities (Sykes et al. 202019).

The preferred habitat of species of *Dipodomys* genus is a landscape with short, sparse vegetation, which allows them to see and hide from potential predators (Hafner 2016; Longland and Dimitri 2021). The presented study areas were composed of dense, tall grassland vegetation with shrubs (Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018), potentially restricting food availability (Thibault *et al.* 2010). These vegetative conditions often cause individuals to search for new habitat areas (Goldingay *et al.* 1997; Bliss *et al.* 2019), despite the associated mortality risks (Zeng and Brown 1987; Thibault *et al.* 2010). *Dipodomys* species are often classified as granivorous, yet many are known to also consume vegetative plant material (Bradley and Mauer 1971; Reichman and Van De Graaff 1975; Soholt 1977; Longland and Dimitri 2021). Controlled grazing has the potential to maintain short and sparse grassland ecosystems free of woody plants (Goldingay *et al.* 1997; Montero-Bagatella *et al.* 2017; Durán-

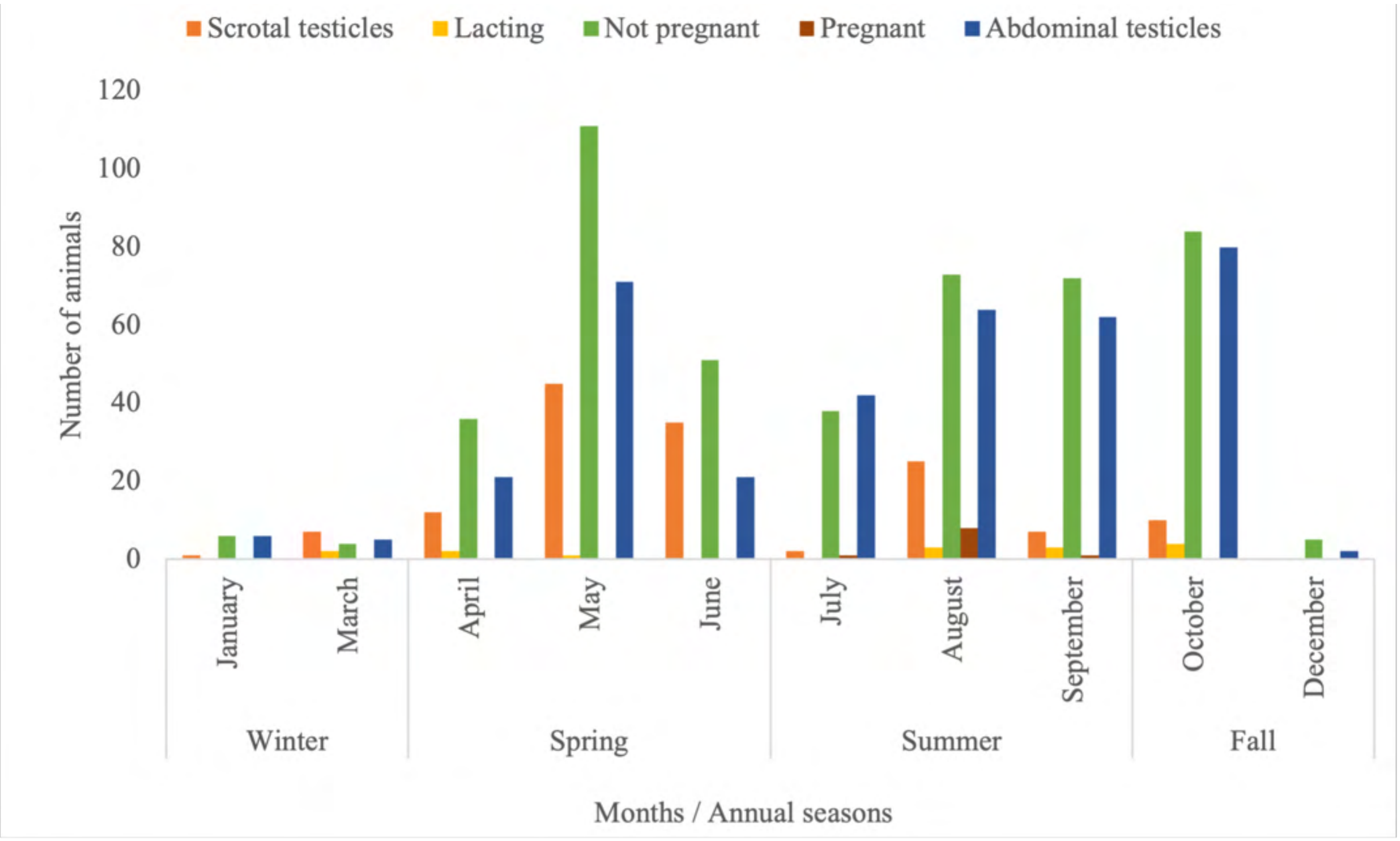

Figure 3. Average sex and age breakdowns of captured Phillips´ kangaroo rat (*Dipodomys phillipsii*) by season for 2012-2016, from Perote, Veracruz.

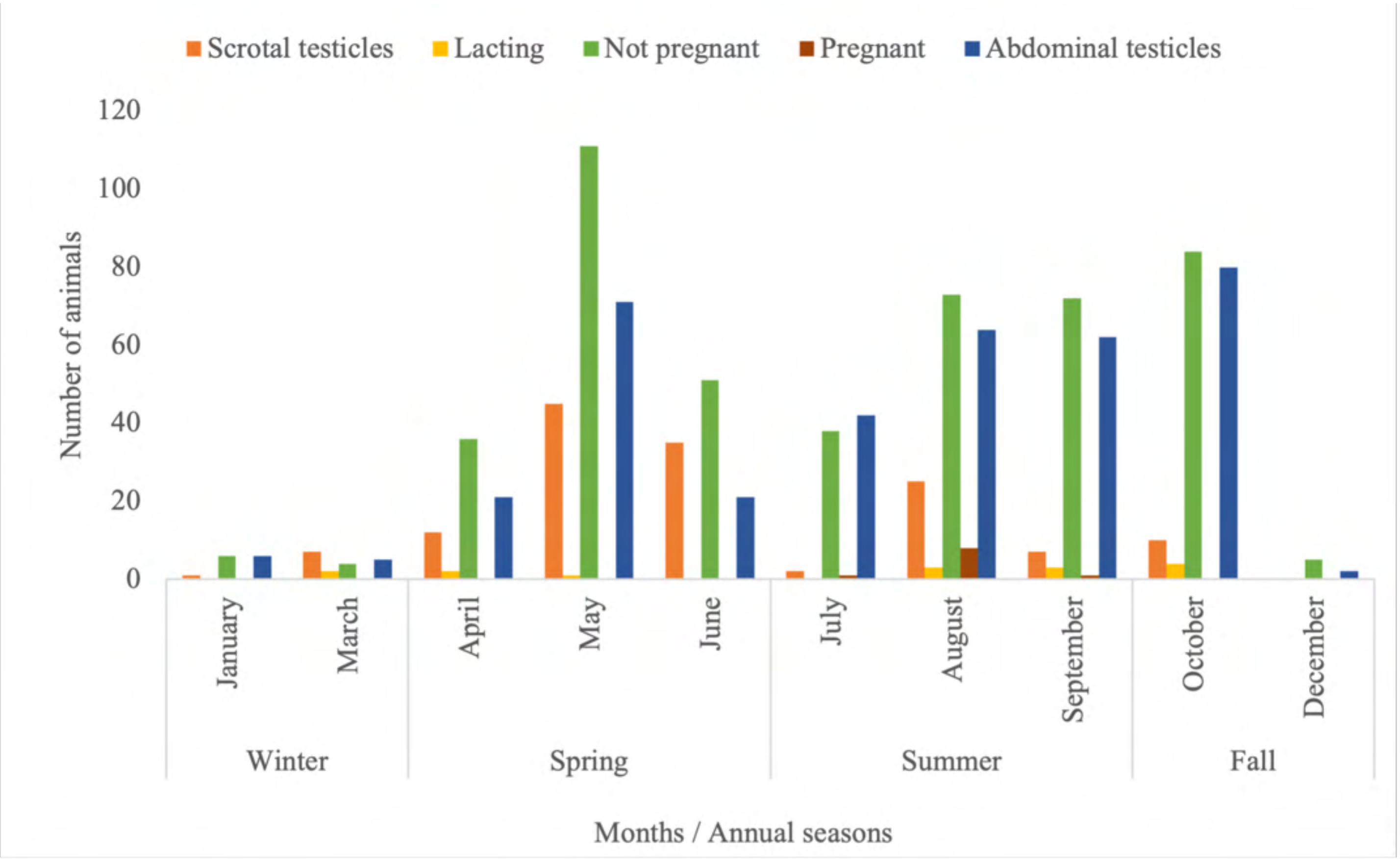

Figure 4. Frequency counts of secondary sexual characteristics for Phillips´ kangaroo rat (*Dipodomys phillipsii*) individuals by month and season, from Perote, Veracruz.

Antonio and González-Romero 2018), providing rodent species with tender shoots, stems and leaves as food resources. *Dipodomys* rats also consume insects (Bradley and Mauer 1971; Longland and Dimitri 2021); it is likely the summer abundance of Orthoptera, as well as mealworm beetles (Coleoptera) which were found daily inside the traps, are part of *D. phillipsii*'s diet. Since such inputs are ephemeral, a diverse diet throughout the year is required to meet the demanding energy requirements for growth and reproduction (Soholt 1977; Zeng and Brown 1987). These energetic demands can be reflected in the weight of the organisms (Bradley and Mauer 1971; Zeng and Brown 1987), which in our study, were like those of Durán-Antonio and González-Romero (2018). The overall weights of individuals decreased significantly in late summer and winter. Such patterns have been observed in *D. merriami* and were attributed to meteorological and food availability changes (Bradley and Mauer 1971; Zeng and Brown 1987) as well as the energetically costly maintenance of homeostasis during temperature lows (Gummer 2005). In winter, these energetic needs are met by the consumption of seasonal vegetation, which is tightly linked to summer rainfall. Consequently, droughts can have serious repercussions on the proliferation and reproduction of these rodents (Beatley 1976; Ernest *et al.* 2000).

Summer food availability is also related to summer reproduction (Lima *et al.* 2008; Thibault *et al.* 2010), where grasses and succulents can provide the necessary requirements for the most demanding stages of gestation and lactation (Soholt 1977). Summer was the season with the highest individual weights, number of captures and was comparatively higher to previously reported numbers for other species of the genus (Zeng and Brown 1987; Goldingay *et al.* 1997). However, in May and June 2018, when the study area was resampled, no individuals were captured (González-Romero personal communication). Human alterations to the landscape surrounding the studied sites may have driven *D. phillipsii* from the area (Thibault *et al.* 2010). The Perote endemic squirrel (*Xerospermophilus perotensis*) also shows lower population densities in these sites than in areas that more closely resemble its original habitat (Montero-Bagatella *et al.* 2017). These two species share habitat preferences and may respond similarly to habitat modifications. Agricultural development and expansion are continuously shrinking their habitat which limits their potential to inhabit new areas (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014; Jiménez-García *et al.* 2014; Flores-Zamarripa and Fernández 2018;). Traditional farming methods that promote native plant diversity and serve as a refuge for the Phillips kangaroo rat (Jiménez-García *et al.* 2014), are being phased out by conventional methods. The low dispersal capacity of the genus, habitat loss, and natural and anthropic barriers combine to limit the flow of individuals to other populations (Zeng and Brown 1987; Bliss *et al.* 2019; Patton *et al.* 2019; Wilkening *et al.* 2019), restricting genetic diversity and increasing the vulnerability to extinction of *D. phillipsii*´s (Patton *et al.* 2019).

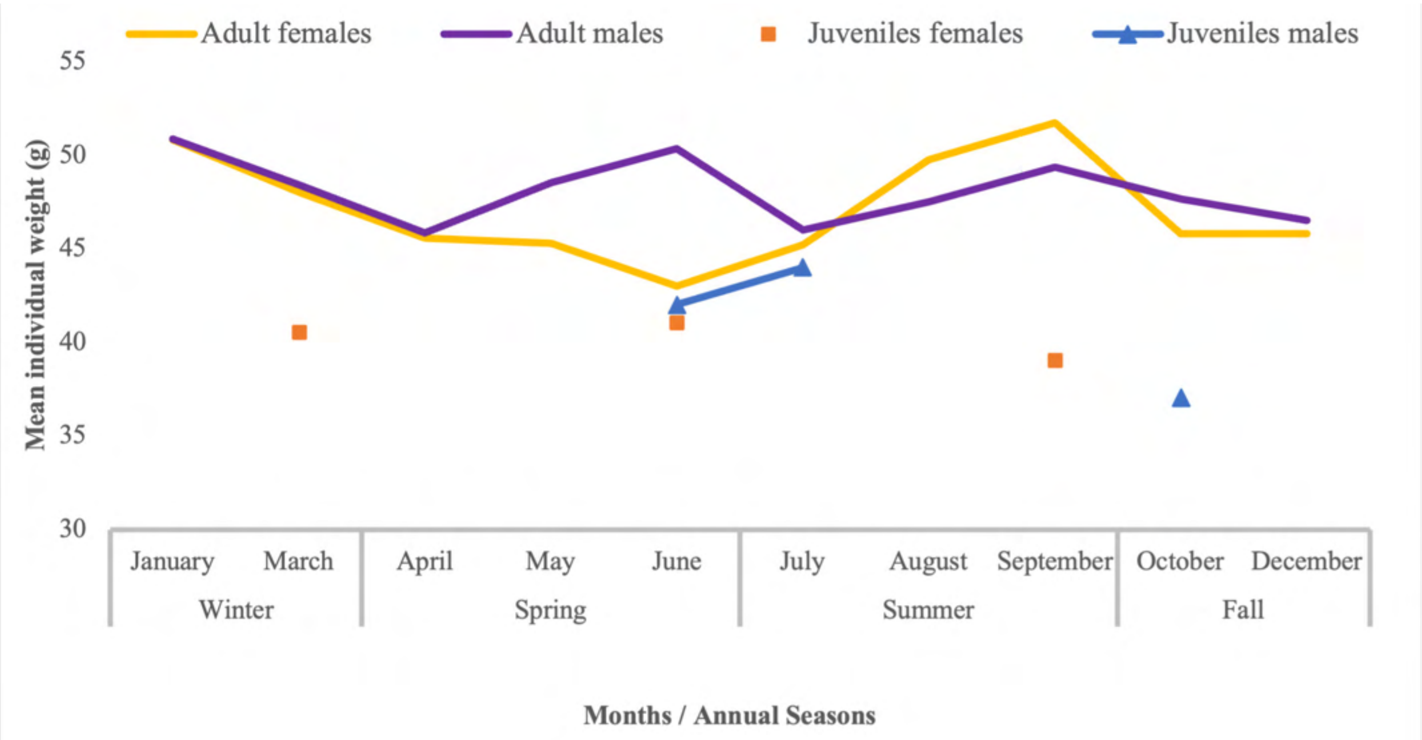

Figure 5. Average weights by age and sex of captured kangaroo rats (*Dipodomys phillipsii*), from Perote, Veracruz.

Further demographic and ecological studies about this species would complement the information presented in this study. The identification and study of additional populations could allow for *ex situ* conservation and reintroduction efforts to be considered (Patton *et al.* 2019; Wilkening *et al.* 2019). The implementation of certain agricultural practices (Jiménez-García *et al.* 2014; Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018) and enforced legal protection of the habitat of *D. phillipsii* has potential to greatly favor the preservation of this and other endemic species. However, the few legal protections that exist are disappearing; the "Natural Protection Area" status that once protected thousands of hectares, including a portion of the distribution range of *D. phillipsii* distribution range, was annulled (Gobierno del Estado deGovernment of the State of Veracruz 2019). The results of this study, together with the physiological and habitual characteristics of this species indicate that its long-term existence is threatened. Actions that support the protection of the Phillips´s kangaroo rat and its habitat are urgent, beginning with changing its national risk category, NOM 059 from "threatened" to "in danger of extinction".

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Variation of mammal diversity along a gradient separated by geographic barriers within the Andes of Perú

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The protection of many mammal species is restrained by anthropogenic pressures. For this reason, using camera traps is critical to learning about the characteristics of their populations and communities, especially when geographic barriers limit their dispersal. This study aimed to measure the variation in mammal diversity in three areas under different protection levels (Piñi Piñi, Manu Learning Centre, and Aguanos), separated by geographic barriers within the Manu Biosphere Reserve. Relative abundance indices, correspondence analysis, non-metric multidimensional scaling, diversity analysis using Hill numbers, similarity analysis, and Bray-Curtis beta diversity partitioning were measured with the recorded data. Overall, 193 individuals of 36 species were recorded, some showing area preference. *Didelphis marsupialis*, *Dicotyles tajacu*, and *Sylvilagus brasiliensis* prefer areas with a lower protection level. According to Hill's diversity indices, the most diverse area is the Manu Learning Centre. The three areas show variations in diversity due to changes in their composition (balanced variation) influenced by geographic barriers, such as Cerro Teparo Punta and the Alto Madre de Dios River.

Muchas especies de mamíferos sufren presiones antrópicas que dificultan su protección, por lo que el uso de cámaras trampa para conocer las características de sus poblaciones y comunidades es muy importante, mucho más cuando se tienen barreras geográficas que podrían limitar su dispersión. El objetivo de este trabajo fue medir la variación de la diversidad de mamíferos en 3 zonas con diferentes grados de protección (Piñi Piñi, Manu Learning Centre y Aguanos), que se encuentran separadas por barreras geográficas dentro de la Reserva de Biosfera del Manu, Perú. Se midieron índices de abundancia relativa, análisis de correspondencia, escalamiento multidimensional no métrico, análisis de la diversidad usando números de Hill, análisis de similitud y partición de la diversidad beta de Bray-Curtis. Se registraron 193 individuos de 36 especies. *Didelphis marsupialis*, *Dicotyles tajacu*, *Sylvilagus brasiliensis* tienen tendencia hacia áreas con menor nivel de protección. El área más diversa según los índices de diversidad de Hill corresponde a Manu Learning Centre. Las tres áreas presentan una variación de la diversidad debida a cambios en su composición (variación balanceada) influenciada por la presencia de barreras geográficas como el cerro Teparo Punta y el río Alto Madre de Dios.

Keywords: Balanced variation; camera trap; disturbance; Madre de Dios; Manu Learning Centre.

Introduction

The Neotropics is characterized by a high mammal richness, with 1,617 of the 6,495 species known worldwide (Burgin *et al.* 2018). Perú is the second most diverse country in mammals in South America, with 573 species grouped into 223 genera (Pacheco *et al.* 2021). Twenty-one of the mammal species registered for Peru are endemic to the country and listed in some threat category. The Manu Biosphere Reserve, in southeast Perú, is home to 222 species, accounting for 39 % of the species recorded in Perú (Solari *et al.* 2006). The number of species recorded in Perú and this reserve may increase because many areas are still unexplored or with little sampling effort (Pacheco *et al.* 2009, 2021). Mammals are frequently used in conservation as key, flag, and umbrella species for various reasons, such as their central role in trophic webs, charisma, and broad distribution (Thornton *et al.* 2016; Figel *et al.* 2018).

The distribution range of a species stretches from a center of abundance to barriers that limit its dispersion (Grinnell 1914; Aliaga-Samanez *et al.* 2020). These can be intangible, such as inter-and intraspecific relationships and climatic factors, or tangible, such as rivers, mountains, and land-use changes (Wallace 1854; Grinnell 1914; Oswald *et al.* 2016; Aliaga-Samanez *et al.* 2020). The permeability of barriers varies depending on the characteristics of each species and may even change over time (Aliaga-Samanez *et al.* 2020). These barriers lead to variations in the composition of communities and their diversity in landscape units or surrounding landscapes (Grinnell 1914; Ayres and Clutton-Brock 1992; Gascon *et al.* 2000).

Some studies have addressed mammal diversity and its differences between landscape types or vegetation units (Pérez-Irineo and Santos-Moreno 2010; Aquino *et al.* 2012; Cruz-Jácome *et al.* 2015; Hernández-Pérez *et al.* 2015; Li *et al.*

2021). In recent years, the use of trap cameras for the study of mammals has increased significantly since they are considered an affordable, reliable, and non-invasive research tool that allows for recording cryptic and evasive species (Pérez-Irineo and Santos-Moreno 2010; Hernández-Pérez *et al.* 2015; Mosquera-Guerra *et al.* 2018). Camera traps facilitate data collection to calculate relative abundance, activity patterns, diversity, and spatial variation (Cruz-Jácome *et al.* 2015; Hernández-Pérez *et al.* 2015; Mosquera-Guerra *et al.* 2018). This information is important to define priority conservation areas with quantitative methods, such as those proposed by Chávez-Gonzalez *et al.* (2014), or to contribute additional information to improve existing proposals in priority areas (Monroy-Vilchis *et al.* 2011; Mosquera-Guerra *et al.* 2018).

Priority conservation areas are threatened by the expansion of the agricultural frontier and road networks, incorporation of pollutants from areas outside their limits, and resource overexploitation due to the intensification of hunting and fishing (Osores-Plenge *et al.* 2012; SERNANP 2019; Shepard *et al.* 2010). In and around priority conservation areas, many mammal species are used as a source of protein (bushmeat) for cultural reasons, subsistence, and growing economic needs (Aquino *et al.* 2007; Fa *et al.* 2013). In this context, 25 % of species consumed as bushmeat in South America are under some category of threat according to IUCN, so their vulnerability is intensified by overhunting (Aquino *et al.* 2007; Fa *et al.* 2013). One of the priority conservation areas in Peru is the Manu Biosphere Reserve (RBM, for its acronym in Spanish; SERNANP 2019).

The RBM comprises an area of 1,881,200 ha, including a core area (Manu National Park) and a buffer zone (SERNANP 2019). This reserve is considered a conservation *hotspot* due to its high biological diversity (Myers *et al.* 2000) as a result of the different climate types and broad altitudinal range within its area (Smith *et al.* 2008; Serrano-Rojas *et al.* 2022). The RBM is home to a wide variety of ecosystems, the most representative of which are the pajonal, the high tropical forest, and the low tropical forest (SERNANP 2019). These and other ecosystems are delimited by geographic barriers that restrain species distribution.

This study aimed to investigate the variation in mammal diversity at three sites within the RBM, each subject to different forms of protection: government-managed, privately-managed, and unprotected. The study also sought to document observations related to both tangible physical barriers, such as the Alto Madre de Dios River and Cerro Teparo Punta, and intangible barriers, including anthropogenic activities and their interactions with mammalian communities.

Materials and methods

Study area. The present work was carried out in the district and province of Manu, in the department of Madre de Dios within the RBM (Figure 1). Phototrapping was carried out at three sites with different degrees of conservation, separated by geographic barriers between them, and at different distances from urban and rural settlements:

Piñi piñi (-12.770769 °S, -71.489761 °W): Region adjacent to the upper Piñi Piñi River at 618 masl in the Manu National Park. This site is under strict protection by the Peruvian government through the Ministry of the Environment. It is located 15 km from the native community of Santa Rosa de Huacaria (-12.886353 °S, -71.4407001 °W and 4.5 km from the Amalia indigenous people in initial contact settlement (-12.742430 °S, -71.524425 °W). Santa Rosa de Huacaria belongs to the Huachperi-Matsigenka tribe and the Amalia settlement to the Matsigenka tribe. The main activities of these communities are small-scale agriculture for self-consumption and bushmeat hunting (*e. g., Ateles chamek, Tayassu peccari, Cuniculus paca, Dasyprocta punctata, Alouatta seniculus,* and *Crax tuberosum*) (Da Silva *et al.* 2005). It is located 19 km from Pillcopata, a major town where there is constant trade and home to hunters who use rifles and similar guns for bushmeat hunting (*e. g., Tayassu peccari, Cuniculus paca, Dasyprocta punctata*, and *Crax tuberosum*). It is separated from the Manu Learning Centre biological field station and Aguanos by the Cerro Teparo Punta, a hill stretching from the Coñec pongo up to 56 km northwestward, from where trap cameras have been installed. According to Servicio Nacional de Metereología e Hidrología del Perú (SENAMHI 2020), the local climate is rainy with a dry and temperate winter (B(i)B′).

The Manu Learning Centre Biological Field Station (MLC; -12.809389 °*S*, -71.396056 °*W*) is situated on the left bank of the Alto Madre de Dios River at an elevation of 524 meters above sea level (asl) in the Manu National Park buffer zone. The station is enveloped by a secondary forest that has been undergoing a self-recovery process for over 30 years. It serves as a hub for biodiversity monitoring and ecotourism activities, and is not supported by government protection but is managed as a private conservation area by the Crees Foundation. It is 19 km from the native Palotoa Teparo community (Matsigenka tribe) on the same left bank of the Alto Madre de Dios River, 2.5 km from the Aguanos village, and 6 km from the Salvacion village, which is the main commercial trade center home to hunters who use firearms. According to SENAMHI (2020), the local climate is rainy with high humidity the year round (*B(r)B′*).

Aguanos (-12.800532 °*S*, -71.372436 °*W*): It is located on the right bank of the Alto Madre de Dios River at 470 m asl in the RBM buffer zone, with neither government nor private protection, administered under the local government of the Manu province. It is a hamlet dedicated mainly to growing bananas (*Musa paradisiaca*) and papaya (*Carica papaya*; Santiago-Corisepa *et al.* 2022). The Villa Salvación village center (-12.836485 °S, - 71.361210 °W) is 5 km away. According to SENAMHI (2020), the local climate is rainy with high humidity the year round (*B(r)B′*).

Sampling with trap cameras. At each study site, eight stations were established, distributed within a system of grids of two quadrants, separated from each other by a minimum distance of 1 km. In each station, we placed a camera trap at a height between 30 and 40 cm from the ground and set to capture 15-second videos with 30-second intervals between captures. At each station, cameras were in operation for three months between June and September, corresponding to the dry season in Peru (with 90 hours of effort per station). Those records separated by more than 1 hour were considered independent records for the analyses (Oliveira *et al.* 2020).

Identification and taxonomic criteria. Species identification was performed by comparison with previous records in the Crees Foundation database and using the descriptions by Emmons and Francois (1990). Species were listed, and scientific names were updated considering the proposal of Pacheco *et al.* (2021).

Data analysis. Potential differences between the three protection levels were investigated using a similarity analysis (ANOSIM) and a non-metric multidimensional scaling (NMDS). ANOSIM is a non-parametric test that uses permutations to calculate differences between groups; in the study, the groups are the eight sampling stations for each forest type (Legendre and Legendre 1983). The NMDS is an ordination method to detect differences between groups using a distance measure, in this case, the Bray-Curtis distance (Legendre and Legendre 1983). The radius of each circle surrounding each point is inversely proportional to the distance to the geometric centroid of the eight sampling points of each forest type.

To determine which of the three forest types is more diverse, we performed Hill's alpha diversity and evenness indices, and rarefaction analyses. Hill's diversity and evenness indices show a better diversity approximation than conventional diversity indices (Hill 1973). Hill's evenness index was calculated by dividing Hill's number of order 0 (N(0)) by the number of order 1 (N(1)).

To define whether the differences in the three protection level types are due to changes in composition, we constructed rank-abundance curves and performed a Bray-Cutis (Bray) beta diversity partitioning analysis. Beta diversity partitioning allows splitting the Bray-Curtis distance into a balanced variation resulting from changes in community composition and variation in gradients associated with the reduction in community richness and abundance (Jost 2007; Baselga 2013, 2017).

Preferences of some mammal species for a given degree of protection were explored through a correspondence analysis (CA). CA is an ordination method that reveals differences between objects and plots the descriptors associated with them using the Chi-square distance (Legendre and Legendre 1983). CA was carried out considering the type-I scaling, excluding species that were only recorded once. All the analyses and graphs were performed using the Python 3.10.9 programming language in the Spyder 5.4.2 IDE, using the packages NumPy 1.24, eCopy 0.1.2.2, Pandas 1.5.3, and Matplotlib 3.7.0.

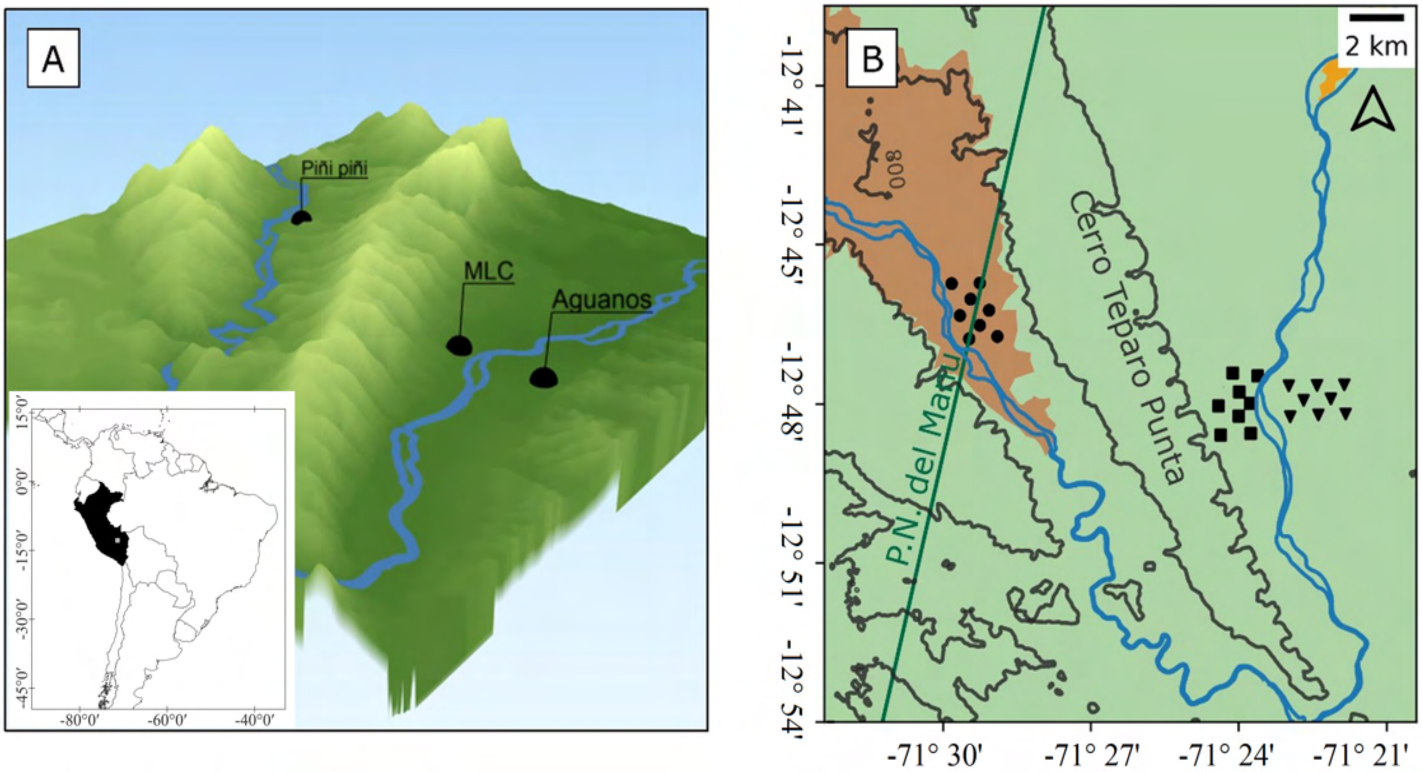

Figure 1. Study area. a) Three-dimensional elevation map showing the mountain formations, Madre de Dios River, Piñi Piñi River, and collection sites. b) Map of the layout of camera traps used in the study area showing mountain ranges, climate types according to SENAMHI (2020). Light green. weather A(r)A'; Light orange. weather B(r)B'; Line green. edge of Manu National Park; Black triangle. Aguanos; Black circle. Piñi piñi; Black square. MLC biological station.

Results

A total of 193 individuals of 36 species were recorded with a sampling effort of 2,160 h. The most abundant species was *Cuniculus paca*, with 21 individuals, followed by *Dasypus novemcinctus* and *Mazama americana*, with 19 individuals each. The families with the highest species richness were Didelphidae and Felidae, with five recorded species each. The most abundant families were Felidae, with 36 individuals; Cuniculidae, with 21; and Dasypodidae and Cervidae, with 19 individuals each. *Cuniculus paca*, *M. americana*, and *D. novemcinctus* are abundantly distributed in the three protection levels, being considered dominant species across the entire study area. Within the family Felidae, the dominant species in the three protection levels was *Leopardus pardalis* (Table 1).

At Aguanos, the most abundant species was *Dicotyles tajacu*, with eight individuals, followed by *C. paca* and *M. americana*, with seven individuals each. Six singleton species were observed, and *Galictis vittata*, *Potos flavus*, *Atelocynus microtis*, *Saimiri boliviensis*, and *Caluromys lanatus* were recorded exclusively in this area (Figure 2 and Table 1). At MLC, the most abundant species were *C. paca* and *D. novemcinctus*, with eight individuals each, followed by *M. americana* and *Tapirus terrestris*, with seven individuals each. Nine singletons with a single record were observed, and *Microsciurus flaviventer, Sciurus ignitus, Callicebus urubambensis, Metachirus nudicaudatus, Procyon cancrivorus, Philander opossum, Sciurus spadiceus,* and *Chironectes minimus* were recorded exclusively in this area (Figure 2 and Table 1). Last, at Piñi Piñi, the most abundant species was *C. paca*, with six individuals; eight singleton species were observed, and *Sapajus apella*, *Dinomys branickii*, and *Lagothrix flavicaudae* were observed only in this area (Figure 2 and Table 1).

According to the correspondence analysis (Figure 3), some mammal species prefer a certain area. This preference is more noticeable in *Didelphis marsupialis*, *D. tajacu*, and *Sylvilagus brasiliensis*, which tend to prefer more open, disturbed, and unprotected areas (such as Aguanos); *and Nasua nasua,* which showed a trend toward protected and conserved areas within the Manu National Park (Piñi Piñi). These preference variations translate into statistically significant differences in the composition of mammal species between the three protection levels in the similarity analysis ($R = 0.159$; $P < 0.05$). Additionally, the above is supported by the non-metric multidimensional analysis (NMDS; Figure 3), showing that, although there is a high similarity between points closer to the centroid of each conservation level, there are also points that allow differentiating them.

The analysis of Hill's alpha diversity numbers (Table 2) revealed that the most diverse protection level is MLC, followed by Aguanos and Piñi Piñi. As for evenness (*E(1.0)*), the most even forest was Aguanos, followed by MLC and Piñi Piñi. The shift of order in the evenness index between MLC and Aguanos occurs because the former recorded more singleton species (9) than Aguanos. Since different numbers of total individuals were recorded in each zone (Aguanos, 73; MLC, 75; and Piñi Piñi, 45), the effort was equalized using the rarefaction index, with MLC attaining the highest index, followed by Aguanos and Piñi Piñi, with very similar index values (Table 2).

In the Bray-Curtis beta diversity partitioning (Table 3), the overall variation is mostly due to balanced variation (63.38 %), indicating that the species composition changes drastically from one protection level to another. When analyzed separately, this prevalence of beta diversity due to balanced variation (B-bal) is maintained when comparing

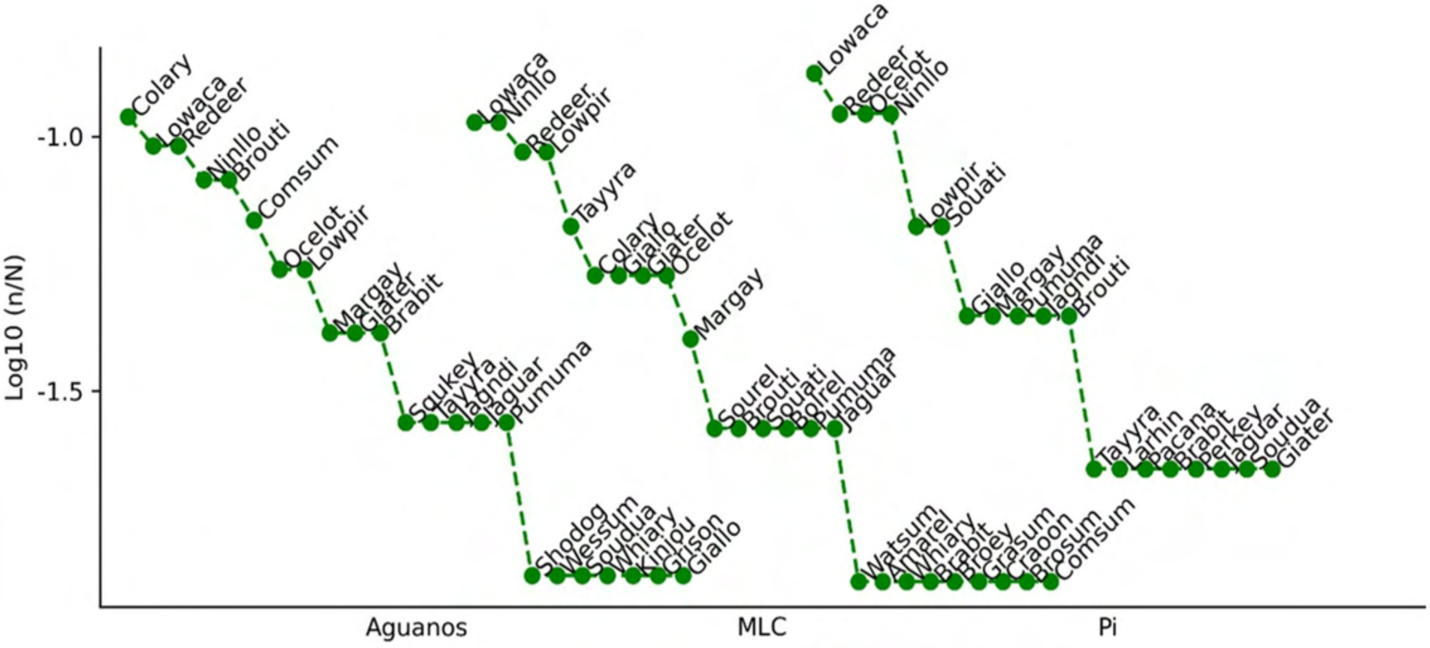

Figure 2. Rank-abundance curves of species recorded by forest type. Graph codes are specified in Table 1.

Table 1. Abundance and richness of mammals collected in the study. Cod, name code; Ag, Aguanos; Pi, Piñi Piñi; M, Biological Station Manu Learning Centre; To, total, CA, conservation level according to SERFOR (2018). IUCN, threat category according to IUCN (2022); LC, Least Concern; EN, Endangered; VU, Vulnerable; NT, Near Threatened

Familia	Especie	Nombre	Cod	Ag.	Pi	M	To	CA	IUCN
Sciuridae	*Microsciurus flaviventer*	Amazon Dwarf Squirrel	Amarel	0	0	1	1	DI	LC
Sciuridae	*Hadrosciurus ignitus*	Bolivian Squirrel	Bolrel	0	0	2	2	-	LC
Leporidae	*Sylvilagus brasiliensis*	Brazilian Rabbit	Brabit	3	1	1	5	-	EN
Pitheciidae	*Callicebus urubambensis*	Brown Titi Monkey	Broey	0	0	1	1	-	-
Didelphidae	*Metachirus myosuros*	Brown Four-Eyed Opossum	Brosum	0	0	1	1	-	-
Dasyproctidae	*Dasyprocta variegata*	Brown Agouti	Brouti	6	2	2	10	-	LC
Tayassuidae	*Dicotyles tajacu*	Collared Peccary	Colary	8	0	4	12	-	-
Didelphidae	*Didelphis marsupialis*	Common Opossum	Comsum	5	0	1	6	-	LC
Procyonidae	*Procyon cancrivorus*	Crab-Eating Raccoon	Craoon	0	0	1	1	-	LC
Chlamyphoridae	*Priodontes maximus*	Giant Armadillo	Giallo	1	2	4	7	V	VU
Myrmecophagidae	*Myrmecophaga tridactyla*	Giant Anteater	Giater	3	1	4	8	V	VU
Didelphidae	*Philander sp.*	Gray Four-Eyed Opossum	Grasum	0	0	1	1	-	-
Mustelidae	*Galictis vittata*	Grison	Grison	1	0	0	1	-	LC
Felidae	*Puma yagouaroundi*	Jaguarundi	Jagndi	2	2	0	4	-	LC
Felidae	*Panthera onca*	Jaguar	Jaguar	2	1	2	5	CA	NT
Procyonidae	*Potos flavus*	Kinkajou	Kinjou	1	0	0	1	-	LC
Cebidae	*Cebus apella*	Large-Headed Capuchin	Larhin	0	1	0	1	-	LC
Cuniculidae	*Cuniculus paca*	Lowland Paca	Lowaca	7	6	8	21	-	LC
Tapiridae	*Tapirus terrestris*	Lowland Tapir	Lowpir	4	3	7	14	CA	VU
Felidae	*Leopardus wiedii*	Margay	Margay	3	2	3	8	DI	NT
Dasypodidae	*Dasypus novemcinctus*	Nine-Banded Armadillo	Ninllo	6	5	8	19	-	LC
Felidae	*Leopardus pardalis*	Ocelot	Ocelot	4	5	4	13	-	LC
Dinomyidae	*Dinomys branickii*	Pacarana	Pacana	0	1	0	1	V	LC
Atelidae	*Lagothrix lagothricha*	Peruvian Woolly Monkey	Perkey	0	1	0	1	EP	VU
Felidae	*Puma concolor*	Puma	Pumuma	2	2	2	6	CA	LC
Cervidae	*Mazama americana*	Red-Brocket Deer	Redeer	7	5	7	19	DI	DD
Canidae	*Atelocynus microtis*	Short-Eared Dog	Shodog	1	0	0	1	V	NT
Procyonidae	*Nasua nasua*	South American Coati	Souati	0	3	2	5	-	LC
Myrmecophagidae	*Tamandua tetradactyla*	Southern Tamandua	Soudua	1	1	0	2	-	LC
Sciuridae	*Hadrosciurus spadiceus*	Southern Amazon Red Squirrel	Sourel	0	0	2	2	-	LC
Cebidae	*Saimiri boliviensis*	Squirrel monkey	Squkey	2	0	0	2	-	LC
Mustelidae	*Eira barbara*	Tayra	Tayyra	2	1	5	8	-	LC
Didelphidae	*Chironectes minimus*	Water Opposum	Watsum	0	0	1	1	-	LC
Didelphidae	*Caluromys lanatus*	Western Wolly Opossum	Wessum	1	0	0	1	-	LC
Tayassuidae	*Tayassu pecari*	White-Lipped Peccary	Whiary	1	0	1	2	CA	VU
Total				73	45	75	193		

MLC with Aguanos (76.14 %) and Aguanos with Piñi Piñi (57.41 %), but changes to a variation by gradients when comparing MLC with Piñi Piñi (59.35 %). Although the variation is mostly balanced, composition changes are also due to gradient variation (B-gra).

Discussion

The protection level of an area determines the presence of human settlements, the activities allowed, and the intensity of resource extraction (Kuamara et al. 2004; Blom *et al.* 2005; Trisurat et al. 200514; Rabanal *et al.* 2010). All these factors influence mammalian communities in different regions and at different scales (Kuamara et al. 2004; Blom *et al.* 2005; Trisurat et al. 200514; Rabanal *et al.* 2010). The present study is one of the few works relating the composition of mammal communities to the protection level of areas within a Biosphere Reserve.

In general, the mammal community varies across the three protection levels as some species exhibit preferences for a given level; as a result, beta diversity is primarily due to balanced variation. This variation may be due to various factors, such as geographic barriers that delimit the distribution of species (Gascon *et al.* 2000; Maciel-Mata *et al.* 2015; Oswald *et al.* 2016), climatic conditions that determine seasonality and its presence (*e. g.*, Cândido-Rocha et al. 2006), and anthropic activities such as hunting (Blom *et al.* 2005; Aquino *et al.* 2007; Fa *et al.* 2013).

Tangible geographic barriers, such as Cerro Teparo Punta and Alto Madre de Dios River, restrain the dispersal capacity of some populations, isolating them. As a result, these may

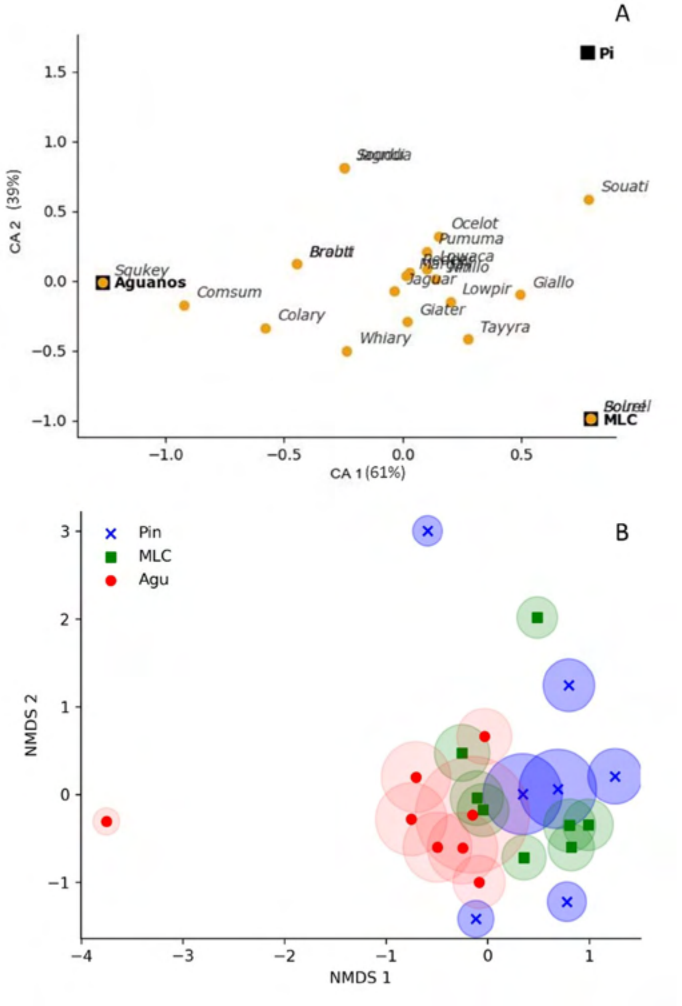

Figure 3. a) Correspondence analysis showing the three collection zones and associated species. b) Non-metric multidimensional scaling of the three forest types, showing camera traps.

produce potential new lineages that respond differently and independently to the local environment (Oswald *et al.* 2016). Mountain ranges are central to species composition and endemism patterns in Neotropical forests (Oswald *et al.* 2016). In this way, Cerro Teparo Punta is a barrier for some mammal populations that cannot move across the peak of this relief form. As regards the Alto Madre de Dios River, more studies should be carried out to determine whether it is a barrier restraining the distribution of mammals because not all rivers limit the movement of species, and their permeability depends on the dispersal capacity of each species (Grinnell 1914; Gascon *et al.* 2000).

Another factor that may explain the variation in the three sampling areas is intangible barriers such as anthropogenic activities, such as hunting, whose preference for some species and strategies differ between regions (Kuamara et al. 2004; Aquino *et al.* 2007; Endo *et al.* 2010; Fa *et al.* 2013). This variation in hunting preference decreases the abundance of the most hunted species and favors the abundance of the least hunted ones in areas surrounding populated centers (Endo *et al.* 2010). In the present work, *Didelphis marsupialis*, *Sylvilagus brasiliensis*, and *Dicotyles tajacu* tend to be present in disturbed areas, maybe cause they are not usually hunted by local or indigenous populations in the surrounding areas (Endo *et al.* 2010; Fa *et al.* 2013; Farfan-Flores *et al.* 2023). The species most hunted and consumed by Matsigenka indigenous communities in the study area are *Ateles chamek*, *Lagothrix lagotricha,* and *Tayassu pecari,* which may explain the low frequency of these species in the present study (Endo *et al.* 2010; Farfan-Flores *et al.* 2023).

Table 2. Analysis of Hill's alpha diversity, rarefaction, and evenness. N(0). zero Hill's number; N(1). First Hill's number; N(2). Second Hill's number; E(1,0). Hill's eveness.

	N (0)	N (1)	N (2)	E (1,0)	rarefy
Aguanos	23.000	18.216	15.446	0.792	19.388
MLC	25.000	19.159	15.756	0.766	20.298
Piñi Piñi	19.000	15.345	12.898	0.808	19.000

All species recorded in the study were previously reported for Peru by Solari *et al.* (2006) and Pacheco *et al.* (2021), so they are common for the Manu Biosphere Reserve. A large part of the recorded species are considered under some threat category. According to Servicio Nacional Forestal y de Fauna Silvestre (SERFOR 2018), 12 (34 %) species are listed under a threat category: four as Vulnerable, one as Endangered, four as Nearly Threatened, and three with insufficient data. According to International Union for Conservation of Nature and Natural Resources (IUCN 2022), 31 species (88 %) are considered under a threat category: 21 species as Least Concern (LC), five as Vulnerable (VU), one as Endangered (EN), three as Nearly Threatened (NT), and one as Data Deficient (DD; Table 1).

Cuniculus paca, *Mazama americana,* and *Dasypus novemcinctus* were the most recorded species in the present work. The three species are widely distributed in Peru and have been recorded in the Pacific rainforest, equatorial dry tropical forest, yungas, and low tropical forest (Pacheco *et al.* 2021). These species can be considered very abundant in the Peruvian Amazon (Aquino *et al.* 2012). Aquino *et al.* (2007) mention them among the species facing heavy hunting pressure, so monitoring strategies are needed to ensure their conservation in the RBM. In addition to these three species, many mammals under a threat category are consumed as a protein source by local and native populations, affecting their diversity and total biomass (Endo *et al.* 2010; Fa *et al.* 2013). Therefore, the effect of hunting and the hunting methods should be considered within and around the current and proposed priority conservation areas.

Table 3. Bray-Curtis beta diversity partitioning analysis. B-bal. balanced partition of Bray-Curtis index; B-gra. gradient partition of Bray-Curtis index; B-total. Bray-Curtis index.

L1	L2	B-bal	%B-bal	B-gra	%B-gra	B-total
MLC	**Aguanos**	0.3263	76.1404	0.1023	23.8596	0.4286
MLC	**Piñi piñi**	0.2000	40.6452	0.2921	59.3548	0.4921
Aguanos	**Piñi piñi**	0.2333	57.4073	0.1731	42.5926	0.4065
MLC-Agu-Piñi		0.3314	63.3859	0.1914	36.6141	0.5228

The present work recorded five feline species, accounting for 62.5 % of the feline species reported for Peru (Pacheco *et al.* 2021). The presence of carnivores such as felines is essential for defining conservation criteria in each area because they play a central role in the ecosystem by limiting the number of herbivores; indeed, they are generally used in conservation strategies (Miller *et al.* 2001; Figel *et al.* 2018; Thornton *et al.* 2016). The most protected areas generally have a greater relative abundance of felines than the least conserved (Pardo Vargas *et al.* 2016). This is consistent with our work, where 26.6 % of felines were recorded at Piñi Piñi and only 14.6 % at MLC. *Puma concolor* and *Panthera onca* inhabit the entire study area, mainly the RBM, so they should be considered in local conservation strategies as umbrella species, replicating previous models (Solari *et al.* 2006; Figel *et al.* 2018; Thornton *et al.* 2016).

From the records, a detailed review of the *Philander* species recorded in the Manu Learning Centre biological station is needed because this genus entails a controversial taxonomy, with eight described species, of which five are reported for Peru (Voss *et al.* 2018; Pacheco *et al.* 2021). Another recorded species for which the distribution should be studied to determine its threat category is *Callicebus urubambensis* (Figure 4), a species endemic to Peru treated as a subspecies of *Callicebus brunneus* before its description as a separate species (Vermeer and Tello-Alvarado 2015).

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Figure 4. Photography of *Callicebus urubambensis.*

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Mesocarnivores activity patterns in the Northern Colombian Andes

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Temporal segregation plays an important role as a coexistence mechanism between potentially competing and closely related species, especially in species with similar morphology and ecological requirements, such as mesocarnivores. This study investigates the temporal niche ecology of mesocarnivores coexisting in the southeastern Aburrá Valley, northern Colombian Andes. Specifically, this study i) evaluated the daily activity patterns of six mesocarnivore species, ii) analyzed the influence of the lunar cycle on the activity patterns of nocturnal species, iii) estimated the temporal overlap between pairs of mesocarnivores, and iv) estimated the functional similarities of these species. We hypothesized that mesocarnivores with similar functional traits exhibit greater temporal niche segregation, thus showing low overlap in their activity patterns to reduce competition. We used data from tracking cameras (10,744 camera-days) and estimated daily activity patterns using Kernel density analysis, non-negative trigonometric summation, and overlap analysis with the *Overlap* package in R. Also, lunar influence was evaluated using circular statistics in the software Oriana 4.02. Functional similarity was analyzed by similarity clustering using Jaccard's index in PAST. Nine species were recorded; six were included in the analyses of daily activity patterns. Activity patterns were not uniform throughout the circadian cycle. *Cerdocyon thous*, *Leopardus tigrinus,* and *Nasuella olivacea* showed mainly nocturnal activity, while *Eira barbara*, *Nasua nasua,* and *Neogale frenata* displayed a diurnal activity pattern. Only *Leopardus tigrinus* showed significant activity related to the lunar cycle. The activity overlap between pairs of species was variable, with a tendency to a low overlap, showing a high ecological similarity between species. This study represents the first estimate of the activity patterns of mesocarnivore species in the southeastern Aburrá Valley. The observed activity patterns are similar to those reported in other works. Species with high overlap showed ecological differences, especially in size and diet. The low number of records for some species may be associated with poor detectability but also with low abundance as a result of urban development and anthropogenic disturbance (*e. g.,* roadkills). Our results suggest that temporal segregation contributes to mediating intra-gremial interactions and coexistence between sympatric and potentially competing species. These results will hopefully contribute to the knowledge of the ecology of mesocarnivores, mainly in ecosystems surrounding large cities in the northern Andes.

La segregación temporal juega un papel importante como mecanismo de coexistencia entre especies potencialmente competidoras y cercanamente emparentadas, especialmente en especies con morfología y requerimientos ecológicos similares como los mesocarnívoros. Aquí, investigamos la ecología del nicho temporal de los mesocarnívoros que coexisten en simpatría al norte de los Andes colombianos, al suroriente del Valle de Aburrá. Específicamente, i) evaluamos los patrones de actividad diaria de seis especies, ii) analizamos la influencia del ciclo lunar en los patrones de actividad diaria de especies nocturnas, iii) estimamos la sobreposición temporal entre pares de mesocarnívoros y iv) estimamos la similitud funcional de estas especies. Hipotetizamos que los mesocarnívoros con rasgos funcionales similares exhiben mayor segregación en el nicho temporal y, por tanto, muestran un bajo sobreposición en sus patrones de actividad para así reducir la competencia. Utilizamos datos obtenidos de cámaras de rastreo (10,744 días-cámara) y realizamos estimaciones de los patrones de actividad diaria por medio de análisis de densidad de Kernel, suma trigonométrica no negativa y análisis de sobreposición con el paquete *Overlap* en el programa R. Asimismo, se evaluó la influencia lunar mediante el uso de estadística circular en el software Oriana 4.02. La similitud funcional se analizó por medio de un conglomerado de similitud, utilizando el índice de Jaccard en el programa PAST. Se registraron nueve especies, seis se incluyeron en los análisis de los patrones de actividad. Los patrones de actividad no fueron uniformes a lo largo del ciclo circadiano. *Cerdocyon thous*, *Leopardus tigrinus* y *Nasuella olivacea* mostraron una actividad principalmente nocturna, mientras *Eira barbara*, *Nasua nasua* y *Neogale frenata* presentaron un patrón de actividad diurno (Figura 2). Únicamente *Leopardus tigrinus* muestra una actividad significativa respecto al ciclo lunar. La sobreposición en la actividad entre pares de especies fue variable, con una tendencia a una sobreposición baja, mostrando una alta similitud ecológica entre especies. Este estudio constituye la primera estimación de los patrones de actividad de las especies de mesocarnívoros del suroriente del Valle de Aburrá. Los patrones de actividad observados son similares a los reportados en otros trabajos. Las especies que mostraron una sobreposición alta, muestran diferencias ecológicas, especialmente en el tamaño y la dieta. El bajo número de registros que se obtuvieron para algunas especies podría estar asociado a una baja detectabilidad, pero también a una baja abundancia como resultado del efecto del desarrollo y la perturbación antrópica (*e. g.,* atropellamientos). Nuestros resultados sugieren que la segregación temporal contribuye a mediar las interacciones intragremiales y la coexistencia entre especie**s** simpátricas y potencialmente competidoras. Esperamos que estos resultados contribuyan al conocimiento sobre la ecología de los mesocarnívoros, principalmente en ecosistemas circundantes a las grandes ciudades al norte de los Andes.

Keywords: Camera trap; ecological traits; non-invasive methods; temporal interactions; temporal segregation.

Introduction

The coexistence of potentially competing species is one of the central topics in ecology and biogeography. It plays a major role in the dynamics of species populations, can profoundly influence the evolution of the ecological traits of interacting species as well as the evolution of species, and also influences underlying ecosystem processes (Broennimann *et al.* 2012; Penteriani *et al.* 2013; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020; Segar *et al.* 2020). For instance, in a community in which closely related species coexist, allopatric mechanisms and some forms of interference (*e. g.,* intraguild predation) are ecological forces with highly relevant implications in structuring communities, with potential effects on the ecology and evolution of the species involved (Rosenzweig 1966; Holt and Polis 1997; Palomares and Caro 1999; de Oliveira and Pereira 2014; Donadio and Buskirk 2006; Hunter and Caro 2008; Arias- Alzate et al. 2022). However, other mechanisms that facilitate the coexistence of potentially competing species remain poorly understood (Godsoe *et al.* 2015; Arias- Alzate et al. 2022).

It could be expected that, at the assemblages level (within the same geographic space), from the competitive exclusion standpoint, the species could coexist if they have distinctive morphological and behavioral adaptations, such as differences in size and diet, changes in habitat use or segregation at spatial or temporal levels (*i. e.,* character segregation or niche differentiation; Case and Gilpin 1974; Schoener 1974a; Chesson and Grubb 1990; Hutchinson 1978; Hunter and Caro 2008; Penido *et al.* 2017; Porto *et al.* 2021; Arias- Alzate et al. 2022). This aspect is an essential part of the ecology of organisms since it provides key information; for example, the use of time directly influences how species interact with the environment, maximize the search for food, seek mating, avoid the risk of predation, and how they continuously cope with the regular changes in the ecosystem (Schoener 1974b; Kronfeld-Schor and Dayan 2003; Laundre *et al.* 2010; Pratas-Santiago *et al.* 2016; Karanth *et al.* 2017; Penido *et al.* 2017; Marinho *et al.* 2020; Vilella *et al.* 2020; Peral *et al.* 2022). Consequently, the daily activity pattern reflects the evolutionary and physiological adaptations that allow species to increase their adequacy while facilitating coexistence (Schoener 1974b; Laundre *et al.* 2010; Tambling *et al.* 2015: Pratas-Santiago *et al.* 2016).

The order Carnivora is one of the most important groups in ecological dynamics. They play a central role in ecosystems through a top-down effect that regulates the populations of their prey, either directly by predation or because of the fear they can produce in the ecosystem (*i. e.,* landscapes of fear; Treves and Karanth 2003; Roemer *et al.* 2009). However, it is one of the most sensitive groups to environmental imbalance, generated mainly by an anthropic effect (Crooks 2002). This group includes a great diversity of species in terms of morphology and function; most are small to medium-sized species (*i.e.*, less than 15 kg), commonly known as mesocarnivores (Roemer *et al.* 2009; Bu *et al.* 2016; Easter *et al.* 2020; Marinho *et al.* 2020).

These species form a diverse group as regards their ecology and behavior; they can be solitary or highly social, with varied diets, and their trophic level is generally just below the top predators (Marinho *et al.* 2020). In general, it has been suggested that mesocarnivores are vitally important in ecosystem dynamics, facilitating nutrient flows between adjacent ecosystems and maintaining the populations of their potential prey in a state of equilibrium (Hunter and Caro 2008; Roemer *et al.* 2009; Penido *et al.* 2017; Marinho *et al.* 2020). In addition, unlike larger carnivores, these species can fulfill unique roles, such as direct or secondary seed dispersal (Hunter and Caro 2008; Roemer *et al.* 2009). Therefore, they play a major role in shaping ecological communities and, therefore, in local and regional ecosystem processes (Hunter and Caro 2008; Roemer *et al.* 2009). For these species, activity patterns may be partly determined by the climate, habitat structure and preference, and anthropogenic influences. On the other hand, these patterns are also driven by interspecific interactions, especially with larger dominant species, where the risk of predation plays a central role and can strongly influence the spatial distribution of resources and the foraging behavior of these species (Crooks and Soule 1999; Bu *et al.* 2016; Ramírez-Mejía and Sánchez 2016; Penido *et al.* 2017; Mpemba *et al.* 2019; Easter *et al.* 2020; Mendes *et al.* 2020). To this end, mesocarnivores must adjust their behaviors and activities in the face of the pressures exerted on these ecosystems while maximizing the search for food and reducing predation risks and antagonistic encounters with other species (Amarasekare 2002; Glen and Dickman 2005; Donadio and Buskirk 2006; Mpemba *et al.* 2019).

However, at a global level, many aspects of the natural history and ecology of mesocarnivores are still unknown, as they are one of the least studied groups about which there are huge gaps in information in the Neotropics (Andrade Ponce *et al.* 2016). For many of them, only their presence in certain regions is known (Andrade Ponce *et al.* 2016); however, little is known about how they interact with each other, their spatial or temporal patterns, and the segregation between them (Easter *et al.* 2020). For example, few studies have investigated the activity patterns of these species in Colombia (González-Maya *et al.* 2015; Cáceres-Martínez *et al.* 2016; Ramírez-Mejía and Sánchez 2016; García-R *et al.* 2019), with limited estimates in the Cordillera Central of Colombia (Delgado-V *et al.* 2011; Ramírez-Mejía and Sánchez 2016). In this region, there are still large information gaps about the ecological dynamics in the group, especially in relevant conservation areas. In the Aburrá Valley, 15 of the 34 carnivorous species registered for Colombia are currently recognized (Ramírez-Chaves *et al.* 2016; Arias-Alzate *et al.* 2021), accounting for 44.1 % of all species of the order Carnivora in Antioquía (Calle and Arango 2003). Among these species, mesocarnivores are one of the most affected groups in the region, mainly due to habitat fragmentation and roadkills (Delgado-V 2007; 2014; Arias-Alzate *et al.* 2015).

This work evaluated the daily activity patterns of mesocarnivore species in the southeast part of the Aburrá Valley (hereafter southeast Aburrá Valley) using non-invasive methods (*i. e.*, tracking cameras). Particularly, we addressed the following questions: What are the activity patterns of the mesocarnivore species inhabiting the southeast Aburrá Valley? What is the degree of segregation in the temporal niche between these species? How does the lunar cycle influence these activity patterns? In functional terms, how similar are the mesocarnivore species living in the area? We hypothesized that mesocarnivores with similar functional characteristics exhibit greater temporal niche segregation, showing a low overlap in their activity patterns to reduce competition. A deeper knowledge of these ecological and natural history aspects of mesocarnivores will support better management and conservation strategies for these ecosystems immersed in landscapes where anthropic activity and urbanization are growing phenomena.

Materials and methods

Study Area. The study was conducted between the San Nicolás Valley and the southeast Aburrá Valley in the south-central department of Antioquia, north of the Central Cordillera of the Colombian Andes. This area harbors an ecosystem of cloud mountain forest or high Andean forest, corresponding to the Tropical Montane Humid Forest life zone (bmh-M, sensu Holdridge 1947). The area comprises mature secondary forests with tree ferns (*Cythea arborea*) and *Chusquea* spp. It stretches across an altitudinal range between 2,100 and 3,050 masl, with a mean annual temperature of 22 °C and precipitation between 1,400 and 3,000 mm (Hermelin 2007). The study area mainly included the municipalities of Envigado and its boundaries with the municipalities of Sabaneta, Caldas, Medellín, and El Retiro (Figure 1).

Sampling Design. Sampling records were obtained by installing tracking cameras (Bushnell Agressor Red-glow and Bushnell Trophy Cam Essential) in forest areas across the study area. For camera installation, the study area was divided into 1 km x 1 km (1 km^2) quadrants, of which 30 sampling quadrants were selected randomly using the Repeating Shapes and Sampling Tools for ArcGIS 10.5 (ESRI 2018). At least 20 of these stations were sampled simultaneously with one camera per station, as follows: Twenty cameras were used from October to December 2015, 28 from August to November 2016, 20 from July to October 2017, seven from January to February 2018, 20 from April to August 2018, and six from December 2019 to December 2020. These monitoring stations were separated from one another by a minimum average distance of 850 m ± 630 m (Figure 1). Each monitoring station operated over a continuous 24-hour sampling period. For installing these

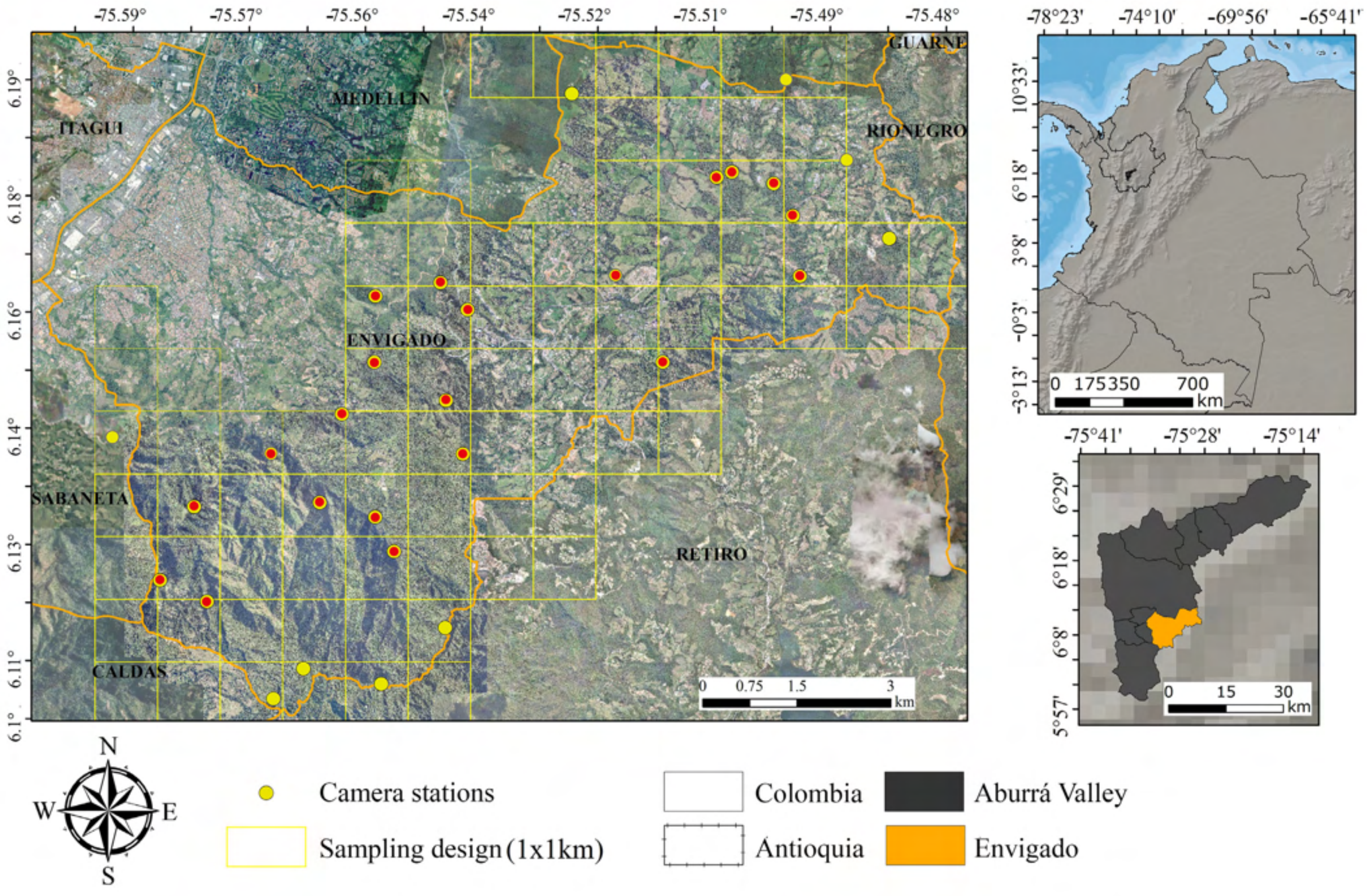

Figure 1. Sampling design for the tracking camera's locations in the study area. A central red dot marks the same stations sampled between 2015 and 2018.

cameras, we searched tracks or signs of the passage of species through existing trails or paths, which are frequently used by wildlife (especially felines, procyonids, and canids), to maximize the probability of capturing species (Navarro-Pelaez *et al.* 2021; Chávez *et al.* 2013; Marinho *et al.* 2018a). The cameras were set in video mode and affixed approximately 20 cm to 30 cm above the ground, with a slight downward-facing inclination and with the following settings: high HD-resolution videos, infrared auto-sensor for day and night, a 40-second video per event, and a 5-minute interval between videos.

Activity Patterns, Lunar Phase, and Temporal Niche Overlap. First, with the circular statistics program Oriana version 4.02 (Kovach 2011), we performed the Rayleigh test (95 % confidence level) to assess whether the species exhibit a regular daily activity pattern over a 24-hour period (Kovach 2011). Afterward, the daily activity patterns of the species were estimated, and their degree of overlap (*i. e.,* temporal niche segregation) was assessed with the *Overlap* package (Ridout and Linkie 2009; Linkie and Ridout 2011; Meredith and Ridout 2018) in R (R Development Core Team 2013). Here, the probability density function of records was evaluated non-parametrically with the Kernel Density (DK) Estimation and the non-negative trigonometric sum (STN) distribution function. These distributions consider each record as a random sample of an underlying continuous distribution (Fernández-Durán 2004; Ridout and Linkie 2009), where individuals of any species have the same probability of being recorded at any time as long as they are active (Linkie and Ridout 2011; Pratas-Santiago *et al.* 2016). In this way, the bias of grouping the records in arbitrarily defined intervals is eliminated to determine the type of activity (Pratas-Santiago *et al.* 2016). To note, we did not consider a measure of independence between records since, according to De Solla *et al.* (1999), Blundell *et al.* (2001), and, recently, Peral *et al.* (2022), the independence assumption (*i. e.*, eliminating the autocorrelation) substantially limits and skews the results, as it does not reflect the continuous activity state. By contrast, considering all data maximizes the performance and accuracy of estimates, for example, in activity pattern analyses.

It is worth mentioning that the tropical zone near the equator is characterized by little variation in the time of sunrise and sunset throughout the year. This situation makes the clock time to approach the solar time (Rowcliffe *et al.* 2014). Therefore, the records obtained were standardized at solar time. Subsequently, these were converted to radians (2π = 24 hrs) before performing the analyses with the *Overlap* package and following the proposals of Ridout and Linkie (2009), Linkie and Ridout (2011), and Vilella *et al.* (2020). Consecutively in *Overlap,* also following the proposal of Ridout and Linkie (2009) and Linkie and Ridout (2011), the daily activity pattern was estimated by splitting the 24-hr period into 4-time intervals, as follows: 00:00-6:00; 6:00-12:00; 12:00-18:00 and 18:00-24:00. In addition, given the little variation between sunrise and sunset times, the sunrise and sunset time are adjusted to $\pi/2$ and $3\pi/2$ (Ridout and Linkie 2009; Bu *et al.* 2016). This allows for classifying the cycle into daytime (the hours elapsed from sunrise to sunset) and nighttime periods (the remaining time), considering sunrise as 06:00 hrs and sunset as 18:00 hrs, respectively (Bu *et al.* 2016; Ridout and Linkie 2009, Meredith and Ridout 2018, Porfirio *et al.* 2016; Rowcliffe *et al.* 2014). Twilight can be considered as the time elapsed one hour before sunrise (*i. e.,* dawn) and one hour after sunset (*i. e.,* dusk; Porfirio *et al.* 2016), corresponding specifically to the astronomical twilight for the study area (https://www.timeanddate.com/).

In this way, it is possible to identify the activity of species according to record density (*e. g.,* Kernel density) identified at the time intervals, classified as diurnal (≥90 % of records during the day), nocturnal (≥90 % during the night), mainly diurnal (~70 % - 89 % during the day), and mainly nocturnal (70 % - 89 % during the night; Azevedo *et al.* 2018; Porfirio *et al.* 2016; Ridout and Linkie 2009). Each daily activity pattern by species was determined using a concentration parameter $K = 1.5$ for the DK function according to Meredith and Ridout (2018); for the STN function, it was identified based on the number of parameters according to the function implemented in *Overlap* (Ridout and Linkie 2009).

We calculated the overlap between pairs of species (*i. e.,* probability density functions sp. 1: $f(x)$ and sp. 2: $g(x)$ using the overlap coefficient Δ, which estimates the degree of overlap between distributions, *i. e.*, the magnitude of the difference between activity patterns (Linkie and Ridout 2011). This coefficient takes values between 0 (no overlap, *i. e.*, different) and 1 (full overlap, *i. e.*, identical; Ridout and Linkie 2009; Linkie and Ridout 2011). For the present analysis, 95 % confidence intervals were estimated through 1000 smoothed Bootstrap replicates,where values are taken from the estimated density function instead of using only those observed (Linkie and Ridout 2011; Meredith and Ridout 2018). For further mathematical and methodological details, please refer to Ridout and Linkie (2009) and Meredith and Ridout (2018). Last, we used the overlap coefficient Δ_1 for small samples (<50 records) and Δ_4 for samples greater than 50 records (Ridout and Linkie 2009). To avoid subjective interpretations of the overlap in activity periods between species, we used the classification proposed by Monterroso *et al.* (2014): low overlap ($\Delta \leq 0.5$), moderate overlap ($0.5 < \Delta \leq 0.75$), and high overlap ($\Delta > 0.75$).

The effect of the lunar phase and light intensity on activity patterns was explored. To this end, the lunar phase was assigned to each species record that showed a mainly nocturnal activity pattern according to the abovementioned analyses. Subsequently, whether there is a uniform distribution related to the lunar phases was evaluated using the Rayleigh test (at a 95 % confidence level) in the circular statistics program Oriana version 4.02 (Kovach 2011). These data were treated as circular data (*i. e.*, scaled to radians) based on the date of each record. These dates are converted to angular data in Oriana by calculating the duration of the lunar month and the day of the lunar cycle according to the time zone of the study area (*i. e.,* GMT-5), where, for example, day one represents the first day of the new moon with 0 % luminosity, so that zero corresponds to the new moon, $\pi/2$ to the first quarter, π to the full moon and $3\pi/2$ to the last quarter (Kovach 2011, Pratas-Santiago *et al.* 2016).

Functional Similarity Analysis. The similarity between the nine mesocarnivore species in the study area was evaluated using their ecological traits and constructing a binary database with the following structure: size, general activity pattern, trophic realm, trophic guild, habit, and social structure (Appendix 1). This information was obtained from previous works (Jones *et al.* 2009; Wilson and Mittermeier 2009; González-Maya *et al.* 2016, 2017; Arias-Alzate *et al.* 2020). These six ecological traits have been identified as major drivers in ecosystem functioning and as important predictors of the competitive capacity between species (de Oliveira and Pereira 20142014; Fergnani and Ruggiero 2015; González-Maya *et al.* 2016; Arias-Alzate *et al.* 2020). Subsequently, the level of similarity between species was determined through a similarity cluster analysis using the Jaccard index. This index takes values between 0 and 1, where zero indicates a greater distance – and therefore a greater differentiation between the species — while values closer to one denote a smaller distance and, therefore, greater similarity. This analysis was performed in the statistical software PAST (Hammer *et al.* 2001).

Results

We obtained a total of 469 records belonging to nine mesocarnivore species with a sampling effort of 10,744 cameras/night (1,118 cameras/night in 2015; 2,852 in 2016, 1,394 in 2017, 1,099 in 2018, 2.211 in 2019, and 2,070 in 2020). Due to the low number of records obtained for three species (*n* = 1 for *Procyon cancrivorus, n* = 2 for *Puma yaguaroundi, n* = 2 and *Leopardus pardalis, n* = 4), these were excluded from the daily activity pattern analysis. Thus, a final total of 461 records were considered, corresponding to six species (Table 1). The species with the highest number of records was *Cerdocyon thous* (*n* = 286), followed by *Eira barbara* (*n* = 76). The species with the lowest number of records were *Nasua nasua* (*n* = 21) and *Neogale frenata* (*n* = 21; Table 1).

Activity Patterns, Temporal Niche Overlap and Lunar Phase. The activity patterns of the species were not uniform throughout the circadian cycle (Table 1). The crab-eating fox (*Cerdocyo thous*), the northern tiger cat (*Leopardus tigrinus*), and the western mountain coati (*Nasuella olivacea*) show mainly nocturnal activity (Figure 2). The crab-eating fox had two peaks of main activity, before dawn at 06:00 hrs and after sunset at 18:00 hrs, with decreased activity near midnight and slight activity at noon (Figure 2). The northern tiger cat starts its activity after sunset, with a slight decrease toward midnight and increased activity

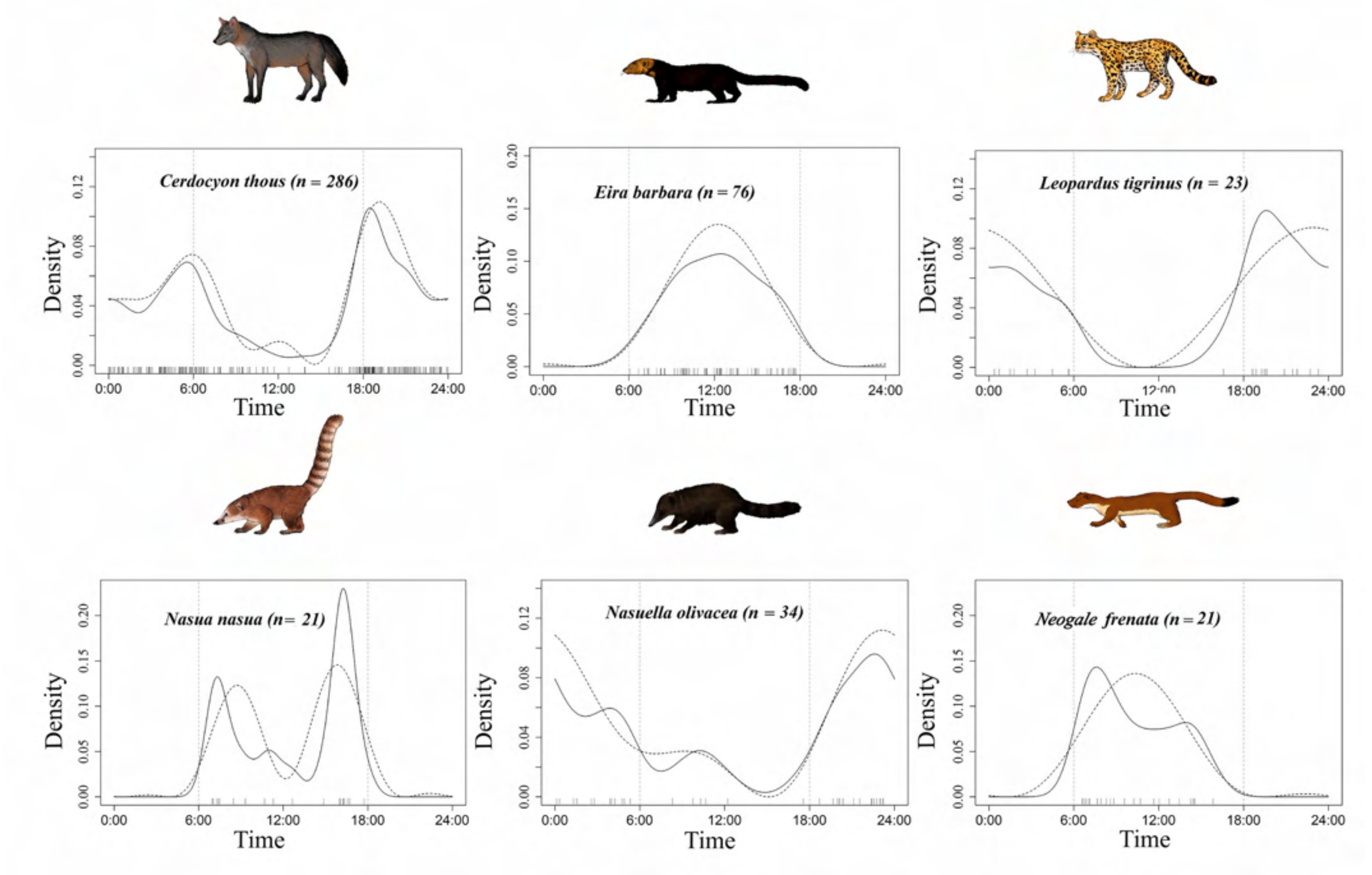

Figure 2. Daily activity patterns of mesocarnivores in the southeast Aburrá Valley. Records are marked as small vertical bars on the time axis. The dotted and solid lines represent estimates by non-negative trigonometric sum (STN) and Kernel density (DK), respectively. Vertical dotted lines mark the dawn (end of astronomical twilight) and dusk (beginning of astronomical twilight).

before dawn (Figure 2). In the case of the western mountain coati, its activity shows two main peaks, one well-marked starting after sunset (18:00 hrs) with an increase toward midnight, followed by a second, much milder peak before dawn (06:00 hrs). This species also shows a slight activity around noon, recorded only under a highway bridge (Via El Escobero; Figure 2).

Tayra (*Eira barbara*), ring-tailed coati (*Nasua nasua*), and long-tailed weasel (*Neogale frenata*) exhibit a mainly diurnal activity pattern (Figure 2). The tayra begins its activity after dawn, with a peak toward noon, followed by a decrease before dusk (Figure 2). The ring-tailed coati has only two marked peaks of activity: one starting after dawn with a descent in activity near noon and a second peak around 14:00 hrs that decreases before dusk (Figure 2). The long-tailed weasel has a marked peak of activity after dawn (06:00 hrs) with a decrease toward noon (12:00 hrs), followed by a slight increase in the early afternoon hours (~14:00 hrs) and decreasing before dusk (Figure 2).

As regards the influence of the lunar phase, only the northern tiger cat shows significant activity around the crescent moon that decreases toward the new moon. The other two species (crab-eating fox and western mountain coati) show no variations in activity throughout the lunar phases (Table 1).

We observed a variable overlap of activity patterns between pairs of mesocarnivore species, with a tendency to a low overlap, as in the case of *C. thous* and *E. barbara* (Figure 3). The greatest overlap levels were recorded between *L. tigrinus* and *C. thous,* and between *L. tigrinus* and *N. olivacea* (Figure 5). Moderate overlap levels were observed between *E. barbara* and *Nasua nasua*, *E. barbara* and *N. frenata*, *N. nasua* and *N. frenata,* and *N. olivacea* and *C. thous* (Figure 3).

Table 1. Rayleigh test of uniformity for the six mesocarnivores activities and the lunar phase for mainly nocturnal species. ***n***: Total number of records, * significant values at 95 % (***P*** < 0.05).

Species	*n*	*P*	Lunar phase	*P*
Cerdocyon thous	286	1.5E-11*	Crescent moon	0.118
Eira barbara	76	1E-12*		
Leopardus tigrinus	23	0.000179*	Waning crescent-new moon	0.000461*
Nasua nasua	21	0.002*		
Nasuella olivacea	34	0.000713*	Waning half	0.091
Neogale frenata	21	2.84E-6*		

Functional Similarity Analysis. The similarity analysis shows two main clusters. The first shows a high similarity between the coaties, followed by their similarity with the tayra. These three species were grouped with the crab-eating fox and the raccoon. Together, these five species show an intermediate degree of ecological similarity (Figure 4). The second cluster shows a high similarity between the tiger cat (~88 %), which is grouped with the yaguarundi and the long-tailed weasel at a similarity of around 70 %. These two main groups show a similarity of about 40 %; that is, they show important segregation in terms of their ecological traits (Figure 4).

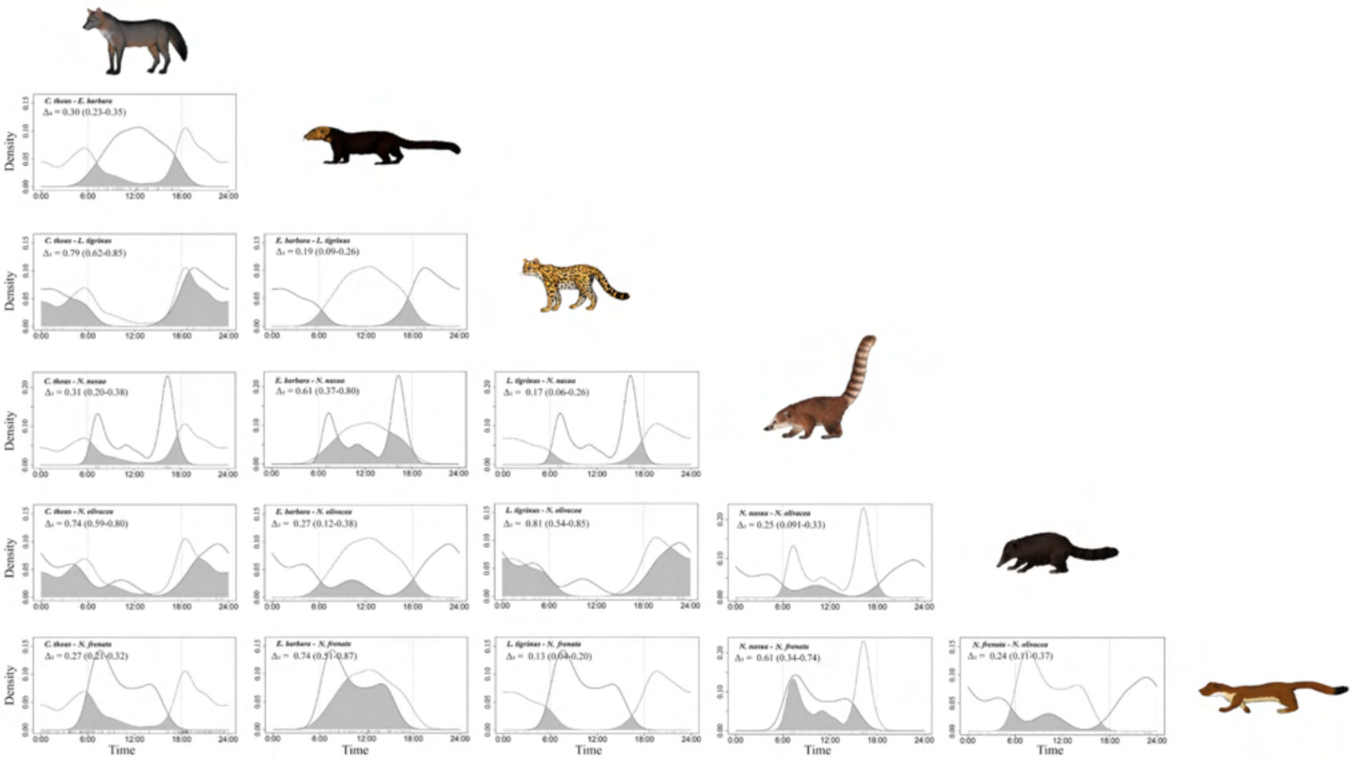

Figure 3. Daily activity patterns overlap between pairs of mesocarnivores species. The gray shaded area represents the overlap level. Δ1 and Δ4 represent the overlap coefficients; 95% confidence intervals are shown in parentheses. Low overlap level (Δ ≤ 0.5), moderate overlap (0.5 < Δ ≤ 0.75), and high overlap (Δ > 0.75*)*. The dashed and solid lines represent the first and second species, respectively. Vertical dotted lines mark the dawn (end of astronomical twilight) and dusk (beginning of astronomical twilight).

Discussion

The species activity patterns may be partly determined by the climate, habitat structure and preference, and by interspecific interactions, where, for example, intra-guild predation plays a central role in the coexistence of potentially competing species (Ramírez-Mejía and Sánchez 2016; Mpemba *et al.* 2019; Easter *et al.* 2020). However, in landscapes surrounded by an important anthropic activity, these dynamics can be affected, disrupting how the different mesocarnivorous groups interact with each other (Easter *et al.* 2020; Mendes *et al.* 2020). In this sense, the low number of records for some species despite the great sampling effort may be associated with their cryptic nature, a low abundance associated with low ecological tolerance to human activity, or poor detectability of cameras located in wooded areas (Boron *et al.* 2019; García-R *et al.* 2019). However, although this study did not directly assess how development and anthropic disturbance can affect mesocarnivores activity and their interactions with each other, it is evident that the development processes have significantly fragmented and reduced the original extent of the habitat for these species, which probably influenced the activity patterns recorded here. For example, different works (Treves and Karanth 2003; Gaynor *et al.* 2018; Van Cleave *et al.* 2018; Wang *et al.* 2019) state that the activity of carnivores may vary to reduce the risk of conflict with humans in areas subjected to heavy anthropic pressure.

In general, the observed activity patterns are similar to those reported in other studies throughout the distribution ranges of these species (*e. g.*, Sheffield and Thomas 1997; Tortato and Oliveira 2005; Faria-Corrêa *et al.* 2009; Delgado-V *et al.* 2011; Oliveira-Santos *et al.* 2012; González-Maya *et al.* 2015; Cáceres-Martínez *et al.* 2016; Ramírez-Mejía and Sánchez 2016; Penido *et al.* 2017; Marinho *et al.* 2018b; Dias *et al.* 2019; Mena y Yagui 2019; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020; Villafañe-Trujillo *et al.* 2021). However, some important aspects are observed, likely associated with adjustments in the behavior, foraging, reduced risk of predation, and antagonistic encounters with other species (Penido *et al.* 2017; Mpemba *et al.* 2019). For instance, although *E. barbara*, *N. frenata*, and *Nasua nasua* show diurnal patterns, as suggested (Sheffield and Thomas 1997; Delgado-V *et al.* 2011; González-Maya *et al.* 2015; Cáceres-Martínez *et al.* 2016; Ramírez-Mejía and Sánchez 2016; Mena and Yagui 2019; Villafañe-Trujillo *et al.* 2021), the first two species show a single peak of activity, while *N. nasua* showed two peaks of activity not previously reported. It is worth noting that Sheffield and Thomas (1997) mention that the large-tailed weasel is active both day and night, contrasting with our observations in the present study. This is likely due to the low number of records, low abundance, lower nighttime activity given the weather conditions in the area, or limited camera detectability. However, the latter is less likely in our study site since we have recorded (at night) smaller mammal species, such as rodents, marsupials, and shrews with the same type of cameras.

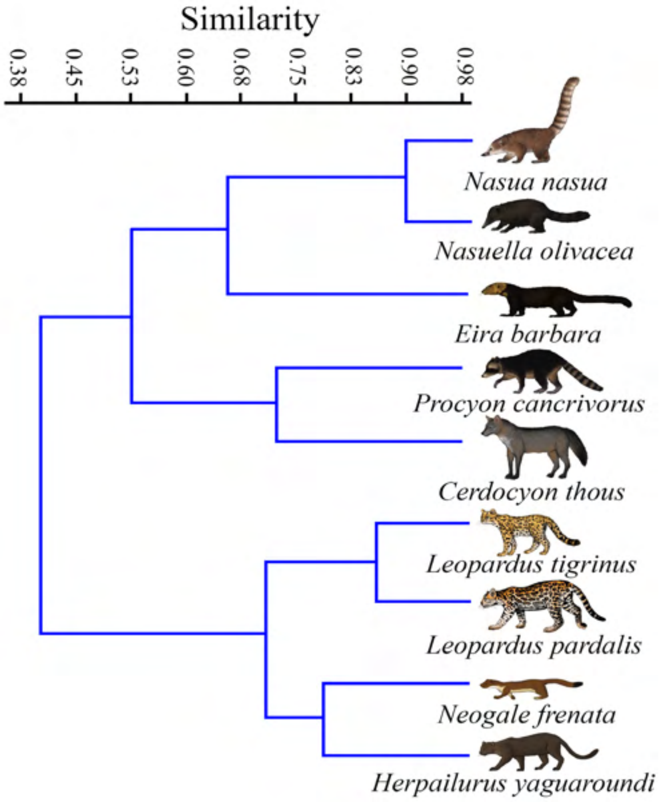

Figure 4. Functional similarity Cluster between mesocarnivores species inhabiting the southeast Aburrá Valley.

With regard to species with a nocturnal activity pattern, although *N. olivacea* has been reported as a mainly nocturnal species (Cáceres-Martínez *et al.* 2016; Ramírez-Mejía and Sánchez 2016; Mena and Yagui 2019), in our study area, the species showed a small peak of activity in the morning hours before noon. These daytime records correspond to activity under a highway bridge, where low light intensity predominates. This could be related to a sense of safety and low predation risk for these individuals, which has important spatial and temporal implications for the species (Easter *et al.* 2020). However, Rodríguez-Bolaños *et al.* (2003) suggested a purely diurnal activity for *N. olivacea* from telemetry data of a single male individual marked in a high Andean forest. The difference in daily activity of the same species is likely due to the reduction of independent records, which may be affecting the effectiveness of activity estimations, for example, by eliminating intermediate or nighttime records (Dde Solla et al. 1999; Blundell *et al.* 2001; Peral *et al.* 2022).

On the other hand, the activity of *C. thous* partly agrees with reports for other regions throughout its range (Penido *et al.* 2017; Marinho *et al.* 2020). Here, north of the Andes, we observed a mainly nocturnal activity, with a slight daytime activity. This contrasts with the findings for the Atlantic Forest and the Catinga in Brazil, where the species is sympatric with other canids of similar size and shows a trend toward being nocturnal, while the other species (*Lycalopex gymnocercus* and *L. vetulus*) display a trend toward diurnal habits (Faria-Corrêa *et al.* 2009; Dias and Bocchiglieri 2016;

Penido *et al.* 2017; Marinho *et al.* 2020). In this sense, sympatry can occur if species of similar size differ in one or more ecological traits, for example, in time activity or the primary food resources used (Easter *et al.* 2020; Godsoe *et al.* 2015, Arias- Alzate et al. 2022). Thus, similar, and potentially competitive sympatric species, such as mesocarnivores, should be segregated according to other ecological niche traits to avoid competition (*i. e.,* competitive exclusion), producing more diffuse patterns of interspecific interaction (Chesson 2000; Arias- Alzate et al. 2022).

Regarding felids, although three species of small felines were recorded, only *L. tigrinus* had a sufficient number of records. The activity of this species is similar to that reported for Cerrado and the Catinga in Brazil, with nocturnal activity after sunset and before sunrise (Tortato and Oliveira 2005; Oliveira-Santos *et al.* 2012; Penido *et al.* 2017; Marinho *et al.* 2018b; Dias *et al.* 2019; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020). However, these authors also report some daytime activity and suggest that this occurs when the species is found in sympatry with other felines. However, this feline inhabiting these two zones has been proposed as two new species (*Leopardus guttulus* and *L. emilie*; Do Nascimento and Feijo 2017). The only areas of Colombia with records of daytime activity for *L. tigrinus* are heavily fragmented areas disturbed by anthropic activities, where some individuals have been roadkilled (Arias-Alzate pers. obs.).

Three other species of felines (*Leopardus pardalis*, *Puma concolor*, and *H. jaguaroundi*) inhabit our study area; although we did not estimate their activity patterns due to the low number of records, they were recorded both at night and during the day. According to observations on these species from camera traps in unpublished information and literature reportes (*e. g.,* Ramírez-Mejía and Sánchez 2016; Penido *et al.* 2017; Massara *et al.* 2018; Marinho *et al.* 2018b; Dias *et al.* 2019; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020), we hypothesize that there is a temporal segregation between these species, mainly between *L. tigrinus* and *H. yaguaroundi*, given their similar sizes and feeding habits (*i. e.,* hypercarnivores). By contrast, the coexistence between the ocelot and the puma (a species recorded in the Aburrá Valley 10 years ago, Arias-Alzate *et al.* 2015) would be mediated by size differentiation and spatial segregation at the local level to avoid inter-guild predation to a large extent (*i. e.*, fear landscapes created by larger predators; Treves and Karanth 2003; de Oliveira and Pereira 2014; Wang *et al.* 2019; Arias- Alzate et al. 2022; Zaman *et al.* 2022). Thus, the segregation of felines according to functional traits would be a driver of sympatry in these species (Penido *et al.* 2017; Massara *et al.* 2018; Marinho *et al.* 2018b; Dias *et al.* 2019; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020; Arias- Alzate et al. 2022).

It should be noted that we found a significant trend in the activity of *L. tigrinus* during the lunar phase waning toward the new moon in the high Andean forests of the study area. This may be a strategy to avoid intra-guild predation when foraging in forested areas while maximizing energy gain by synchronizing their activity pattern with that of their potential prey, as proposed for other carnivorous species (Harmsen *et al.* 2011; Foster *et al.* 2013). However, Marinho *et al.* (2018a), in a study in the Catinga (lowlands) in Brazil, found no direct influence of the lunar cycle on this species, which, as mentioned above, has been proposed as a different species (Do Nascimento and Feijo 2017).

These activity patterns and the different trends in the overlap between these species seemingly result from the segregation of their functional ecological attributes (*i. e.,* functional niche) to reduce interspecific competition, the predation risk, and, therefore, facilitate coexistence, as suggested in other works (Nagy-Reis *et al.* 2019; Marinho *et al.* 2020, Arias- Alzate et al. 2022). This segregation would be mediated mainly by size, *i. e.*, species of similar size would become segregated in one or more functional attributes (Arias- Alzate et al. 2022).

Thus, time segregation appears as an additional mechanism to reduce and avoid interference competition between ecologically similar and potentially competing species (Monterroso *et al.* 2014; Massara *et al.* 2018; Nagy-Reis *et al.* 2019; Marinho *et al.* 2020; Arias- Alzate et al. 2022).

This hypothesis would be consistent with our findings, as more than 86 % of the pairs of species studied exhibited a low or moderate activity overlap. Only a few pairs of species showed a high overlap but displayed additional niche segregation, suggesting more diffuse interactions between these species (Chesson 2000, Arias- Alzate et al. 2022). For example, although *N. nasua* and *N. olivacea* showed a similar food pattern, they differ in size and are segregated in their temporal niche, as observed in areas where the two species are sympatric, mainly in high areas (Ramírez-Mejía and Sánchez 2016; Mena and Yagui 2019). Likewise, species with intermediate (*i. e., E. barbara* and *N. frenata*) and high (*i. e., C. thous*, *L. tigrinus*, and *N. olivacea*) temporal overlap show segregation based on their traits, particularly size and dietary preferences (Dias and Bocchiglieri 2016; Ramírez-Mejía and Sánchez 2016; Mena and Yagui 2019; Marinho *et al.* 2020). This suggests that resource partitioning would also be recognized as another mechanism that facilitates coexistence (Hearn *et al.* 2018; Nagy-Reis *et al.* 2019). For instance, Bubadué *et al.* (2016) noted that when in sympatry with other canids from the south of the continent (*e.* g., *Lycalopex vetulus* and *L. gymnocercus*), *C. thous* tends to be far more carnivorous, unlike individuals of the same species inhabiting the north of the continent.

Although this study did not directly assess how development and anthropic disturbance can affect mesocarnivore activity and their interaction in peri-urban ecosystems, it is clear that development processes have caused a reduction of the original habitat of these species. In this sense, the low number of records obtained for some species may be associated not only with poor detectability but also with low abundance as a consequence of these anthropic pressures. To note, abundance would also be declining due to deaths from collisions with motor cars on roads adjacent to these ecosystems, where a large number of individuals of these species have been found (*e. g.,* more than 14 individuals of northern tiger cat over the past ten years; Delgado-V 2007, 2014; Arias-Alzate *et al.* 2014, 2016).

Our results suggest that mesocarnivore species inhabiting the Aburrá Valley show variable temporal segregation, with a tendency to a low overlap, which would help mediate interactions and coexistence between these species. These results contribute to the knowledge about the ecology of these species and the interactions between them, mainly in ecosystems surrounding large cities north of the Andes. It is important to highlight the need to implement conservation strategies to generate tools and management strategies for preserving these ecosystems by identifying priority conservation areas or restructuring poorly functional protected ones. This would greatly favor the connection between populations of these and other species, both across the Aburrá Valley and at the regional level, as well as the conservation of ecological and evolutionary processes and, hence, of the environmental services of the territory.

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Appendix 1

Ecological trait descriptions and used for assessing similarity between mesocarnivore species. This information was obtained from previous works (Jones *et al.* 2009; Wilson and Mittermeier 2009; González-Maya *et al.* 2016, 2017; Arias-Alzate *et al.* 2020). Trait codification in the database was present (1), absent (0)

Body mass (Bm): this ecological trait provides considerable information about the ecology and life history of species and has proven informative for most of the fundamental characteristics of an organism in terms of adaptation to their environment and interaction with other species. The variability in body mass is a good predictor of the ecological niche of species, therefore is considered a proxy of functional diversity due to its relationship with ecosystem functioning.

Locomotor behavior (LB): this ecological trait provides information about the locomotive adaptations to different substrate, indicating a relationship between the species and their environment. This is important because it reflects details of their feeding strategy. Likewise, this trait could reveal much more about carnivore species history life, preferred habitat, foraging behavior, and escape strategy. One species may have one or more locomotor behavior, Aquatic (Ac); Terrestrial (T); Arboricolal (Ar); Scansorial (Sc); Fossorial (F).

Social organization (SO): this ecological trait represents the mean number of individuals of the species present during most of the year outside of the breeding season. Group size is considered as an anti–predator response, since larger groups reduce the risk of predation per capita, by increasing collective vigilance and predator detection, or by collective defense. Groups (G); Solitaries (S); Group size (GS).

Activity pattern (AP): this ecological trait represents the active period where the species is most active during a 24 h cycle. The active period is related to resource use and is influenced by physiological constraints. Diurnal (D), Nocturnal (N); Catameral (C).

Trophic realm (TR): this trait represents the main indicator of resources used and covers several dietary attributes that reflect amplitude of species diet. carnivore (TrC); herbivores (TrHe); Omnivores (TrOm).

Trophic guild (TG): this ecological trait represents the main feeding specialization of the carnivoran species. It describes the different feeding types and allows to distinguish species more precisely. Carnivore big (TgCb); carnivore medium (TgCm); carnivore small (TgCs); carrion (Car); piscivores (TgPis); invertebrates (TgIn); frugivores (TgF).

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Chiropteran diversity and diet of fruit bats in a tropical dry forest of northern South America

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Remnants of Tropical Dry Forest persist in urban and peri-urban areas and are essential for maintaining biodiversity and ecosystem services. However, the challenges facing the conservation of these respective forests have intensified with the encroachment of the urban frontier, mining activities, deforestation, and cattle ranching. In this context, our study aims to estimate the diversity of the order Chiroptera and characterize the diet of the family Phyllostomidae. This approach allows us to gain insights into the ecological dynamics and assess the status of Tropical Dry Forest fragments located within the urban and peri-urban areas of Cúcuta, Colombia. Field sampling was conducted from January to September 2018, with a total sampling effort of 2,160 hours/meter/net. Bats were sexed, morphometrically characterized, and had their feces collected for diet analysis before being tagged and released. We identified three families, nine genera, and 11 species. A total of 276 individuals were captured. Seven species were observed in the urban area and ten in the peri-urban zone; *Artibeus lituratus* and *Carollia perspicillata* were the most abundant species in both locations. The diet included seeds from the families Moraceae, Anacardiaceae, and Rosaceae. Our findings reveal that in areas with dense vegetation, such as peri-urban zones, frugivorous bats prefer to consume fruits of domesticated species, including economically significant fruits like guava and tomato. This dietary shift could alter seed dispersal patterns and the dynamics of the Tropical Dry Forest, highlighting the ecological importance of these flying mammals in ecosystem regeneration.

En las zonas urbanas y periurbanas, perduran fragmentos de bosque seco tropical que desempeñan un papel fundamental en la conservación de la biodiversidad y los servicios ecosistémicos. Sin embargo, los desafíos para preservar estos remanentes forestales han aumentado debido al avance de la urbanización, la minería, la deforestación y la ganadería. En este contexto, nuestro estudio tiene como objetivo estimar la diversidad del Orden Chiroptera y caracterizar la dieta de la familia Phyllostomidae como una estrategia para comprender las dinámicas ecológicas y evaluar la situación de los fragmentos de bosque seco tropical situados en el área urbana y periurbana de Cúcuta, Colombia. Llevamos a cabo muestreos de campo durante los meses de enero a septiembre de 2018, con un esfuerzo de muestreo total de 2,160 horas/metro/red. Los murciélagos fueron sexados, caracterizados morfo-métricamente, y se tomaron muestras de heces para determinar su dieta antes de ser marcados y liberados. Se capturó un total de 276 individuos, Identificamos tres familias, nueve géneros y once especies de murciélagos. Encontramos siete especies en el fragmento urbano y diez en la zona periurbana, con *Artibeus lituratus* y *Carollia perspicillata* siendo las especies más abundantes en ambos sitios. En cuanto a la dieta, se obtuvieron semillas de las familias Moraceae, Anacardiaceae y Rosaceae. Nuestros hallazgos revelan que, en áreas con mayor cobertura vegetal como zonas periurbanas, los murciélagos frugívoros prefieren frutos de especies domesticadas, incluyendo frutas de relevancia económica como guayaba y tomate. Esta tendencia dietética podría alterar la dispersión de semillas y la dinámica del Bosque Seco Tropical, subrayando la importancia ecológica de estos mamíferos voladores en la regeneración del ecosistema.

Keywords: Abundance; bioindicator; Colombia; peri-urban; Phyllostomidae; urban ecology.

Introduction

Tropical dry forests (TDF) represent valuable biodiversity reservoirs linked to essential ecosystem services, including water, recreational, and genetic resources (Pizano and García 2014). Globally, TDFs cover an impressive 42 % of the total area of tropical forests (Quesada *et al.* 2009). However, the extent of these forest remnants has been severely reduced due to multiple factors, including the expansion of urban areas, mining activities, deforestation, and livestock raising, in sharp contrast to adjacent biomes like Andean forests. These anthropogenic pressures have sculpted the TDF landscape, posing a significant risk to biodiversity and the ecological interactions they support (Miles *et al.* 2006). As a result, TDFs are considered one of the most threatened biomes, facing the loss of biodiversity, decline of genetic diversity, and fragmentation of landscape connectivity, resulting in isolated mosaic patterns and the risk of local extinctions (Pizano and García 2014).

In Colombia, TDFs historically cover a wide geographic range, estimated at approximately 80,000 km^2 (Pizano and García 2014). However, these forests currently cover only 8 % of their original extent (Garcia et al. 2014). The areas once covered by TDF have been converted to urban areas, forest remnants, and agricultural (28 %) and livestock (34 %) production areas (Etter 2008; Pizano and García 2014).

In the Norandina region of Colombia, about 47 % of the 80,000 km^2 identified as TDF correspond to natural fragments, while the remaining 53 % is dedicated to agricultural and livestock activities that still conserve small remnants of secondary forest (Garcia et al. 2014). This situation has led to substantial changes in the spatial configuration of the available habitats at the local landscape level, exerting apparent effects on the abundance and diversity of the regional fauna and flora.

In Colombia, bats play a central role, representing 30.9 % of the mammal richness in the country, with a total of 217 species. This positions Colombia as the second most chiropteran- diverse country worldwide, after Indonesia (Ramírez-Chaves *et al.* 2021). In the context of the Neotropics, Colombia is a leading country in number of bat species, surpassing countries such as Brazil (182), Ecuador (178), and México (140; Ceballos and Arroyo-Cabrales 2012; Abreu *et al.* 2022; Tirira *et al.* 2022). Bats, being more numerous than other mammal groups, play a central role in multiple ecosystem processes and are of particular interest in the analysis of environmental changes in ecosystems (Jones *et al.* 2009). Some authors have formulated the idea that variations in the diversity and composition of bat populations may be influenced by food availability and the preservation of their environments (Medellín *et al.* 2000; Chávez and Ceballos 2001; Jiménez-Ortega and Mantilla-Meluk 2008). This is due to the close relationship of bats with particular groups of plants; for example, they participate in the pollination of dozens of plants and control of insect populations, besides playing a major role in seed dispersal (Medellín *et al.* 2000; Willig *et al.* 2007; Ávila-Cadabilla *et al.* 2009).

Despite the continuous degradation of TDFs in Colombia (MINAMBIENTE 2021) and the importance of bats in diagnosing the state of ecosystems (García-Morales *et al.* 2013), little is known about the ecology of bats in northeast Colombia. The studies on TDFs include those conducted in Área Natural Única Los Estoraques (ANULA), which report a list of seven bat species (Anteliz-Pallares *et al.* 2021), the use of shelters by three species of phyllostomid bats (Suárez-Payares and Lizcano 2011), and aspects associated with the diet (Alviz and Pérez-Torres 2020), and body size (Acevedo and Pabón 2020).

Although studies have been conducted on bat assemblages associated with anthropogenic disturbances, most have focused on evaluating the effects of habitat fragmentation associated with the establishment of agricultural, extensive livestock and silvo-pastoral systems (Estrada and Coates-Estrada 2001; Numa *et al.* 2005; Ortegón-Martínez and Pérez-Torres 2007; Vela- Vargas and Pérez-Torres 2012). The resulting changes in the structure and composition of bat assemblages in TDF fragments occupied by urban settlements are unknown. A study by Ramos (2021) addressed the effects of habitat reduction on species richness and abundance of phyllostomid bats in TDF fragments of the Colombian Caribbean zone. This study reported that the ecological effects of habitat fragmentation and loss in bats are species-specific, which could lead to the local extinction of some species while being beneficial or may not affect others.

Most studies on habitat loss have evaluated its effect according to fragment size (Santos and Telleria 2006), finding that species diversity and abundance increase in larger fragments that offer greater resource availability (Mena 2010). Habitat reduction is clearly one of the anthropic processes with the greatest effects on biodiversity (Santos and Tellería and Santos 2006). However, the responses can differ according to the particular ecology of the species (Mena 2010; Cabrera 2011).

In a context of high anthropic disturbance, such as the one observed in the TDF in the Cúcuta metropolitan region (Norte de Santander, Colombia), examining the impacts of habitat reduction on the diversity and diet of animal species has become imperative. Therefore, we first carried out a comprehensive description of the bat diversity and composition, classifying them into guilds and covering all possible families. Subsequently, we analyzed the diet composition of frugivorous bats of the family Phyllostomidae in two TDF fragments immersed in urban and peri-urban areas.

The central hypothesis of this study was that habitat reduction caused by human activities in the urban area has impacted both the diversity of chiropterans from different guilds and the availability of food resources used by the family Phyllostomidae, compared to peri-urban fragments. This process led to substantial modifications in the diversity and abundance of bat species inhabiting these areas. This study aims to provide key information for biodiversity conservation in the Cúcuta Tropical Dry Forest, highlighting the importance of protecting and restoring habitats in urban and peri-urban areas. By understanding how anthropogenic disturbance impacts bat diversity and diet, we hope to contribute to implementing effective conservation strategies that promote the coexistence of these key species in these ecosystms.

Materials and Methods

Study area. The study was carried out in two TDF fragments of the municipality of Cúcuta, Norte de Santander, Colombia: 1) TDF peri-urban fragment located on the outskirts of the Cúcuta City urban zone in the corregimiento of San Pedro (7° 48' 17.0'' N, -72° 31' 32.5' W), comprising an area of 23,289 m^2 with secondary (*e. g.*, *Licania apetala*) and atypical (*e. g.*, *Ficus carica* L., *Solanum lycopersicum*) plant species. 2) TDF urban fragment located among urbanized areas in the EcoParque theme park, one of the largest green areas in Cúcuta City (7° 51´51.8" N, -72° 30´ 24" W), comprising an area of 20,939 m^2; the TDF fragments are highly altered, and largely comprise dry scrub vegetation (Figure 1). The study areas have an average elevation of 300 masl, characterized by a warm climate, with mean annual temperature of 25 °C, annual relative humidity of 75 %, and mean annual precipitation of 867 mm to 2,063 mm.

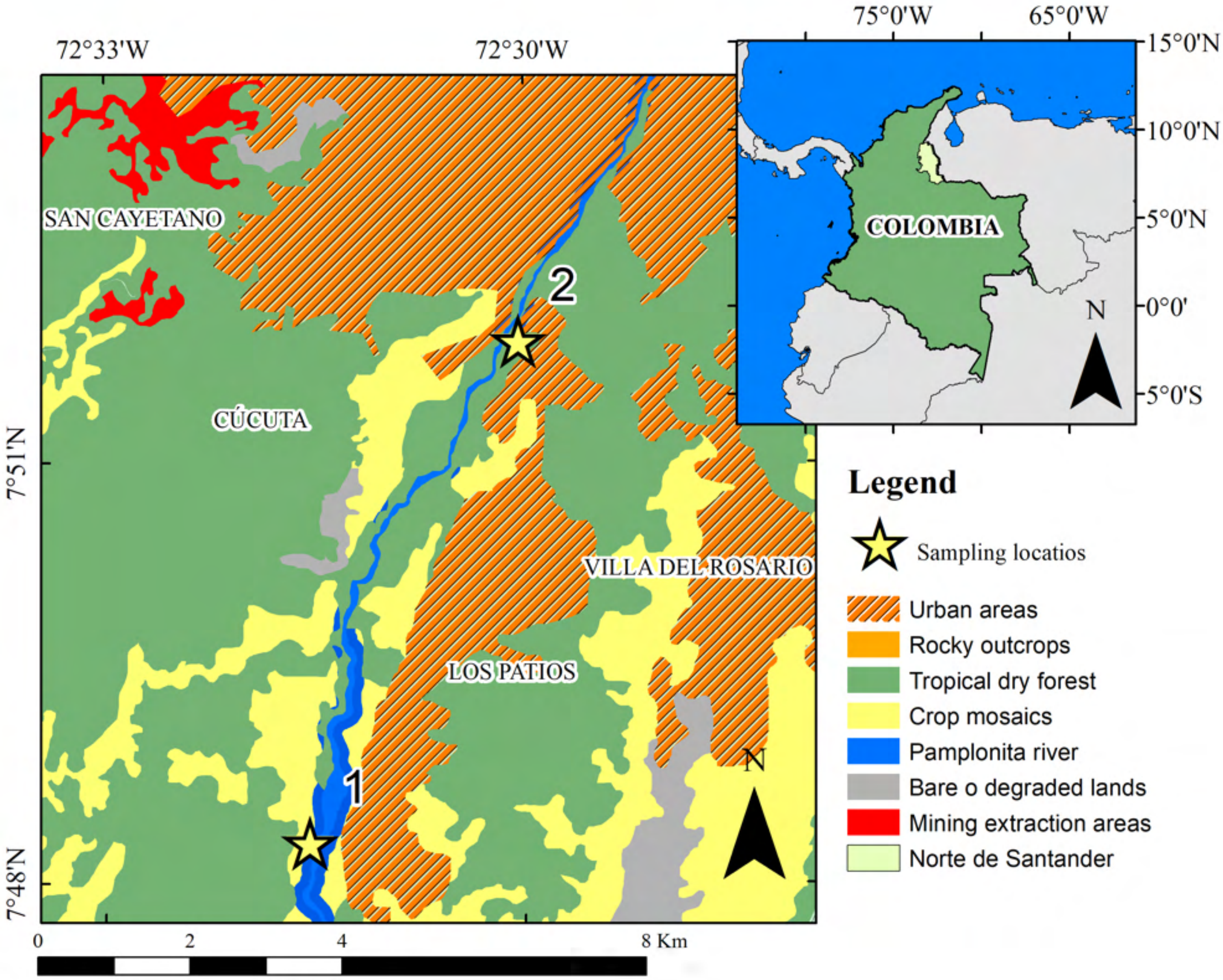

Figure 1. TDF fragments selected for the present study in the Cúcuta metropolitan area, Colombia. 1) Peri-urban zone. 2) Urban zone.

Field data collection. We conducted a general survey of the plants in the fragments studied, capturing photographic records and collecting samples of plants with fruits for subsequent identification to obtain general information on the food resources available to the bat community. Plant species were identified using the taxonomic keys of Linares and Moreno (2010) by comparison with plant specimens deposited in the botanical collection of the Catatumbo Sarare Regional Herbarium (HECASA) at Universidad de Pamplona.

Eight field trips were carried out between January and September 2018, each lasting 16 nights in each TDF fragment. Bats were captured using two mist nets measuring 12 m long by 3 m high, with 15 mm x 15 mm mesh size, which were kept open between 18:00 and 24:00 and reviewed every 10 to 15 minutes. In each sampling campaign, full-moon nights were avoided to the extent possible because they may affect bat capture due to lunar phobia (Santos-Moreno *et al.* 2010). All captured individuals were weighed, and their morphometric measurements were recorded for identification following the guidelines of Díaz *et al.* (2011). To avoid re-sampling, each captured bat was marked using a four-digit X 3/8" Lhaura® tattoo machine and released in places adjacent to the study area. Specimens were collected under the research framework license number 200 granted by the Corporación Autónoma Regional de la Frontera Nororiental (CORPONOR, in Spanish) to the Universidad de Pamplona. Specimens were preserved following the protocols of Simmons and Voss (2009) and were deposited in the mammal collection of the "José Celestino Mutis" Museum of Natural Sciences at the Universidad de Pamplona.

Seeds consumed by phyllostomid bats. The captured bats were placed in cloth bags to subsequently take fecal samples, which were stored in Eppendorf tubes with 70 % alcohol for preservation. The seeds and plant remains were separated with tweezers and distilled water under a Carl Zeiss stereo microscope; then, these were dried at room temperature (Ríos-Blanco and Pérez-Torres 2015). Seeds were identified by comparison against HECASA specimens, botanical samples, and photographic records captured in the sampling area. Plant species were identified using the guide for the taxonomic identification of seeds of Dueñas *et al.* (2011).

Data analysis – diversity. The relative abundance of bat species in the urban and peri-urban areas was estimated by constructing rank-abundance curves, transforming the values to log10 (Magurran and Henderson 2011). We used sampling completeness with the true diversity estimator based on Hill numbers (Chao and Jost 2012; Chao *et al.* 2014). This estimator is based on the species with one and two samples relative to the total abundance of individuals (Ortiz and Henao 2014). To know the percentage of completeness of the sampling, the "sample coverage" technique was performed, which calculates the proportion of each species in the sample relative to the total number of individuals through the standardization of the communities sampled (Chao and Jost 2012; López-Mejía *et al.* 2017). The analysis was performed with the iNEXT package (Hsieh *et al.* 2016) in R v. 3.6.3 (R Core Team 2013). The diversity of three orders was calculated (Jost 2007): 1) Order ^0q, representing the species richness or total number of species. 2) Order ^1q, based on the exponential Shannon index, which weights the most common species. 3) Order ^2q, based on the inverse Simpson index associated with abundant species.

Beta diversity was estimated through a dissimilarity analysis using Sorensen's index ($Ss = 2a/[2a + b + c]$), where a = number of common species; b = number of unique species occurring only at site one; c = number of unique species occurring only at site two (Koleff *et al.* 2003). The data were analyzed with the betapart package (Baselga and Orme 2012) in R v. 3.6.3 (R Core Team 2013).

Diet. The diet of phyllostomid bats was determined through the following parameters. 1) The absolute frequency of seeds (FA) based on the number of times a seed type was recorded in all the feces obtained per individual collected. 2) The percentage of occurrence (PO) for each seed species, obtained using the ratio of the absolute frequency (FA) relative to the total number of feces: $(PO) = (FA)/\text{Total number of feces} \times 100$; Kunz and Whitaker 1983). We assumed that the number of times a seed is found in the feces indicates its importance in the diet of bats. In addition, direct observations were made of the direct consumption of fruits of some species not usually recorded in the diet of these species.

Importance as seed dispersers. The importance of each frugivorous bat as a seed disperser in each community was evaluated with the Disperser Importance Index (DII; Galindo-González *et al.* 2000). This index uses the relative abundance of each captured bat species (B) and the percentage of feces samples containing seeds from each bat species (S). Samples with at least one seed were counted as one event, samples with two different seed species were counted as two events, and so on. $DII = (S*B)/1{,}000$. The index ranges between a minimum value of 0 (zero), indicating seedless feces (rare bat species dispersing a few seeds will have values close to zero), and a maximum of 10, indicating that a bat species disperses all seeds from a particular plant in the community.

Results

A total of 276 individuals distributed in three families, nine genera, and 11 species were recorded (Figure 2, Table 1) using a sampling effort of 2,160 hours/meter/net, corresponding to 90 hours over sixteen nights, for successful capture of 0.1255 individuals/hour/meters/net.

In the peri-urban area, we collected 164 individuals belonging to ten of the 11 bat species found in the study. According to the rank-abundance curve (Figure 3), the following categories were observed: Rare species: *Desmodus rotundus* (0.6 % of the captured species) and *Pteronotus parnellii fusco* (0.6 %). Moderately abundant: *Platyrrhinus fusciventris* (4.2 %), *Sturnira lilium* (1.8 %), *Glossophaga soricina* (3.6 %), *Carollia brevicauda* (4.2 %), and *Myotis nigricans* (2.4 %). Abundant: *Artibeus lituratus* (43.2 %), *Carollia perspicillata* (33.5 %), and *Uroderma bilobatum* (5.4 %). Of the ten species recorded, 60 % belong to the frugivorous guild, 20 % to the arthropodophagous guild, and 10 % to the nectarivorous and hematophagous guilds (Table 1).

In the urban area, we collected 112 individuals belonging to seven of the 11 bat species recorded in the study. The only rare species was *C. brevicauda* (0.8 %). Moderately abundant: *G. soricina* (5.3 %), *Artibeus obscurus* (5.3 %), and *S. lilium* (2.6 %). Abundant: *A. lituratus* (52.6 %), *C. perspicillata* (24.1 %), and *U. bilobatum* (8.9 %). Regarding guilds, the study recorded that 85.7 % of the seven species corresponded to the frugivorous and 14.7 % to the nectarivorous guilds (Table 1).

The sampling completeness in the urban and peri-urban areas recorded values of 95 %. The species richness in the sampled areas showed that the peri-urban area obtained the highest richness, with ten species, followed by the urban area, with seven species (Figure 4).

Table 1. Relative abundance of each species in urban and peri-urban TDF fragments in the Cúcuta metropolitan area, Norte de Santander, Colombia. Each species are classified according to its guild. A = arthropodophagous, F = frugivorous, H = hematophagous, and N = nectarivorous. Habitat type: urban fragments (UF) and peri-urban fragments (PUF).

Bat species	Guild	UF	PUF
Family Phyllostomidae			
Artibeus lituratus	F	59	71
Artibeus obscurus	F	6	0
Carollia perpicillata	F	27	55
Platyrrhinus fusciventris	F	0	7
Glossophaga soricina	N	6	6
Carollia brevicauda	F	1	7
Sturnira lilium	F	3	3
Desmodus rotundus	H	0	1
Uroderma bilobatum	F	10	9
Family Vespertilionidae			
Myotis nigricans	A	0	4
Family Mormoopidae			
Pteronotus parnellii fusco	A	0	1
Total		112	164

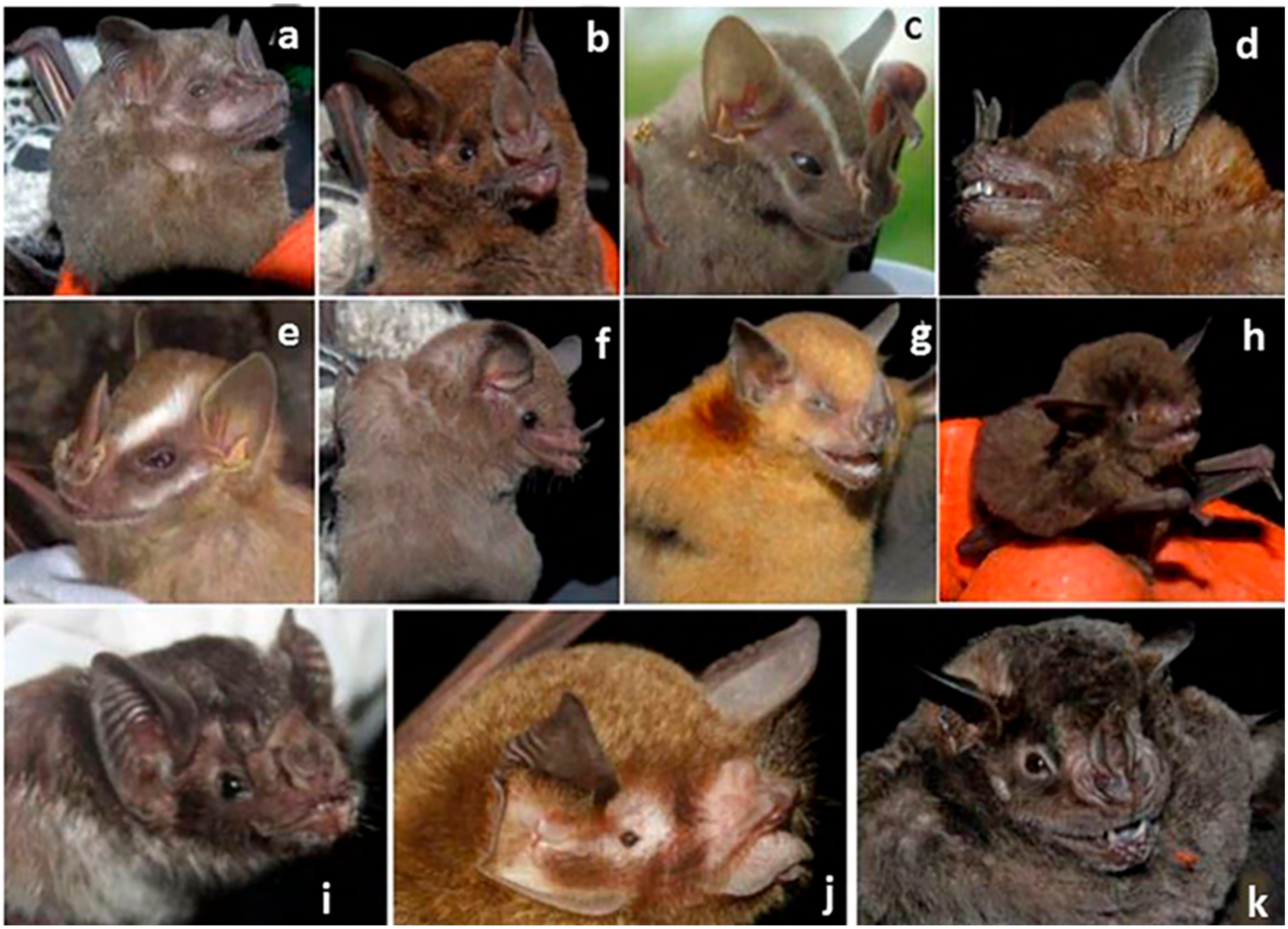

Figure 2. Bat species recorded in the peri-urban and urban TDF fragments studied. (a) *Artibeus lituratus*, (b) *Carollia perspicillata*, (c) *Uroderma bilobatum*, (d) *Carollia brevicauda*, (e) *Platyrrhinus fusciventris*, (f) *Glossophaga soricina*, (g) *Sturnira lilium*, (h) *Myotis nigricans*, (i) *Desmodus rotundus*, (j) *Pteronotus parnellii fusco*, and (k) *Artibeus obscurus* (Photographs a–j by Friedman Pabón and k by Roberto L. Morim).

For the diversity of order ^{1}q, the peri-urban area had the highest number of common species, with 4.50 effective species, compared to the urban zone, which reported 3.85. For order ^{2}q, the peri-urban area recorded the highest number of dominant species, with 3.23 effective species, having 1.13 times more dominant species than the urban zone, which reported 2.85 effective species (Figure 5).

The beta diversity estimated by the Sorensen index showed that the two communities (urban and peri-urban) may correspond to the same chiropteran assemblage with a variation between 0.2 and 0.6. However, some species were only recorded in a single community (peri-urban: *P. fusciventris, M. nigricans, P. parnellii fusco*, and *D. rotundus*; Urban: *A. obscurus*; Figure 3)

Percentage of occurrence (PO) of fruits consumed by bats. For the urban area, 49 feces samples were collected from five species of phyllostomid bats. In total, five types of plants were recorded from seeds (four at the species level; Table 2). The fruits with the highest percentage of occurrence in the diet of *A. lituratus* were *Ficus obtusifolia* (fig), with 40 %, and *Piper aduncum* L. (cordoncillo), with 30 % (Table 2). For *C. perspicillata*, the seeds of *F. obtusifolia* and *Cecropia* sp. (yarumo) showed the highest occurrence in their diet, with 55.6 % and 50 %, respectively. *Uroderma bilobatum* feeds on the fruits of four plant species, namely, *F. obtusifolia*, with a 50 % occurrence in its diet, followed by fruits of *Cecropia* sp., *P. aduncum*, and *Psidium guajava* (guava), which showed a 33.3 % occurrence. *Glossophaga soricina* consumed two types of fruits, where the seeds of *Cecropia* sp. showed a 33.3 % occurrence in the diet and *P. aduncum*, with 66.7 % occurrence. On the other hand, *S. lilium* consumed *F. obtusifolia* and *P. aduncum*, with frequencies of 50 % and 100 %, respectively. Additionally, direct field observations recorded the consumption of *Mangifera indica* (mango) fruits by *C. perspicillata*.

For the peri-urban area, 87 feces samples were collected from seven species of phyllostomid bats. A total of five seed species were recorded (Table 2). The seeds with the highest percentage of occurrence in the diet of *A. lituratus* were *F. obtusifolia* (50 %) and *Cecropia* sp. (40.6 %). *Carollia perspicillata* recorded the consumption of five types of seeds, where *Solanum lycopersicum* (tomato) and *F. obtusifolia* (fig) were the fruits with the higher occurrence in their diet, with 41.7 % and 33.3 %, respectively (Table 2). For

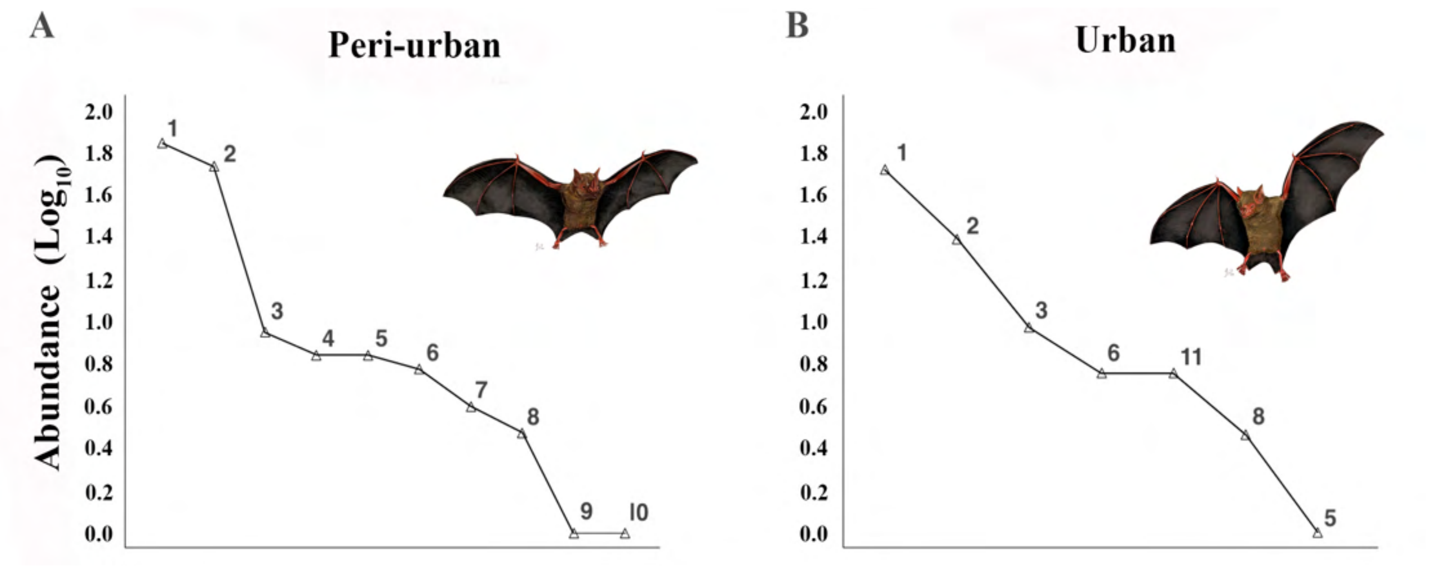

Figure 3. Abundance distribution plots for bat species in the urban and peri-urban TDF fragments in the Cúcuta metropolitan area, Colombia. *Artibeus lituratus* (1), *Carollia perspicillata* (2), *Glossophaga soricina* (3), *Platyrrhinus fusciventris* (4), *Carollia brevicauda* (5), *Uroderma bilobatum* (6), *Myotis nigricans* (7), *Sturnira lilium* (8), *Pteronotus parnellii fusco* (9), *Desmodus rotundus* (10), and *Artibeus obscurus* (11).

G. soricina, the seed with the highest percentage of occurrence was *P. aduncum,* with 66.7 %, while *S. lilium* recorded three seed species with the same proportion (*F. obtusifolia, P. aduncum,* and *S. lycopersicum*), with 33.3 %. *Uroderma bilobatum* feeds mainly on *F. obtusifolia,* with 80 %. *Carollia brevicauda* feeds on three types of fruits, mainly *S. lycopersicum* (75 %). Finally, *P. fusciventris* feeds mainly on *F. obtusifolia,* with 66.7 %. On the other hand, direct field observations recorded the consumption of *Manilkara zapota* (zapote) and *Mangifera indica* (mango) fruits by *A. lituratus* (Table 2).

Disperser importance index (DII). The values of the disperser importance index for the peri- urban area (DII = 1.205) suggest that *A. lituratus* is the most important disperser species, followed by *C. perspicillata* (DII = 1.049) and *U. bilobatum* (DII = 0.023). Likewise, for the urban area, *A. lituratus* (DII = 0.530) is the most important disperser species, followed by *C. perspicillata* (DII = 0.212) and *U. bilobatum* (DII = 0.026; Table 3).

Discussion

The present research assessed how the areas with urban growth that maintain relicts of TDF have affected the species composition and diversity for different bat guilds and the composition of the food resources for the family Phyllostomidae. Our results support this hypothesis by showing a marked difference in bat species richness and abundance between the urban (112 individuals, seven species) and peri-urban (164 individuals, ten species) TDF areas. In the urban area, we observed a notable reduction in species richness and total bat abundance compared to the peri-urban area. This discrepancy may be linked to habitat size and structure (Garcés-Restrepo *et al.* 2016; Chacón-Pacheco *et al.* 2017) since the peri-urban area maintains greater continuity in its floristic composition and a lower degree of alteration due to human activity. In addition, the importance of natural corridors between forest fragments

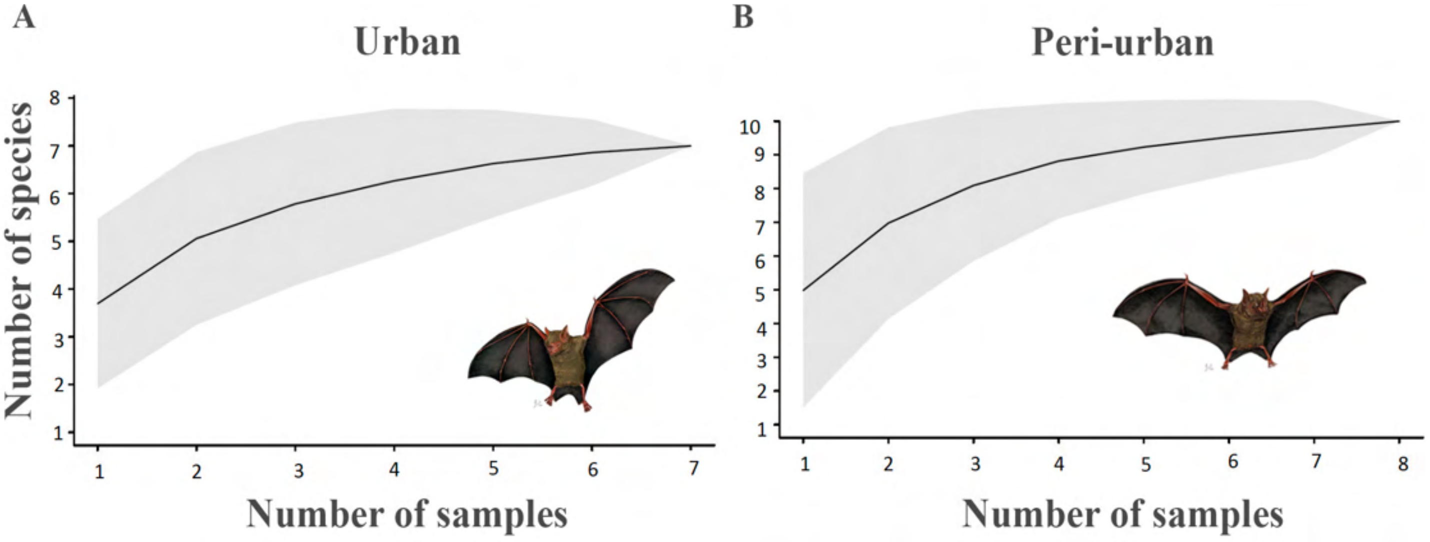

Figure 4. Rarefaction curve of the bat assemblage in the study areas.

Table 2. Percentage of occurrence (PO) of fruit species consumed by bats inhabiting urban and peri-urban TDF fragments.

Fragments	Bat species	Fruit species						
		***Cecropia* sp.**	***F. obtusifolia***	***P. aduncum***	***P. guajava***	***S. lycopersicum***	***M. indica****	***M. zapota****
Urban	*A. lituratus*	20.0	40.0	30.0	30.0	0	25.0	0
	C. perspicillata	50.0	55.6	22.2	22.2	0	1.7	0
	G. soricina	33.3	0	66.7	0	0	0	0
	S. lilium	0	50.0	100.0	0	0	0	0
	U. bilobatum	33.3	50.0	33.3	33.3	0	0	0
Peri-urban	*A. lituratus*	40.6	50.0	25.0	21.8	25.0	21.8	43.7
	C. perspicillata	19.4	33.3	30.6	13.9	41.7	0	0
	G. soricina	33.3	33.3	66.7	0	0	0	0
	S. lilium	0	33.3	33.3	0	33.3	0	0
	U. bilobatum	40.0	80.0	40.0	0	0	0	0
	C. brevicauda	0	25.0	0	25.0	75.0	0	0
	P. fusciventris	0	66.7	33.3	0	33.3	0	0

* Direct field observations

is worth highlighting, as these favor the dynamics and stability of animal communities in urbanized areas (Gehrt and Chelsvig 2004; Hale *et al.* 2012). Our results are consistent with previous studies indicating a decrease in bat richness in urban areas and suggest that species of the family Phyllostomidae, with their generalist adaptability, play a central role in the colonization of disturbed habitats (Quinto-Mosquera *et al.* 2013). Taken together, these findings underline the relevance of considering the effects of habitat reduction on the conservation of bat diversity in urbanized landscapes and emphasize the need to implement strategies that promote the connectivity between habitats to preserve the local fauna (Hahs *et al.* 2023).

The 11 species of bats recorded in the Cúcuta urban and peri-urban areas account for 5.33 % of the species known for Colombia. In turn, the diversity reported in this work agrees with similar figures reported for other TDF ecosystems. For example, Sánchez *et al.* (2007) reported 12 species in Chicamocha and Patia. Cabrera et al. (2016) found nine species in three dry ecosystems transformed by crops in Nariño. For their part, Vela-Vargas and Pérez-Torres (2012) reported 20 species in a livestock area in the department of Cordoba. However, this variation in richness is generally associated with habitat deterioration (Ortega and Mantilla-Meluk 2008). This can be represented by high abundance records of common species (*e. g.*, *U. bilobatum*, *C. perspicillata,* and *S. lilium*).

Diet composition of phyllostomid bats. Nine species of the family Phyllostomidae were recorded (Table 1), corresponding to 9 % of the total phyllostomid species recorded for Colombia, where the most abundant species are *A. lituratus* and *C. perspicillata*. The richness observed in the urban and peri-urban areas is consistent with the results repored by Aroca *et al.* (2016) in dry forest patches in the Department of Caldas, where eight frugivorous bat species were recorded, with a higher relative abundance of *C. perspicillata*, followed by *U. bilobatum* and *A. lituratus*. The studies by Ríos-Blanco and Pérez-Torres (2015) in a native TDF fragment in the municipality of Buenavista, Cordoba, recorded 17 phyllostomid species, coinciding with our study in that the most abundant species were *A. lituratus*, *C. perspicillata*, and *U. bilobatum*.

Our study on the diet of urban and peri-urban bats identified a recurrent presence of plants belonging to the genera *Piper*, *Cecropia*, *Ficus,* and *Solanum*. On the other hand, the genera *Manilkara*, *Psidium,* and *Mangifera* were less represented. Although it has been documented that Neotropical frugivorous bats show a preference for species of the genera *Ficus* and *Solanum* (Muscarella and Fleming 2007; Estrada-Villegas *et al.* 2010; Suárez-Castro and Montenegro 2015; Anteliz-Pallares *et al.* 2021; Velásquez-Roa *et al.* 2023), our study highlighted a particular trend: these bats demonstrate a marked preference for domesticated species, especially those from crops, plantations, or orchards near TDF patches (refer to Figure 1, crop mosaics). Such a preference may influence seed dispersal, potentially favor-

Table 3. Percent values of captures, samples containing seeds, and disperser index (DII) for each frugivorous bat species inhabiting the urban and peri-urban communities.

Fragments	Bat species	Percentage of catches	Samples with seeds	DII
Urban	*A. lituratus*	54.1	9.80	0.530
	C. perspicillata	24.1	8.82	0.212
	U. bilobatum	9.1	2.94	0.026
	G. sorcsina	5.5	1.47	0.008
	S. lilium	2.7	0.98	0.002
	A. obscurus	0	0	0
Peri-urban	*A. lituratus*	43.8	27.52	1.205
	C. perspicillata	33.9	30.96	1.049
	U. bilobatum	5.5	4.30	0.023
	C. brevicauda	4.3	3.44	0.014
	P. fusciventris	4.3	2.58	0.011
	G. soricina	3.7	2.58	0.009
	S. lilium	1.8	2.58	0.004
	D. roduntus	0	0	0
	P. parnellii fusco	0	0	0

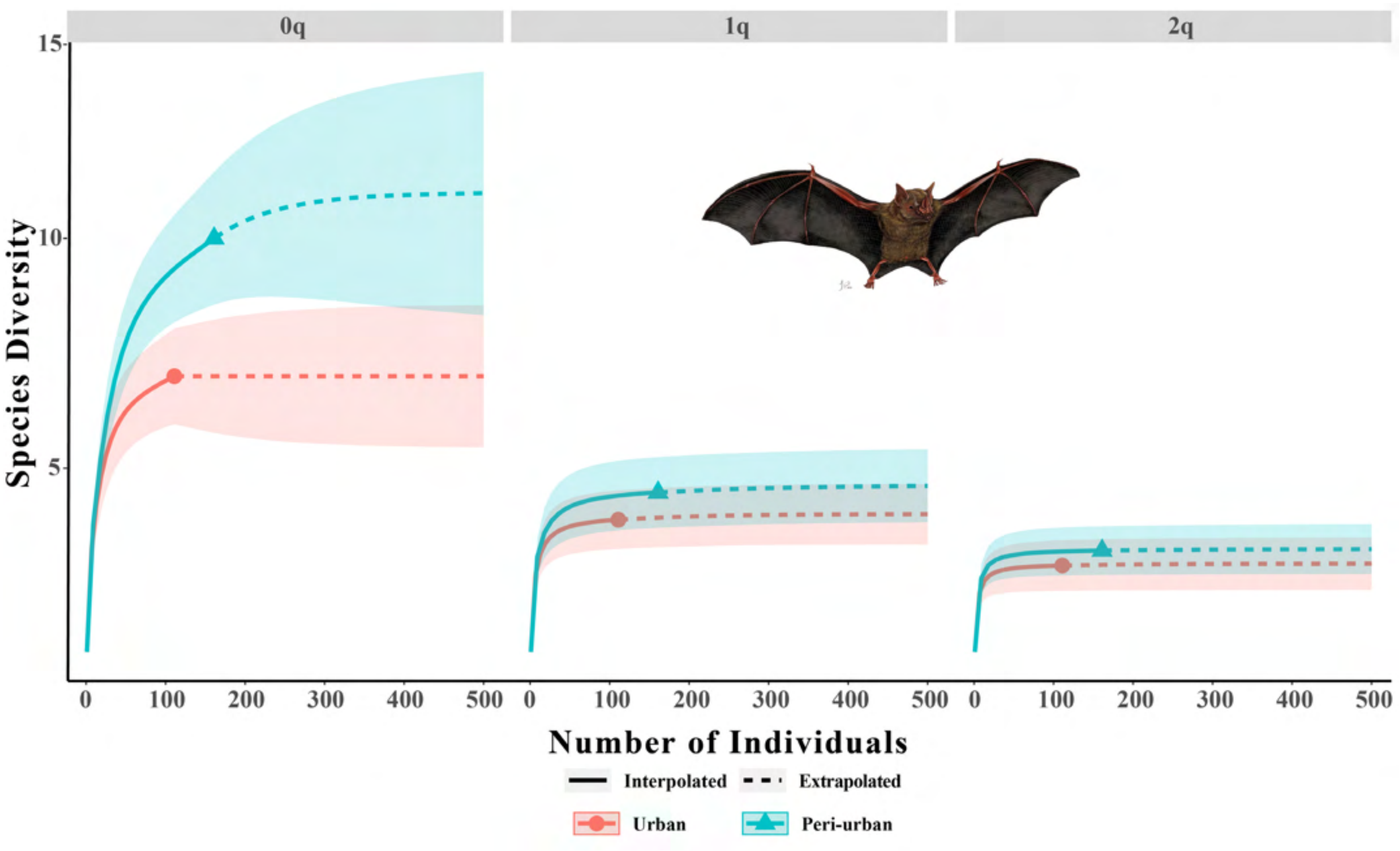

Figure 5. Diversity profiles of bats in the urban and peri-urban TDF fragments in the Cúcuta metropolitan area. Diversity orders: ^0q; ^1q; ^2q.

ing these domesticated species at the expense of wild ones. This relationship between bats and domesticated plants emphasizes the importance of further investigating its effect on the structure and composition of the TDF, as well as its role in the natural regeneration processes in central and peripheral zones of the Cúcuta metropolitan area.

However, two plant records, *Cecropia* sp. and *P. aduncum*, are characteristic of the TDF. In particular, *Cecropia* sp. was found in four of five bat species in urban areas and four of seven species in peri-urban zones. For its part, the shrub *P. aduncum* (family Piperaceae) was detected in the feces of all urban and six peri-urban bat species (Table 2). Given its ability to colonize perturbed areas, this plant probably plays a role as a pioneer or early-succession plant in dry forests, rapidly establishing in open or altered zones. These characteristics favor colonization by other species since environmental conditions are modified, either by enriching the soil or providing shade (Fleming 2004). Interestingly, mid-sized to large species, such as *S. lilium* (total length of 62 to 65 mm; forearm 36.6 to 45.0 mm; Gannon *et al.* 1989), showed a less varied diet in urban and peri-urban zones, as detailed in Table 2. However, they showed 100 % occurrence (PO) for *P. aduncum*. This affinity may involve significant consequences because fruit dispersal by bats may boost regeneration in perturbed zones within urban and peri-urban areas, in agreement with the ecological role proposed for *Piper* in dispersal and ecological succession (Fleming 2004). In this regard, Muscarella and Fleming (2007) state that Neotropical frugivorous phyllostomid bats are essential in the early forest succession stages, given the importance of fruits of early-succession shrubs and trees in their diet. These phyllostomid bats are vital facilitators of early forest regeneration, indirectly boosting the incorporation of plant species characteristic of TDFs. Besides, some reports mention that *S. lilium* feeds mainly on fruits of the families Solanaceae, Piperaceae, and Moraceae (Calonge 2009), emphasizing its key role in the regeneration process in TDF patches.

Separately, *C. brevicauda* is a mid-sized species (forearm 36 to 43 mm; mid-sized tibia 16 to 20 mm) that thrives in the low forest stratum that concentrates most shrubs and plants that produce the seeds it consumes (Emmons and Feer 1999). For *C. brevicauda*, this study recorded that it consumes three types of fruits in the peri-urban area, *Solanum* being the most frequent in the diet (75 %), followed by *Ficus* and *Psidium* (25 %). These findings contrast with those of Estrada-Villegas *et al.* (2010), who recorded that *C. brevicauda* consumed mostly fruits of the family Piperaceae and, to a lesser extent, of the family Solanaceae. However, *C. brevicauda* is able to exploit a broad range of food resources according to fruit availability and abundance in the areas where it lives (Aroca *et al.* 2016; Anteliz-Pallares *et al.* 2021), as well as to the degree of alteration and, hence, the vegetation structure and composition in these zones relative to the study area. On the other hand, *Platyrrhinus fusciventris* consumed fruits from three genera of plants in the peri-urban area, *Ficus* being the most frequent (66.6 %), followed by *Piper* and *Solanum* (33.3 %). Our findings are consistent with other studies that reported a preference for the genera *Solanum, Piper,* and *Ficus* by *Platyrrhinus* spp. (Aroca *et al.* 2016).

Likewise, other studies report that *Artibeus* spp. feed mainly on *Ficus* spp. (Gardner 2008), similar to the findings in the present study (Thies and Kalko 2004) in urban and peri-urban areas. However, Gorchov *et al.* (1995) found a larger number of *Cecropia* seeds in the feces of *Artibeus* spp. than in other species. Also, *C. perspicillata* showed a diet including fruits of the genus *Ficus*, with 41.6 % for the peri-urban zone and 55.5 % for the urban area. This finding contrasts with the reports for *Carollia* spp., where the main food sources are plants of the genera *Solanum* and *Piper* (Giannini and Kalko 2004). The feeding patterns of some bat species in TDFs may be influenced by limited food availability, particularly in the fragments studied, given the degree of alteration, in contrast with other tropical forests (Apgaua *et al.* 2014). Regarding the diversity of plant families in the TDF, Suárez *et al.* (2004) reported that *Machaerium* sp. (Fabaceae) showed the highest density, with 12.20 %, followed by *Croton cucutencis* and *C.* aff. *croizatti* (Euphorbiaceae), with densities of 11.08 % and 10.70 %, respectively. Despite that García-Herrera *et al.* (2019) documented the interaction of bats with plants of these families, our study did not show the presence of plants with the highest density in the TDF in the diet of bats. It is worth highlighting that although the families Asteraceae and Euphorbiaceae are dominant in TDFs, it is vital to understand the relationship between the abundance of these plants and the consumption of their fruits by bats. This interaction becomes even more relevant considering the expansion of crops and orchards, which have increased the presence of domestic plants.

The findings of the present study indicate that *A. lituratus* is one of the most important disperser bat species in urban and peri-urban areas, so it might greatly influence the restoration of areas perturbed by agriculture and livestock raising, as was the case of the areas assessed in this study. Hahs *et al.* (2023) found that bats in urban zones show traits typical of mobile generalists, favored by urbanization in species with strong dispersal abilities, versatile diets, and reproductive strategies that allow them to use the available resources efficiently. Novoa *et al.* (2011) reported a similar pattern in a dry forest, where the genera *Artibeus* and *Carollia* were also the main dispersers within the bat assemblage. According to the Disperser Importance Index (Table 3), all species in the urban and peri-urban areas showed lower values than those reported by Galindo-González *et al.* (2000) but were similar to those reported by Ríos-Blanco (2015). This may be due mainly to the number of samples collected: when the number of samples per species is low, this index probably underestimates the importance of the disperser; therefore, a greater sampling effort is needed to collect a larger number of samples. Previous works applying the disperser importance index (Galindo-González *et al.* 2000; Loayza *et al.* 2006) reveal that the highest value generally corresponds to the most abundant species that attain the largest number of samples analyzed, consistent with our findings in the present study.

This research shows that bats inhabiting urban and peri-urban areas preferentially consume fruits of domesticated plant species. In the urban landscape, the fruits consumed preferentially by bats are those of *F. obtusifolia* (fig) and *P. guajava* (guava), although native species, such as *P. aduncum* and *Cecropia* sp., are also included in the diet of all the bat species collected. In the peri-urban environment, we observed an even more pronounced preference for fruits of domesticated species, particularly fruits of high economic importance such as *P. guajava, S. lycopersicum* (tomato), *F. obtusifolia, M. zapota* (zapote), and *M. indica* (mango). These results suggest that in peri-urban areas, the food preference of bats may be shifting from wild species to domesticated and cultivated plants. Our findings underline the need to carry out further in-depth studies to understand the impact of this shift in the diet on seed dispersal and ecological dynamics in the study areas.

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Academics, academia, and intellectual fulfilment: lessons from the career of an eminent mammalogist

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Dr. William (Bill) Lidicker, Jr., was a classically trained mammal biologist who played an important role in pushing the field of mammalogy from largely descriptive beginnings into conceptual arenas soundly rooted in theory and principles. Whereas many readers will know Bill primarily as the architect of a "multifactorial approach" to understanding population cyclicity in arvicoline rodents, less well-known is how Bill's thematic focus shifted over the years. In an career that often prioritizes high-level productivity, I argue that Bill's willingness to pursue novel themes provides an compelling model of how to live a rich and fulfilling life in academia.

Dr. William (Bill) Lidicker, Jr., fue un biólogo de mamíferos de formación clásica que desempeñó un papel importante en impulsar el campo de la mastozoólogo desde comienzos en gran parte descriptivos hasta arenas conceptuales sólidamente arraigadas en la teoría y los principios. Mientras que muchos lectores conocerán a Bill principalmente como el arquitecto de un "enfoque multifactorial" para comprender la ciclicidad de poblaciones en roedores de arvicolina, menos conocido es cómo el enfoque temático de Bill cambió a lo largo de los años. En una carrera que a menudo prioriza la productividad de alto nivel, propongo que la voluntad de Bill de perseguir temas novedosos proporciona un modelo convincente de cómo vivir una vida rica y satisfactoria en la academia.

Keywords: Academic diversity; conservation biology; landscape ecology; mammalogy; population ecology; systematics; thematic diversity; William Z. Lidicker, Jr.

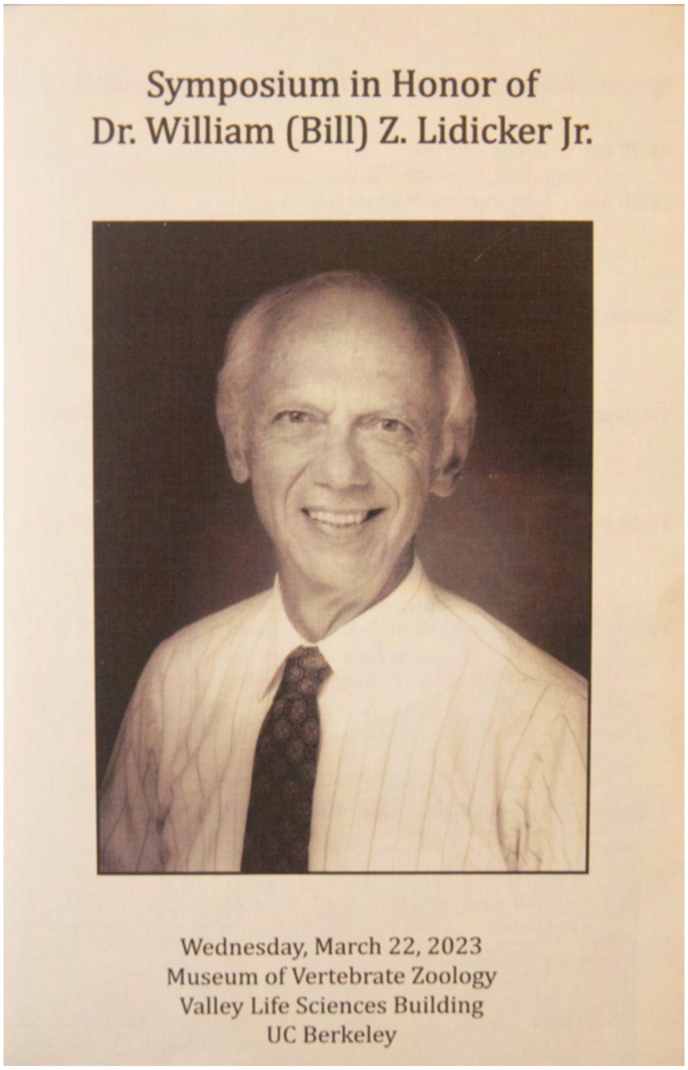
Dr. William (Bill) Zander Lidicker, Jr. (1932-2022) was perhaps best known as a population ecologist, with an emphasis on arvicoline rodents. However, I share the view espoused by Heske *et al.* (2023), that Bill was a systems biologist, albeit one focused clearly on mammals, and throughout his career he moved across at least four thematic arenas, which I believe reflects his unbridled intellectual curiosity and his endless desire to expand his own limits. As such, I believe that Bill's career highlights the joys of following one's intellectual passions wherever they may take one. Perhaps more fundamentally, it underscores the benefits that accrue when we avoid feeling canalized by our own experiences.

Reflecting his stature, colleagues at the UC Berkeley Museum of Vertebrate Zoology, where Bill spent his career, organized a symposium to reflect on Bill's legacy and impact (Figure 1). I was invited to speak to Bill's influence on the field of mammalogy, but as I prepared my presentation, I found that a larger message gradually emerged. Heske *et al.* (2023) had already penned an outstanding obituary, and this journal hosted a special issue (Vol. 13(1)) in honor of Bill's career and legacy. Rather than repeat what these authors have so capably highlighted, I wish to emphasize what I think may be a different message from Bill's career, and one that may carry some weight in the current academic marketplace.

Bill started out as a classically trained mammalogist, although it wasn't long before his publications turned to population biology, and he later extended this to the spatial realm of landscape ecology and ecological corridors (Figure 2). Perhaps not surprisingly in a world facing significant anthropogenic threats to biodiversity, Bill added conservation biology to his retinue in later years.

If the data from Figure 2 are adjusted to show the *proportion* of Bill's publications in four themes, a pattern of gradual transition becomes more clear (Figure 3). In particular, Bill's early publications emphasized systematics and taxonomy, and (mostly upon arrival at Berkeley) population ecology. Overall, population ecology was a dominant theme throughout his career, but this was gradually complemented with papers at broader spatial scales, and finally in the arena of conservation.

Word clouds can provide visual depictions of the differential dominance of key words among a series of items. A word cloud based on the titles of Bill's research publications (Figure 4) highlights his career in California and with a focus on populations (and the role of dispersal) and factors regulating these, and in particular with the California Vole (*Microtus californicus*). However, his early work in New Guinea and Australia also stand out, as does his interest in landscapes, conservation, and corridors. These latter two figures set a stage for viewing Bill Lidicker's career, and in turn highlight the value of never limiting the potential avenues for pursuit, a message that I think may be particularly important for younger investigators in a competitive academic marketplace.



Symposium in Honor of
Dr. William (Bill) Z. Lidicker Jr.

Wednesday, March 22, 2023
Museum of Vertebrate Zoology
Valley Life Sciences Building
UC Berkeley

Figure 1. Cover of the flyer distributed at the MVZ Symposium in Honor of Dr. William (Bill) Z. Lidiker Jr. This one-day event comprised a morning session and an afternoon session, with three presentations in each. Morning speakers were Drs. Richard Ostfeld and Felicia Keesing ("The Lidickerian Approach to Vole Ecology"), Dr. Sergio Ticul Álvarez-Castañeda ("Chat for a Friend"), Dr. Alex Hon-Tsen Hu ("Encounters in Corridors: Reflection of my personal Interactions with Professor William Z. Lidicker, Jr."). Afternoon speakers included the author ("William Z. Lidicker, Jr., and the Development of Contemporary Mammalogy"), Dr. Eileen Lacey ("A Legacy of Service to Mammalogy"), and Dr. Jim Patton ("Bill Lidicker – Mammalian Systematist").

Act 1: Systematics and Taxonomy. North America, Australia.—As noted, Bill Lidicker's publication record began with notes on range extensions and some descriptive morphology (Davis and Lidicker 1955a, b, c; Davis *et al.* 1955; Davis and Lidicker 1956). However, he also conducted extensive field research. His dissertation was a traditional (albeit quite thorough) evaluation of morphological variation within a species, in his case Merriam's Kangaroo Rat, and included recognition of a new subspecies (*Dipodomys merriami collinus*—Lidicker 1960b). With MVZ colleagues he continued this tradition, including the discovery of a new subspecies of Cliff Chipmunk (*Neotamias dorsalis*) in Chihuahua, Mexico (Lidicker 1960a—Figs. 5, 6).

Less widely known is Bill's attempt to quantify the nature of subspecies boundaries (Lidicker 1962b). In this he devised a complex metric to quantify relative morphological change across subspecific boundaries, but as Jim Patton noted in his presentation at the Lidicker Symposium, this was published just as the field of numerical taxonomy was emerging, and Bill's contributions appear to have been lost in the flood of novel quantitative tools (Sokal 1963; Sokal and Sneath 1963). Nonetheless, as Ruedas (2020) noted in an editorial commentary, Bill's contribution was important in refuting arguments (Wilson and Brown 1953) that subspecies were neither objective nor practicable, and this paper continues to be cited in contributions addressing diverse taxa (BioSis lists 45 citing articles, Google Scholar lists 81, as of 17 August 2023).

Although Bill rapidly diversified his thematic foci, he never lost his interest in systematics, which included Australasian rodents and marsupials (Lidicker 1968; Lidicker and Follett 1968: Lidicker and Ziegler 1968; Ziegler and Lidicker 1968; Lidicker and Marlow 1970; Lidicker 1973a; Lidicker and Brylski 1987) – even describing a new genus and species of fossil rodent (Martinez R. and Lidicker 1971) – and later addressing the taxonomic status of the Southern Sea Otter (*Enhydra lutris nereis*—Davis and Lidicker 1975), and ultimately returning to the kangaroo rat of his nascent years, helping with the revision of *D. merriami* in Baja California, México (Álvarez-Castañeda *et al.* 2009).

Act 2: Population Ecology (mostly voles). Bill's interests clearly extended beyond taxonomy and evolutionary systematics, and immediately upon arriving at Berkeley he initiated studies on the local fauna. This included surveys on the House Mouse (*Mus musculus*) population on Brooks Island, located close to Richmond in the San Francisco Bay and populated at that time almost solely by house mice, but at very high abundances; Norway Rats (*Rattus norvegicus*) occupied beach areas. At about the same time, California Voles were accidentally introduced from an adjacent islet (Lidicker 1966:27), ultimately leading to the extirpation of *Mus* from the island. Observations on these and other populations of small mammals led to a brief but highly influential paper (Lidicker 1962a) that remarkably included no data. In a contribution to the *Therya* festschrift, Krebs (2022) noted that at that time, few authors had given much thought to a role for emigration in regulating populations. He noted that David Lack (1954), in his seminal book, had emphasized the role of food, predation, and disease, but gave little consideration to animal movement as a regulating factor. Nearly three decades earlier, Elton (1927) also discussed dispersal, but largely phenomenologically, as did Andrewartha and Birch (1954) in their influential contribution. Lidicker (1962a) emphasized the potential role of emigration but carried this further, addressing the selective advantages of dispersal and several corollary themes. Indeed, Krebs (2022:19) concluded: "If you go back to Lidicker (1962[a]) you will find threads of [many subsequent] developments in the study of dispersal", including: emigration, dispersal, and population regulation; social and genetic consequences of dispersal; the adaptive advantage of dispersal; selection for dispersal tendency; frustrated emigration; lack of food limitation.

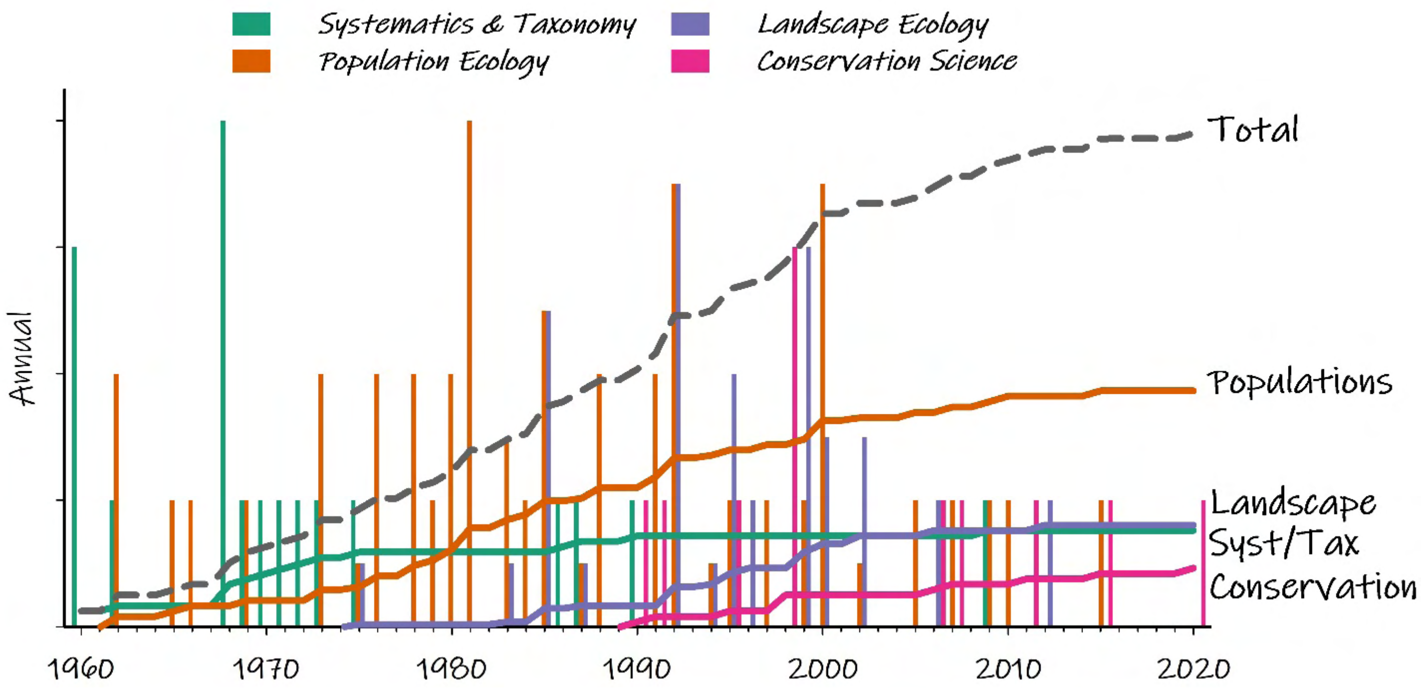


Figure 2. Bill Lidicker's research publication record, segregated in four general themes. Vertical bars illustrate the number of papers published in each year, whereas the line show the cumulative number of papers in each theme over Bill's career. What stands out is that Bill gradually transitioned from classical systematics and taxonomy to a career-dominant theme of population ecology, which in turn was complemented by papers (and books) that extended population biology to landscape scales and finally integrated conservation themes in the face of increasing societal concerns over habitat loss, climate change, and related challenges.

After collecting 13 years of data on California Voles from Brooks Island, Bill published his observations in *Ecological Monographs*, where he initiated what would become a hallmark of his legacy, as he questioned the value of single-factor models to explain regular cyclicity in these populations. Bill wrote (Lidicker 1973b:272): "The quasi 2-year cycle of regularly recurring peaks every year and alternating high and low winter densities which came to characterize the Brooks Island vole population is considered to be the result of a regulation process in which a *multiplicity of factors interact to achieve regulation*. Both density-unresponsive and responsive factors are involved" (emphasis mine). He concluded his paper by noting: "It is clearly apparent to me that one cannot triumphantly point to *the* regulating factor

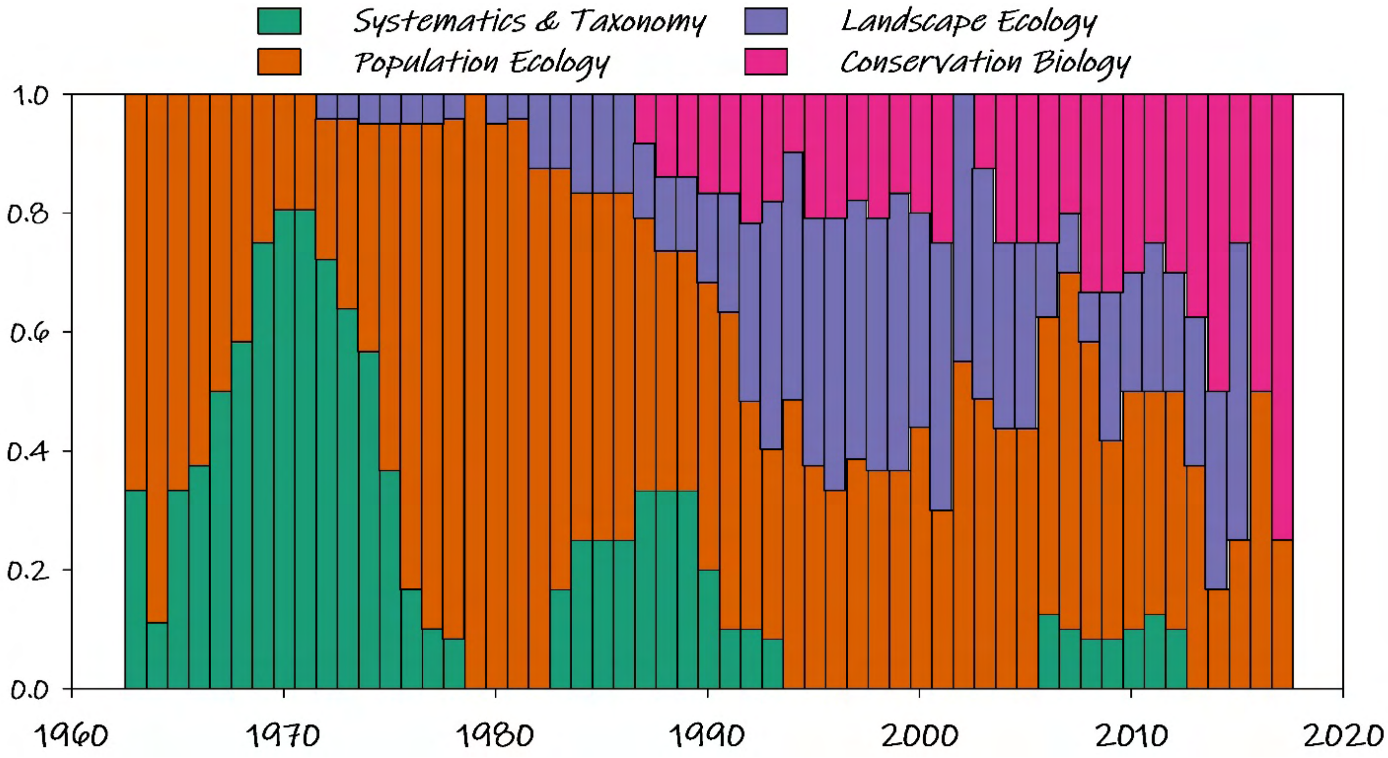


Figure 3. Using the same data as in Figure 2, this figure illustrates the proportion of Bill's publications in four themes, using a 7-year rolling window.

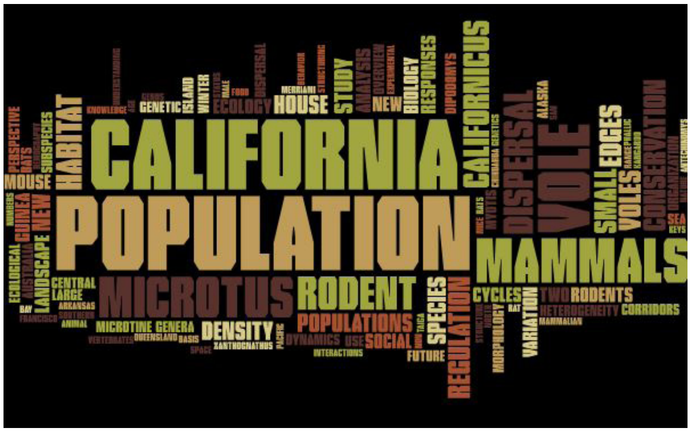


Figure 4. A word cloud based on the full titles of Bill Lidicker's research publications.

influencing vole density. Rather, a multiplicity of factors are found to be interacting, and one is led to some integrated or synthetic theory of regulation" (emphasis his).

It was in 1978, when Bill was invited to contribute to a symposium on small mammal populations (Lidicker 1978), that he formally coined the term "multi-factorial model of vole demography". He returned to this theme when the American Society of Mammalogists recognized Bill's career with the Merriam Award; in his resulting talk and publication, Bill highlighted four extrinsic factors and four intrinsic factors that he argued were important in regulating populations of California voles (Lidicker 1988). Of course, a number of these had been discussed by other authors, and Bill didn't disagree with the potential role of each of these factors individually; rather, he argued that none of them in and of themselves could explain cyclicity in California Vole numbers, and probably not in other species either.

Another seminal contribution was Bill's invited contribution of a chapter for an edited volume in the IBP book series (Lidicker 1975). In this he reiterated and built upon his developing theory of population regulation, but two key sets of concepts emerged from this paper. First, Bill formally distinguished "pre-saturation dispersal" from "saturation dispersal", noting that animals in these two phases are different in numerous respects, including rates of maturity, reproduction, and the very likelihood of their survival: whereas the former are in relatively good condition, and they have a much greater chance of surviving and re-establishing themselves elsewhere, the latter tend to be social outcasts, juveniles, very old individuals, and generally in poor condition, with limited capacity to cope with local conditions. As such, the former category includes individuals for which there may actually be "greener pastures" on the other side of the hill, whereas the latter category includes individuals faced with the immediate choice of staying in the population and almost certainly dying, versus moving out and probably dying.

A second concept that emerged from this publication was that of a "dispersal sink". For an animal to emigrate there has to be somewhere to go; in the absence of another patch where the animal could at least survive for some time, it would most likely return home, which Bill called frustrated dispersal. This concept was picked up by others and contributed significantly to the development of source/sink dynamics by Ron Pulliam (1988), which in turn has contributed to metapopulation (and metacommunity) theory.

It should be noted that pushing boundaries carries risks, and Bill was roundly denounced by many research-

Figure 5. Bill Lidicker (right) conducting field research in the Sierra del Nido, Chihuahua, Mexico, 1961. These efforts resulted in the description of a new subspecies of the Cliff Chipmunk (*Neotamias dorsalis nidoensis* —Lidicker 1960a). Other members of this photo include (left to right) Ned Johnson, Gene Christman, Mike Pontrelli, and Jim Anderson (Courtesy of the MVZ Archives; Image #10065; © Museum of Vertebrate Zoology, University of California, Berkeley).

ers on demographic cyclicity, not so much because they disagreed with his argument that no single factor could explain all cycles (neither within nor – certainly! – across species) as because Bill's multifactorial approach is exceedingly difficult to test. Hence began what Ostfeld (2015) called the "vole wars", which unfortunately pushed at least some young researchers away from this exciting field. In the face of seemingly personal attacks, however, Bill remained remarkably unperturbed, and he epitomized the heart of scientific debate by responding calmly yet succinctly to his critics (e.g., "Science without controversy would be dull indeed . . ."—Lidicker 1991b:631).

Act 3: Landscape and Corridor Ecology.—it is perhaps inevitable that Bill's interest in dispersal led to curiosity over how and where animals disperse, but understanding such dynamics required that he put population ecology into the broader spatial context of landscapes. Of course, in a world of growing appreciation of habitat fragmentation, it may seem logical that a demographer interested in dispersal would ask about the corridors through which individuals move between populations. In the 1980s, with Andy Cockburn, Bill published on the role of microhabitat heterogeneity in structuring the population dynamics of California Voles (Cockburn and Lidicker 1983). This work evidently stimulated Bill's interest in population ecology across landscapes, leading to a symposium at the sixth *International Theriological Congress* in Sydney in 1993, and a subsequent edited volume, *Landscape Approaches in Mammalian Ecology and Conservation* (Lidicker 1995a). In turn, this was followed by chapters on vertebrate responses to habitat edges and corridors in which Bill and his colleagues summarized the state of knowledge at the time. They emphasized the importance of understanding emigration and immigration in a metapopulation context, given growing anthropogenic fragmentation and degradation of habitats globally (Lidicker and Koenig 1996; Lidicker and Peterson 1999).

Figure 6. Bill Lidicker named two subspecies new to science. Heske *et al.* (2023) illustrated one of these (*Dipodomys merriami collinus*), based on his dissertation work and published in (Lidicker 1960b). His field research in Chihuahua, Mexico (Figure 5) resulted in discovery of this new subspecies of chipmunk. Photo by William Stone (Courtesy of CalPhotos and the MVZ Archives; MVZ Image #16834; © Museum of Vertebrate Zoology, University of California, Berkeley).

Perhaps culminating this section of his career, with Jodi Hilty and Adina Merenlender he co-edited the first volume on the growing field of corridor ecology (Hilty *et al.* 2006). This book has had a substantial influence on the field, and recently was updated and revised in a second edition (Hilty *et al.* 2019). This trajectory illustrates how Bill continued to expand his research focus; while remaining largely focused on small mammals and population ecology, he contributed importantly to placing this in the proper spatial framework that furthered understanding of nuance in population ecology and demographic cycles. In a retrospective article, Bill's co-editors (Merenlender *et al.* 2022) wrote that Bill repeatedly urged consideration of the *species* for whom corridors were being considered. He always emphasized the ecology and natural history of species, and how spatial dynamics and environmental structure influenced population demography and viability.

Act 4: Conservation Biology. The final broad theme to Bill's career, as I see it, is perhaps common to many contemporary scientists. Studying population ecology of small mammals in an increasingly fragmented world under the specter of desertification and climate change leads many to be concerned over the future of entire biomes, not to mention the particular taxa we have dedicated our lives to study. Bill's interest in conservation appears to have initiated in earnest in the late 1980s, when he edited the first ever global survey of rodent species of conservation concern (Lidicker 1989a). Soon thereafter he published chapters on "Impacts of non-domesticated vertebrates on California grasslands" (Lidicker 1989b) and "Introduced mammals in California" (Lidicker 1991a), and three years after that by an essay on "Biodiversity: what is it and what is it good for?" (Lidicker 1995b). Bill recognized the magnitude of this title, noting that "[t]o confront such a profound question in any substantive way is beyond the scope of this essay", but underscoring his appreciation of diverse perspectives he highlighted

Figure 7. Bill Lidicker was well known for his spatial memory. Speakers at the MVZ Symposium commented that in spite of the apparent mayhem of paperwork in his office, he could locate "just the paper you need" with ease. One has to wonder if this spatial memory contributed to the ease with which Bill integrated spatial dynamics into his population research, ultimately leading to a focus on landscape-scale processes. Photo by O. P. Pearson (Courtesy of the MVZ Archives; Unnumbered image; © Museum of Vertebrate Zoology, University of California, Berkeley).

three broad categories of reasons why biodiversity is good – "moral and aesthetic", "educational and scientific", and "mental health". Bill continued to publish papers and chapters on conservation, initially emphasizing conservation of rodents but gradually broadening his focus to all mammals and, finally, to humanity itself. A few select contributions include: "Revisiting the human dimensions of conservation biology" (Lidicker 1998); "Some neglected aspects of rodent conservation" (an extended abstract—Lidicker 2006); "Issues in rodent conservation" (Lidicker 2007); "Hope and realism in conservation biology" (Lidicker 2011); "Mammalian conservation: scientific frontiers and sociopolitical pitfalls" (Introduction to a Special Contribution on mammal conservation—Lidicker 2015); "A scientist's warning to humanity on population growth" (Lidicker 2020).

Synthesis, Conclusions, and Bill's Big Message. Bill Lidicker's passion for the biology of small mammals and his seemingly endless curiosity, combined with a legendary memory, helped to push the boundaries of mammalogy, perhaps most notably in population ecology, but also in several themes that are linked to, but distinct from, this field. Bill fended off numerous arguments concerning his multi-factorial model and he appears to have done so with good grace and diplomacy. His curiosity may inevitably have drawn him from traditional systematics to population biology, and thence to landscape and corridor ecology. As I began preparing to speak to Bill's influence on mammalogy, I was increasingly drawn to the broader message that is exemplified by his career but which has been overlooked by his biographers. Bill Lidicker was trained in classical mammalogy, but through his career he followed his passions to new intellectual arenas. Academic careers often involve intense selection for productivity, and this in turn can disincentivize intellectual diversification and personal growth and discovery – publishing more papers on a topic one knows well often is easier than pursuing novel themes, often involving a new literature. I have tried to highlight how Bill avoided being pigeon-holed or intellectually constrained. The thematic breadth illustrated through his career was founded on a deep appreciation of natural history and organismal biology, and promoted by a diverse set of personal interests and broad curiosity. If there is an overarching message from Bill Lidicker's career, it may be to remind us all that there is value in following your interests. If these lead you to new fields, then so be it – be the intellectual presaturation disperser who earns the satisfaction of experiencing new intellectual arenas, and perhaps you'll even have an impact in these fields. Even if you don't, the challenge likely is worth the effort. Nobody goes into science to be bored or to be intellectually constrained. I'll close by quoting Rick Ostfeld, who commented on this facet of Bill's career in an email to me (12 August 2023): "[Bill's] thematic breadth, derived from broad curiosity and the ability to self-inform, is in short supply these days." "[F]requency-dependence applies way beyond natural selection, and . . . rare phenotypes are often more valuable for their rarity."

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I first met Bill Lidicker when, as an undergraduate, I visited MVZ to look at specimens of kangaroo rats. I still remember Bill noticing what surely was a gawking young man, and he immediately came down from his second-floor office to ask if he could help me. That such a figure would so unquestioningly offer to help left me with a career-long appreciation for the impact that one can have by simple acts of generosity (Bill then passed me to Jim Patton who was equally generous, and until I began meeting other leading mammalogists at ASM meetings I wondered if this was just something in the water at Berkeley). I am grateful to Michael Nachmann, Eileen Lacey, and Jim Patton for inviting me to speak at the Lidicker Symposium, and to all the speakers of that memorable and inspirational day. Ed Heske oversaw coordination of the *Therya* volume in honor of Bill, and subsequently built upon this to produce an outstanding obituary in the *Journal of Mammalogy*. For any readers curious to read more about Bill I highly recommend these contributions. Thanks to Peter Meserve, Ed Heske, and Jim Patton for comments on this manuscript. Finally, I owe a special thanks to Charley Krebs for his paper in *Therya*, highlighting the role of Bill's 1962 *American Naturalist* article, and to Rick Ostfeld for the elegant synthesis that I quote at the end of this manuscript.

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