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Diversity and activity of medium- and large-sized mammals in agroforestry systems, Santander, Colombia

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The expansion of the agricultural frontier for food production is one of the main threats to biodiversity in Colombia. Agroforestry systems represent a productive strategy based on mixed cropping with timber, fruit, or native species that enhance production and can provide resources for diverse animal species. In Colombia, cacao is generally cultivated under agroforestry systems, with Santander being the main national producer. Because these systems harbor species sensitive to anthropogenic disturbance, such as mammals, the objective of this study was to evaluate the taxonomic diversity and activity patterns of medium- and large-sized mammals associated with cacao agroforestry systems. The study area included three cacao agroforestry systems located on different farms between San Vicente de Chucurí and Zapatoca, Santander, Colombia. Three Bushnell Essential E3 camera traps were installed on each farm and remained active from January 2022 to July 2023. Relative abundance indices, diversity based on Hill numbers, activity patterns, and overlap were estimated. Based on an effort of 1,529 camera-trap nights and 1,154 independent detections, 17 species of medium- and large-sized mammals were recorded, some of which were categorized as Near Threatened (NT) and Vulnerable (VU). The assemblage exhibited predominantly nocturnal–crepuscular activity. Possible shifts in activity patterns in response to human presence were identified, as observed in *Dasyprocta punctata*. Additionally, comparisons among potentially competing species revealed temporal segregation in rodents and overlap in marsupials and cingulates. These results highlight the potential of cacao agroforestry systems to provide resources such as water, food, and shelter for these mammals.

Keywords: Camera trapping, human presence, relative abundance, temporal overlap, *Theobroma cacao*.

La expansión de la frontera agrícola para la producción de alimentos es una de las principales amenazas para la biodiversidad en Colombia. Los sistemas agroforestales representan una estrategia productiva basada en cultivos mixtos con especies maderables, frutales o nativas que favorecen la producción y pueden proporcionar recursos a diversas especies animales. En Colombia, el cacao se desarrolla generalmente mediante sistemas agroforestales, siendo Santander el principal productor nacional. Debido a que estos sistemas albergan especies sensibles a la intervención antrópica, como los mamíferos, el objetivo del estudio fue evaluar la diversidad taxonómica y los patrones de actividad de mamíferos medianos y grandes asociados a sistemas agroforestales de cacao. El estudio se desarrolló en tres sistemas agroforestales de cacao ubicados en diferentes predios entre San Vicente de Chucurí y Zapatoca, Santander, Colombia. Se instalaron tres cámaras-trampa Bushnell Essential E3 en cada predio, las cuales permanecieron activas de enero de 2022 a julio de 2023. Con la información obtenida se estimaron índices de abundancia relativa, diversidad mediante números de Hill, patrones de actividad y solapamiento. Como resultado de 1.529 noches/trampa y 1.154 detecciones independientes, se registraron 17 especies de mamíferos medianos y grandes, algunas de ellas categorizadas como Casi Amenazadas (NT, Near Threatened) y Vulnerables (VU, Vulnerable). El ensamblaje presentó principalmente actividad nocturna-crepuscular. Se identificaron posibles ajustes en el patrón de actividad frente a la presencia humana, como en el caso de *Dasyprocta punctata*. Además, se comparó la actividad entre especies potencialmente competidoras observando segregación temporal en roedores y solapamiento en marsupiales y cingulados. Estos resultados destacan el potencial de los sistemas agroforestales de cacao para proveer recursos como agua, alimento y refugio a estos mamíferos.

Palabras clave: Abundancia relativa, fototrampeo, presencia humana, solapamiento temporal, *Theobroma cacao*.

Agriculture is one of the anthropogenic activities that sustain human populations (Godfray *et al.* 2010; Bula and Tessmer 2020). This activity generally depends on large land areas for food production (Dirzo and Raven 2003), leading to large-scale tree clearing that affects plant and animal biodiversity, including mammals (Haddad *et al.* 2015). As an alternative, agroforestry systems (AFS) have been implemented for food production (Zermeño-Hernández *et al.* 2016). Agroforestry systems consist of combinations of crops with timber, fruit, or native species that provide shade to cultivated plants (Moreno-Calles *et al.* 2013). In this context, AFS have been considered as productive systems capable of providing shelter and resources for different mammal species (Beer 1999; Bhagwat *et al.* 2008). One of the crops commonly grown under this modality is cacao (Jaimes-Suárez *et al.* 2022).

In Colombia, cacao cultivation is generally carried out under AFS, with Santander Department being the main producer (Jaimes-Suárez *et al.* 2022). This department has more than 59,000 hectares under cultivation and contributes 41% of the national production of dry cocoa beans (Ministerio de Agricultura y Desarrollo Rural 2021). Within this region, San Vicente de Chucurí and El Carmen de Chucurí are the municipalities with the highest cacao production, accounting for 48.7% of departmental production. Due to its importance, cacao agroforestry is considered a sustainable production system from social, economic, and biophysical perspectives (Jaimes-Suárez *et al.* 2022), as well as a strategy to reduce pressure on primary forests, preserve biodiversity, and contribute to food security (Palencia-Calderón and Mejía-Flórez 2004). Among the ecosystem services provided by these systems are carbon sequestration, water cycle regulation, and the provision of habitat for diverse species of birds, insects, and mammals (Jaimes-Suárez *et al.* 2022).

Mammals play a fundamental role in ecosystems (Racero-Casarrubia and Reyes-Cogollo 2022), fulfilling important ecological functions such as seed dispersal, soil aeration and water infiltration, and the regulation of plant, animal, and insect populations (Martín-Regalado and Briones-Salas 2024). They are generally considered indicators of ecosystem health because they can be sensitive to anthropogenic disturbances such as habitat loss and fragmentation, which may lead to changes in their activity, structure, composition, and distribution (Rumiz 2010; Buchmann *et al.* 2013). In agricultural landscapes, their presence can provide valuable information about the sustainability of management practices and the capacity of production systems to conserve biodiversity.

Studies conducted in agricultural systems have shown that plantations can affect mammal species diversity in surrounding areas and agricultural landscapes (Navarro and Gómez 2015; De Giorgi Peirano 2016). Conversely, research carried out in Costa Rica, Brazil, and Mexico suggests that cacao cultivation can provide shelter and food resources for a wide variety of animal and plant species (Guiracocha *et al.* 2001; Cassano *et al.* 2012; Sánchez-Soto *et al.* 2025). In Colombia, studies by Peralta-Zapata *et al.* (2019) and López-Ramírez *et al.* (2020) have reported similar findings. Therefore, the objectives of this study were to: 1) estimate taxonomic diversity, 2) describe activity patterns, and 3) determine temporal overlap in the activity patterns of medium- and large-sized mammals in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca, Santander, Colombia.

Materials and methods

Study area. The study was conducted in three cacao agroforestry farms located in the municipalities of San Vicente de Chucurí and Zapatoca, Santander Department, northeastern Colombia (Figure 1). The sites correspond to: A) Montegrande Farm, located at 6.9252° N, –73.3997° W, and 480 m above sea level (masl); B) Villa del Rosario Farm, located at 6.9177° N, –73.4086° W, and 428 masl; and C) Miraflores farm, located at 6.9355° N, –73.3611° W, and 995 masl (Figure 1).

Montegrande Farm (23 ha) and Villa del Rosario Farm (43 ha), both located in the municipality of San Vicente de Chucurí, are cacao farms managed under agroforestry systems integrated with cattle production. In these systems, cacao is cultivated in association with avocado and citrus trees, while cattle graze within the agroforestry areas. In contrast, Miraflores Farm (20 ha), located in the municipality of Zapatoca, consists of a cacao-based agroforestry system in which cacao is cultivated in association with orange trees and plantain. Together, the three farms exhibit a vegetation structure comprising tree, shrub, and herbaceous strata, which enhances habitat heterogeneity, provides resources and shelter for wildlife, and promotes landscape connectivity (Guzmán *et al.* 2016).

The region exhibits low annual thermal variation, with temperatures ranging from 20 to 28 °C and a bimodal rainfall pattern, with rainy seasons during March–May and September–November, ensuring relatively constant water availability throughout the year (Instituto Geográfico Agustín Codazzi 2025).

Sampling design. A camera-trapping survey using single-station setups was conducted between January 2022 and July 2023 in cacao agroforestry systems. Nine Bushnell Essential E3 (Bushnell, USA) camera traps were installed, with three cameras deployed per farm (sampling unit). Camera-trapping stations were established opportunistically (*ad libitum*) within the cacao plantations, considering internal footpaths, sites with evidence of mammal activity (e.g., tracks and feces), and recommendations from the landowners. A minimum distance of 100 m was maintained between stations, following the recommendation of Moreno *et al.* (2025).

Cameras were mounted on tree trunks approximately 30 cm above ground level. In one case, a camera was installed at a height greater than 1 m due to terrain conditions. Camera traps were programmed to record 30-s videos with a 15-s interval between consecutive trigger events and operated continuously over a 24-h period (Díaz-Pulido and Payán-Garrido 2012). Video recordings facilitated species identification by allowing the observation of morphological and behavioral characteristics. Each camera-trapping station was georeferenced using a Garmin GPS 60CSx and checked monthly to ensure proper functioning and to retrieve recorded data (Ministerio de Medio Ambiente *et al.* 2021).

Collected data were organized in a database including farm name, camera identification, record code, coordinates, date (dd/mm/yyyy), time, species, common name, number of individuals, sex (when identifiable), conservation status, and general observations. Medium-sized (>101 g and <10 kg) and large (>10 kg) mammals were defined following Hernández-Hernández *et al.* (2018). Specialized literature was used for species identification (Pérez-Gómez *et al.*

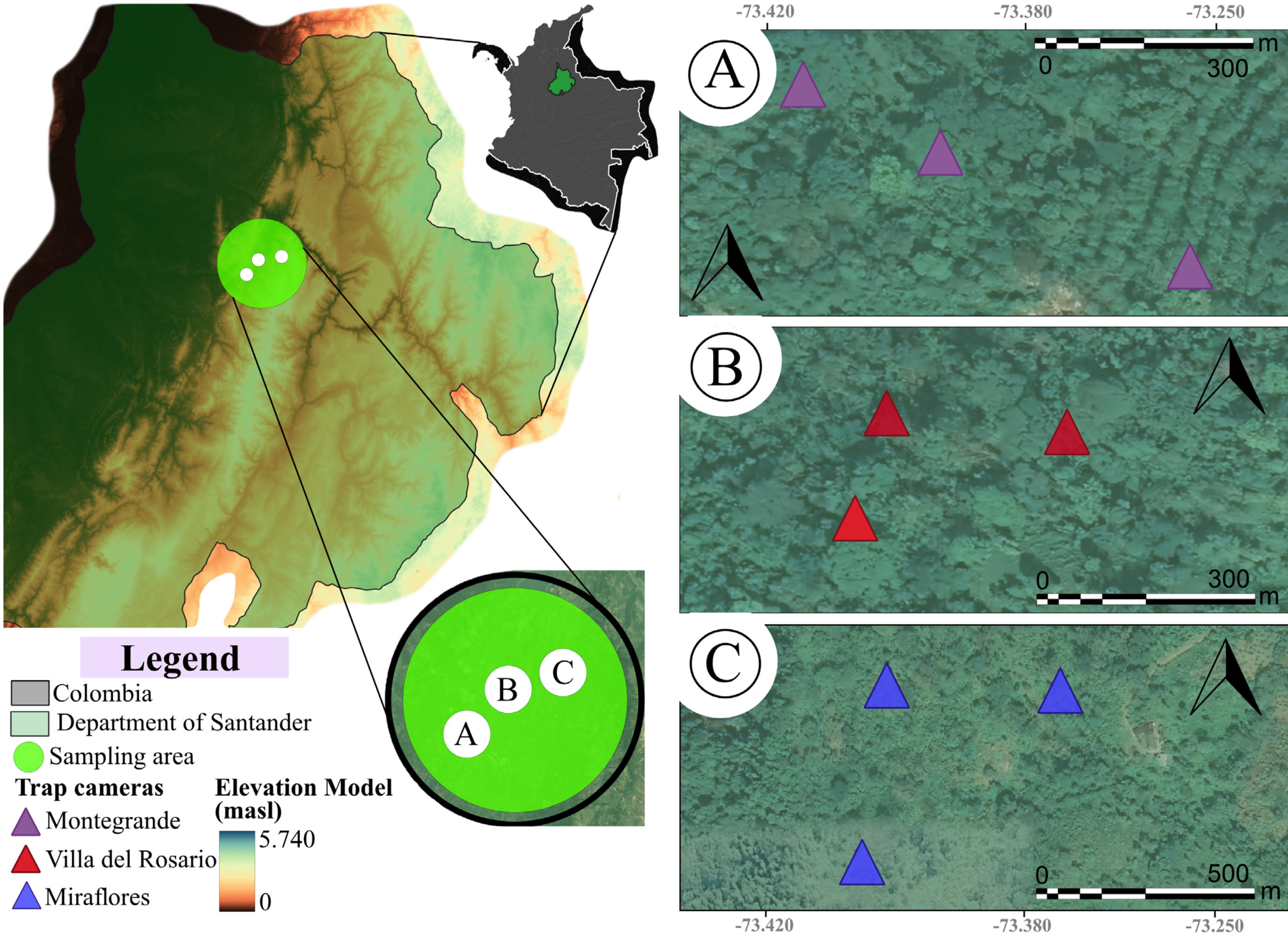

Figure 1. Location of camera-trapping stations (triangles) at Montegrande (A), Villa del Rosario (B), and Miraflores (C) farms, in the municipalities of San Vicente de Chucurí (A–B) and Zapatoca (C), Santander, Colombia.

2025; Ramírez-Chaves *et al.* 2025). Trophic guilds were classified according to López-Ramírez *et al.* (2020) and Pérez-Gómez *et al.* (2025). Conservation status followed Resolution 0126 issued by the Colombian Ministry of Environment and Sustainable Development (2024) and the International Union for Conservation of Nature (IUCN) Red List (IUCN 2025). Human activity was recorded incidentally by the camera traps and corresponded primarily to farmers carrying out cacao crop management. Records were identified through the visual recognition of complete individuals or visible body parts, during both diurnal and nocturnal periods.

Data analysis. Sampling effort (camera-trap nights) was calculated as the total number of nights that each camera remained active (O'Brien *et al.* 2003).

Relative abundance. Relative abundance was estimated using the relative abundance index (RAI), calculated as the number of independent detections divided by sampling effort and multiplied by 100 (Pardo-Vargas and Payán-Garrido 2015). Independent detections were defined as consecutive records of different species, or consecutive records of the same species separated by more than 60 min (Tobler *et al.* 2008). In a capture or record the total number of individuals was counted when they could be reliably distinguished (Rowcliffe *et al.* 2008).

Taxonomic diversity. Diversity was assessed using Hill numbers with the iNEXT package in R version 4.4.1, with a minimum of 100 permutations, 1,000 bootstrap replications, and 95% confidence intervals (Hill 1973; Jost 2006; Hsieh *et al.* 2016). Hill numbers partition diversity into three orders: Order 0 diversity (q^0) corresponds to species richness, order 1 diversity (q^1) represents common species according to their abundance, and order 2 diversity (q^2) accounts for dominance (Chao and Jost 2012).

Activity patterns. Only species (including humans) with more than 20 independent records were included (Pardo *et al.* 2021). Daily activity patterns were estimated using the overlap package in R version 4.4.1, which fits kernel density functions to the temporal distribution of species activity records (Meredith and Ridout 2017). Temporal distribution was evaluated using the Rayleigh test implemented in the circular package over a 24-h period for each species; values close to 1 indicate a stronger temporal preference, whereas values close to 0 indicate a more uniform temporal distribution (Agostinelli and Lund 2017). Species were classified according to their activity pattern as diurnal

Table 1. Medium- and large-sized mammal species recorded in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca, Santander, Colombia. NI: number of independent records. RAI: relative abundance index (%). N: nocturnal, D: diurnal, EV: evening crepuscular, MC: morning crepuscular, and DD: data deficient. (*) Species recorded at all farms.

Scientific name	Common name / local name	NI	RAI	Activity pattern	Trophic guild
Artiodactyla					
Cervidae					
*Andinocervus rufinus**	Northern Andean Red Brocket / Venado	392	25.64	N-CV	Herbivore
Carnivora					
Canidae					
Cerdocyon thous	Crab-eating Fox / Zorro perro	8	0.52	DD	Omnivore
Felidae					
Leopardus pardalis	Ocelot / Ocelote	4	0.26	DD	Carnivore
Leopardus wiedii	Margay	6	0.39	DD	Carnivore
Herpailurus yagouaroundi	Jaguarundi / Gato pardo	1	0.07	DD	Carnivore
Mephitidae					
Conepatus semistriatus	Striped Hog-nosed Skunk / Mapuro	1	0.07	DD	Omnivore
Mustelidae					
Galictis vittata	Greater Grison / Hurón	4	0.26	DD	Carnivore
Eira barbara	Tayra / Zorro umba	14	0.92	DD	Omnivore
Procyonidae					
Procyon cancrivorus	Crab-eating Raccoon / Zorra patona	29	1.9	N-CV	Omnivore
Cingulata					
Chlamyphoridae					
Cabassous centralis	Northern Naked-tailed Armadillo / Armadillo cola de trapo	22	1.44	N-CV	Insectivore
Dasypodidae					
*Dasypus fenestratus**	Western Andean Long-nosed Armadillo / Armadillo de nueve bandas	27	1.77	N-CV	Omnivore
Didelphimorphia					
Didelphidae					
*Didelphis marsupialis**	Northern Black-eared Opossum / Faro or Fara	239	15.63	N-CV	Omnivore
Metachirus myosuros	Common Brown Four-eyed Opossum / Cuatrojos	25	1.64	N-CV	Omnivore
Pilosa					
Myrmecophagidae					
Tamandua mexicana	Northern Tamandua / Hormiguero	16	1.05	DD	Insectivore
Rodentia					
Cuniculidae					
*Cuniculus paca**	Lowland Paca / Tinajo	163	10.66	N	Frugivore
Dasyproctidae					
*Dasyprocta punctata**	Central American Agouti / Ñeque	160	10.46	D-CM	Frugivore
Sciuridae					
*Syntheosciurus granatensis**	Red-tailed Squirrel / Ardita	43	2.81	D-CM	Frugivore

(08:00–18:00 h), nocturnal (20:00–06:00 h), morning crepuscular (06:00–08:00 h) and evening crepuscular (18:00–20:00 h) (Monroy-Vilchis *et al.* 2011).

Activity overlap. Temporal overlap between species was estimated using the coefficient Δ (delta), a non-parametric measure that quantifies the degree of coincidence between activity patterns, taking values close to 0 when overlap is low and close to 1 when it is high (Ridout and Linkie 2009; Mandujano and Pérez-Solano 2019). This coefficient is derived from the area of intersection between the activity density curves of two species (Schmid and Schmidt 2006). Given the available sample size, the Δ1 estimator was used, as it is recommended for datasets with fewer than 50 records and provides more robust estimates for small sample sizes than Δ4 and Δ5, which require more than 70 records (Mandujano and Pérez-Solano 2019). Overlap analysis was conducted under two comparison criteria: (1) between diurnal wild mammal species and human activity, represented by records of farmers carrying out cacao crop management; and (2) among potentially competing species, belonging to the same taxonomic order and trophic guild. Finally, Δ values were interpreted following

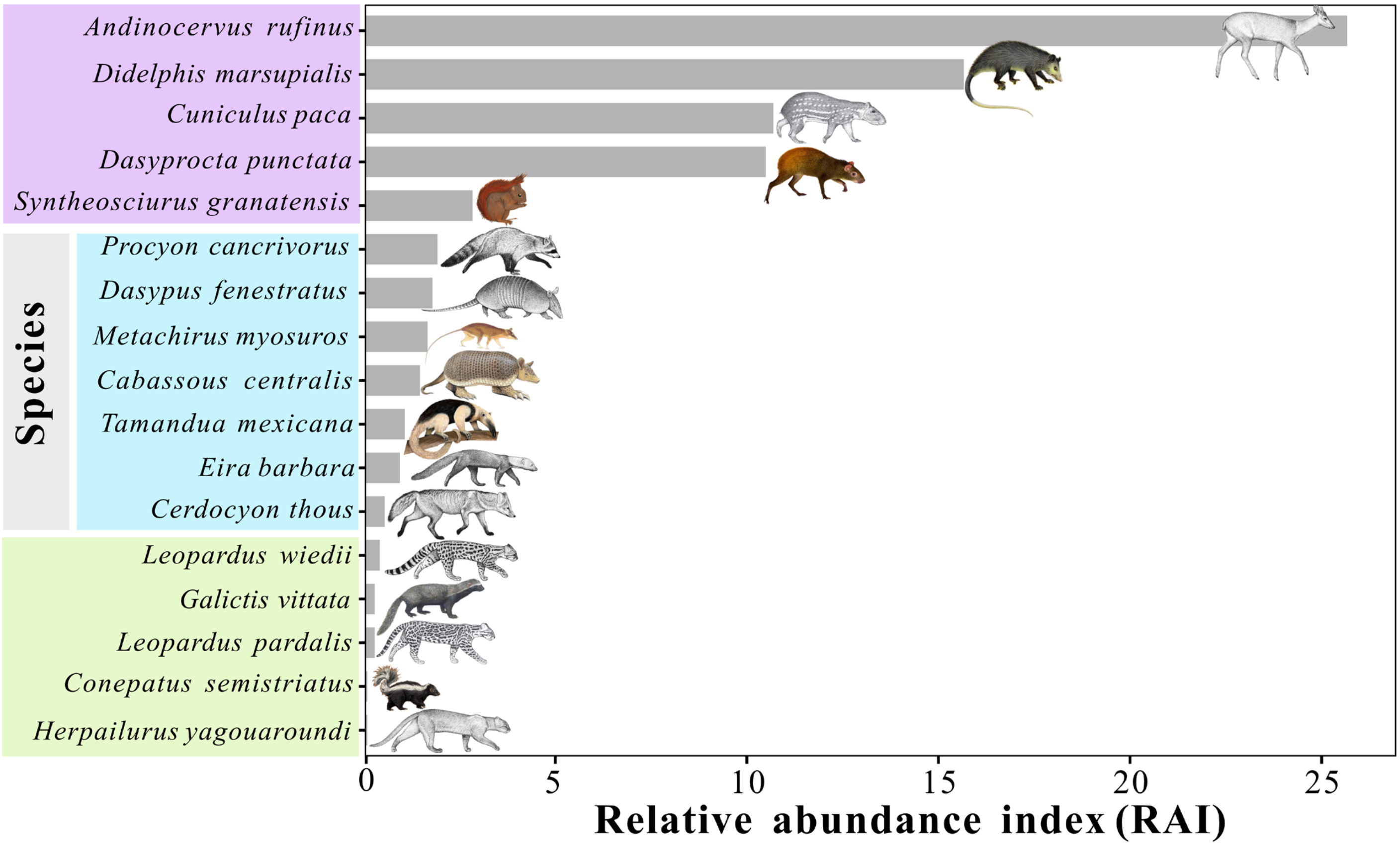

Figure 2. Relative abundance index of the species recorded in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca, Santander, Colombia. Species are grouped according to their relative abundance as high (purple), intermediate (blue), and low (green). Illustrations were obtained from Navarro and Muñoz (2000); Superina and Trujillo (2023) and Navarro *et al.* (2024).

the classification proposed by Monterroso *et al.* (2014), which defines low overlap (Δ ≤ 0.5), moderate overlap (0.5 < Δ ≤ 0.75), and high overlap (Δ > 0.75).

Results

With a sampling effort of 1,529 camera-trap nights, a total of 1,154 independent records of 17 species of medium- and large-sized mammals were obtained, distributed across six orders, 13 families, and 16 genera (Table 1). The most representative order was Carnivora, represented by five families, followed by Rodentia and Cingulata, with three and two families, respectively. Artiodactyla, Didelphimorphia, and Pilosa were each represented by a single family. Among families, Felidae contained the highest number of species (3), followed by Didelphidae and Mustelidae (2 each).

Relative abundance. The species with the highest relative abundance was *A. rufinus* (RAI = 25.64; 392 independent records), clearly exceeding all other species (Table 1; Figure 2). This was followed by *D. marsupialis* (15.63), *C. paca* (10.66), and *D. punctata* (10.46), all showing RAI values considerably higher than the overall average. Species with intermediate RAI values included *S. granatensis* (2.81), *P. cancrivorus* (1.90), *D. fenestratus* (1.77), *M. myosuros* (1.64), and *C. centralis* (1.44) (Table 1; Figure 2). In contrast, the lowest relative abundances corresponded to species with RAI values < 1, including *E. barbara* (0.92), and *C. thous* (0.52) (Table 1; Figure 2). Finally, the lowest number of independent records were observed for *L. wiedii*, *L. pardalis*, and *G. vittata*, whereas *C. semistriatus* and *H. yagouaroundi*, were each represented by a single independent record (Table 1; Figure 2).

Taxonomic diversity. Hill number analyses indicated that estimated richness was equivalent to observed richness (17 species), suggesting that no additional species were

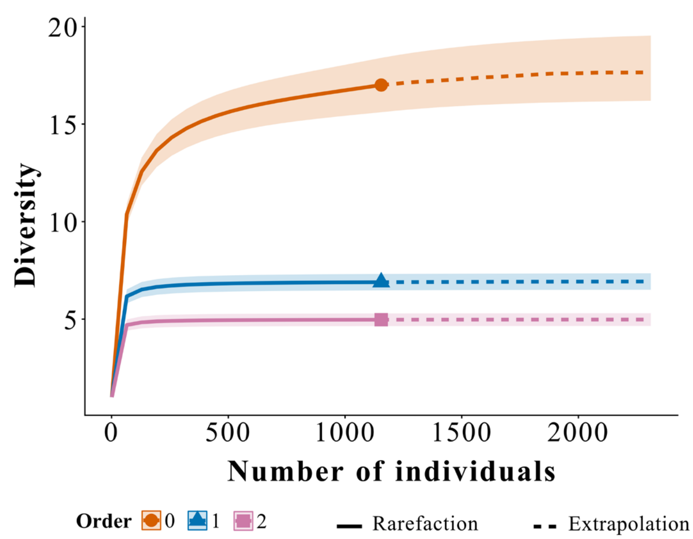

Figure 3. Rarefaction–extrapolation curves based on Hill numbers of orders q^0, q^1, and q^2 in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca, Santander, Colombia. The solid line indicates interpolation, the dashed line indicates extrapolation, and the shaded area represents the 95% confidence interval.

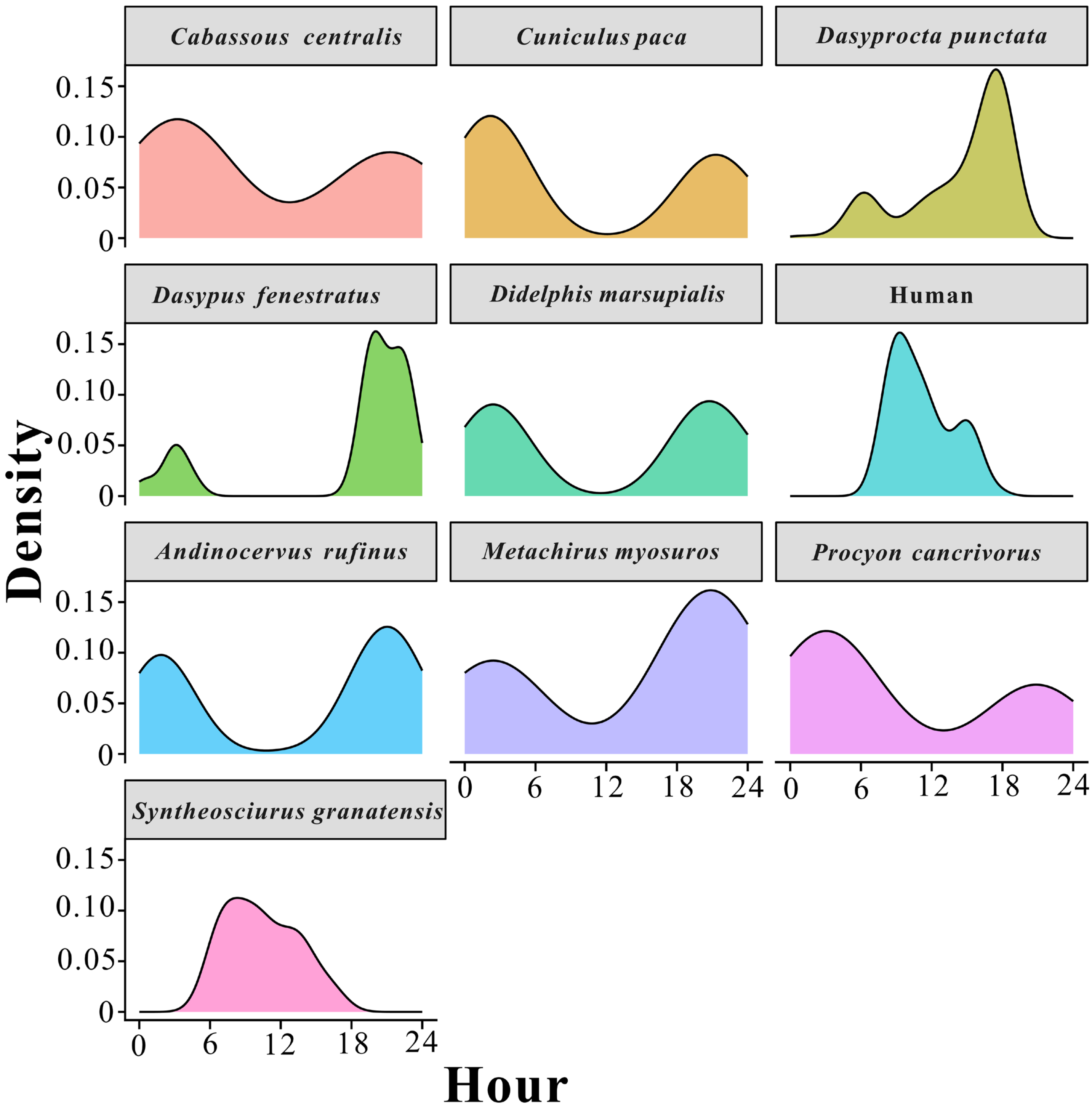

Figure 4. Kernel density of daily activity patterns of nine species of medium- and large-sized mammals recorded in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca, Santander, Colombia (including humans). The x-axis represents a 24-hour period, and the y-axis indicates activity density.

detected beyond those recorded during sampling (Figure 3). Likewise, sample coverage values were high (SC = 0.9983), indicating that the sampled assemblage was nearly completely represented (Figure 3). Although asymptotic estimators showed a slight tendency toward higher values (estimated richness ≈ 18 species), they did not differ significantly from the observed richness (p-value = 0.723). This suggests that sampling reached an asymptote and that the sampling effort was sufficient to characterize the taxonomic diversity of the assemblage (Figure 3).

In terms of diversity in the cacao agroforestry system, 17 species were recorded (q^0; s.e. = 17.99 ± 0.98; 95% CI = 17.00–19.93), of which approximately 7 correspond to common species (q^1; s.e. = 6.95 ± 0.19; 95% CI = 6.47–7.32) and 5 to dominant species (q^2; s.e. = 4.99 ± 0.16; 95% CI = 4.61–5.33). These results indicate that, despite the high species richness, most records were concentrated on a relatively small number of species, reflecting a community with marked dominance and an uneven distribution of abundances (Figure 3).

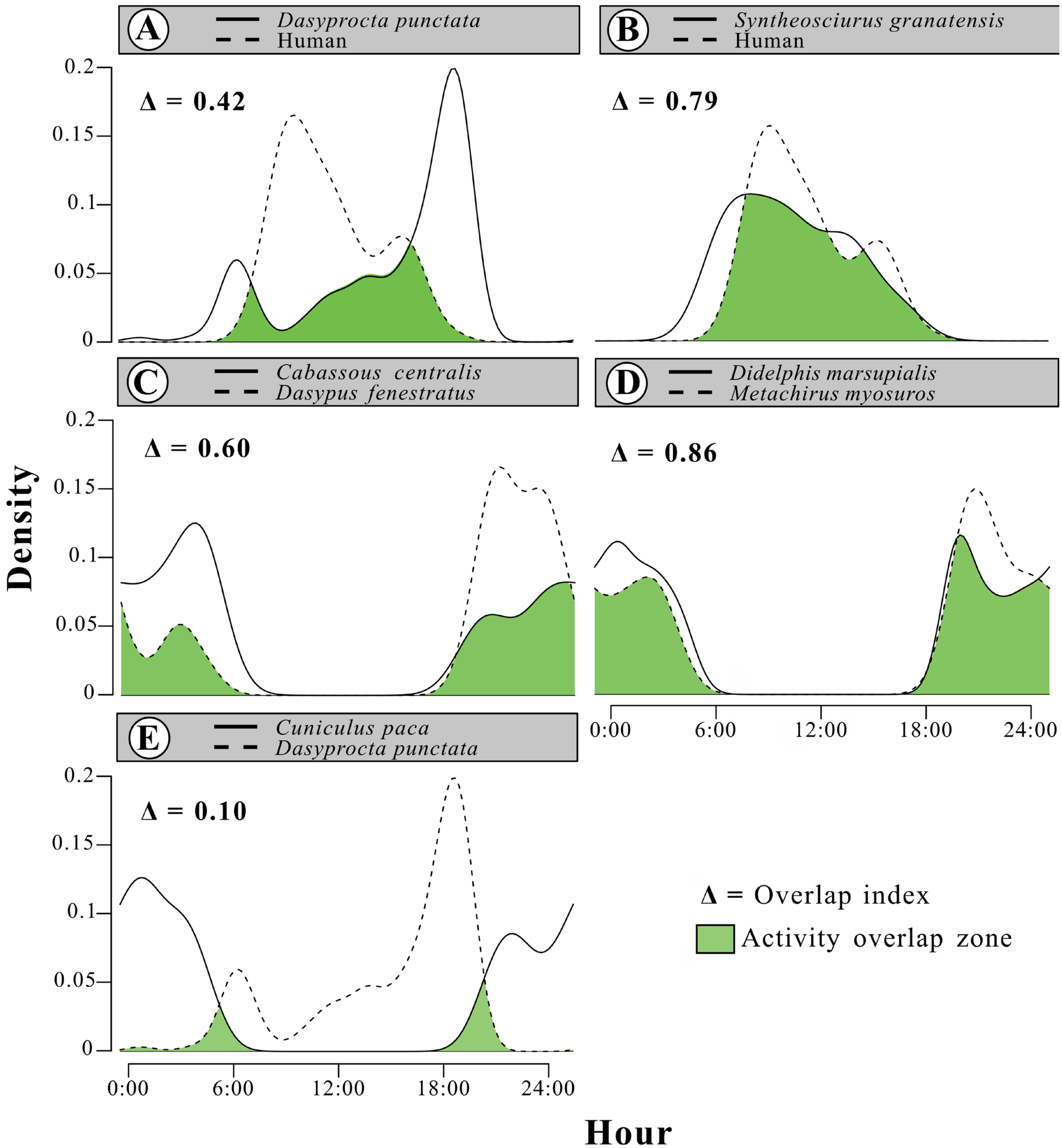

Figure 5. Activity overlap between diurnal species and humans, and among ecologically similar species in San Vicente de Chucurí and Zapatoca, Santander, Colombia. Panels A and B correspond to comparisons based on the wildlife–human activity criterion. Panels C, D, and E correspond to comparisons between ecologically similar species, selected according to taxonomic order and trophic guild.

Activity patterns. Activity patterns were described for nine of the 17 recorded mammal species. The assemblage exhibited predominantly nocturnal–crepuscular activity. Five species showed nocturnal and crepuscular activity, two showed diurnal and crepuscular activity, and two were strictly nocturnal (Table 1; Figure 4). Species with nocturnal and evening crepuscular activity included *D. fenestratus*, which was active from 19:00 to 00:00 h, with activity peaks between 19:00–21:00 h and 22:00–23:00 h; *A. rufinus*, active between 18:00 and 05:00 h, with a peak between 01:00–02:00 h; *M. myosuros*, active from 19:00 to 04:00 h, with greater activity between 19:00–21:00 h; *D. marsupialis*, active from 19:00 to 05:00 h, with peaks between 01:00–03:00 h and 19:00–20:00 h; and *P. cancrivorus*, active from 18:00 to 07:00 h, with higher activity between 01:00–03:00 h and 19:00–21:00 h (Figure 4).

The species with diurnal and evening crepuscular activity was *D. punctata*, whose activity was recorded from 05:00 to 19:00 h, with higher activity between 17:00–19:00 h, whereas *S. granatensis* exhibited diurnal and morning crepuscular activity between 06:00 and 17:00 h, with a peak between 06:00–10:00 h. In contrast, the species with strictly nocturnal activity included *C. centralis*, active from 19:00 to 06:00 h, with a peak between 04:00–05:00 h, and *C. paca*, active between 20:00 and 06:00 h, with greater activity between 01:00–02:00 h. Additionally, human activity was recorded between 07:00 and 18:00 h, with a peak between 08:00–10:00 h (Figure 4).

Activity overlap and comparisons. Temporal overlap was evaluated between human activity and species exhibiting diurnal activity (*D. punctata* and *S. granatensis*; Figure 5). *D. punctata* and humans showed low temporal overlap (Δ = 0.42; Figure 5A), whereas *S. granatensis* and humans showed high temporal overlap (Δ = 0.79; Figure 5B).

Comparisons among species with similar ecological traits revealed different levels of overlap (Figure 5). Among armadillos, *C. centralis* and *D. fenestratus* showed moderate temporal overlap (Δ = 0.60), indicating partial overlap in their activity patterns. In contrast, the opossums *D. marsupialis* and *M. myosuros* exhibited high temporal overlap (Δ = 0.86), suggesting very similar activity patterns. Finally, among large rodents, *C. paca* and *D. punctata* showed low temporal overlap (Δ = 0.10), reflecting marked temporal segregation in their activity (Figure 5E).

Discussion

The richness recorded in cacao agroforestry systems in San Vicente de Chucurí and Zapatoca constitutes an important proportion of the mammals reported for Colombia and the Santander Department (Vélez *et al.* 2018; Ramírez-Chaves *et al.* 2025), including species with different conservation statuses such as *L. wiedii* (NT) and *A. rufinus* (VU), as well as species with limited information such as *C. centralis* (DD) (IUCN 2026). The 17 documented species are consistent with previous studies conducted in cacao agroforestry systems and other transformed landscapes, where similar or higher values have been reported, supporting ecological value of these systems compared to more homogeneous matrices such as oil palm plantations (Pardo-Vargas and Payán-Garrido 2015; Peralta-Zapata *et al.* 2019; López-Ramírez *et al.* 2020). Comparable species richness has also been reported in natural ecosystems (Cáceres-Martínez *et al.* 2016; Hernández-Hernández *et al.* 2018; Mosquera-Guerra *et al.* 2018) suggesting that cacao agroforestry systems may contribute to landscape connectivity and the maintenance of mammal diversity in human-modified landscapes (Ferreira *et al.* 2020; Bedoya-Durán *et al.* 2023).

In studies monitoring medium- and large-sized mammals with high dispersal capacity, methodological aspects such as the independence of records for estimating relative abundance require careful consideration (Tobler *et al.* 2008). This is particularly relevant in local cacao agroforestry systems, where the sampling area is constrained by the size of individual farms and camera traps are typically installed 100–300 m apart (López-Ramírez *et al.* 2020). Under these conditions, standardization criteria based on the temporal separation of records are valuable, whereby records are considered independent after a predefined time interval has elapsed (Tobler *et al.* 2008). An important consideration of these approaches is the difficulty of drawing causal inferences about behavior and intraspecific interactions, focusing instead on describing activity patterns and the degree of temporal overlap among the species studied (Tobler *et al.* 2008).

Species with higher relative abundance, such as *A. rufinus* and *D. marsupialis*, may be favored by resource availability and their capacity to adapt to disturbed environments, allowing them to perform key ecological roles such as seed dispersal and population regulation (Ceballos and Oliva 2005; Franco-Quimbay and Rojas-Robles 2015; Saldaña-Garro *et al.* 2019). Similarly, species such as *C. paca* and *D. punctata* reflect tolerance to disturbance and fulfill important functions in ecosystem dynamics, particularly through herbivory and seed dispersal processes (Wright and Duber 2001; Naughton-Treves *et al.* 2003). In contrast, the low number of records of carnivores such as *H. yagouaroundi*, *L. pardalis*, and *L. wiedii* may be associated with their large home ranges, low population densities, and the limitations inherent to the sampling design; however, their presence supports the availability of prey and the ecological functionality of these agroforestry systems (Dillon and Kelly 2008; Payán-Garrido and Soto-Vargas 2012; Pinilla-Buitrago *et al.* 2015).

Species exhibiting nocturnal and crepuscular activity generally showed patterns consistent with previously reported for these taxa (Blake *et al.* 2012; Mosquera-Guerra *et al.* 2018). However, some differences were observed, as in *A. rufinus*, whose activity has been described as both diurnal and nocturnal (Blake *et al.* 2012), but which in this study showed a predominantly nocturnal pattern. Similarly, the nocturnal–crepuscular activity of *D. marsupialis*, *D. fenestratus*, and *P. cancrivorus was* consistent with previous studies (Lira-Torres and Briones-Salas 2012; Fonseca-Prada *et al.* 2023), whereas the diurnal patterns of *D. punctata* and *S. granatensis* also agreed with reports from other contexts (Cáceres-Martínez *et al.* 2016; Mosquera-Guerra *et al.* 2018; Fonseca-Prada *et al.* 2023). However, *D. punctata* has been reported to exhibit variable activity patterns, ranging from diurnal to crepuscular or nocturnal depending on factors such as resource availability, predation risk, and human activity (Hernández-Pérez *et al.* 2015; Albanesi *et al.* 2016; Encalada 2018).

Overlap with human activity revealed species-specific responses. *S. granatensis* showed high temporal overlap, suggesting greater temporal coincidence with human activity, consistent with reports describing variable behavioral responses to humans (Nitikman 1985) and its frequent occurrence in cultivated areas, where it may directly interact with cacao resources (Monje 2018; Peralta-Zapata *et al.* 2019; López-Ramírez *et al.* 2020). In contrast, *D. punctata* exhibited lower temporal overlap, indicating reduced temporal coincidence with human activity recorded within the cacao agroforestry system (Gálvez *et al.* 2024). This difference may be associated with their contrasting ecological habits: squirrels are arboreal and generally remain above human activity, whereas *D. punctata*, being terrestrial, may be more exposed to human presence and hunting pressure (Torres *et al.* 2018).

Among species with similar ecological characteristics, the degree of overlap varied according to their activity strategies. In armadillos, partial coincidence in activity periods was observed, suggesting a shared use of the temporal niche with some degree of differentiation (Fonseca-Prada *et al.* 2023). In contrast, opossums exhibited highly overlapping activity patterns, indicating greater similarity in their temporal organization (Moreno *et al.* 2025). Likewise, large rodents, showed marked temporal segregation, which may reflect temporal niche partitioning that could reduce competition for resources (Lira-Torres and Briones-Salas 2012).

In summary, these results suggest that cacao agroforestry systems may promote the coexistence of medium- and large-sized mammals with different ecological requirements by providing conditions that facilitate temporal segregation among species, a mechanism that may help reduce the potential for competition (Guiracocha *et al.* 2001; Guzmán *et al.* 2016). Furthermore, the differences observed in the degree of temporal overlap with human activity indicate that some species exhibit greater tolerance to productive environments, whereas others may adjust their activity patterns in response to human presence (Torres *et al.* 2018). In this context, cacao agroforestry systems may play an important role in biodiversity conservation by providing complementary habitats that support the presence of wildlife in transformed landscapes and contribute to landscape connectivity (Guzmán *et al.* 2016).

The conservation value of cacao agroforestry systems may also be influenced by the surrounding landscape configuration. In the municipalities of San Vicente de Chucurí and Zapatoca, cacao plantations are embedded within a heterogeneous matrix composed of forest remnants, riparian vegetation, secondary forests, and other productive systems, which promotes connectivity with less transformed areas (Solarte-Soto *et al.* 2025). This landscape configuration may facilitate the movement of medium and large-sized mammals among habitat fragments, allowing cacao agroforestry systems to function as complementary habitats for foraging, shelter, and movement rather than as isolated environments (López-Ramírez *et al.* 2020). The presence of species with large home ranges and those sensitive to habitat transformation suggests that these systems maintain a certain degree of connectivity for wildlife (Higuera-Mora *et al.* 2026). The contribution of cacao agroforestry systems to mammal conservation depends not only on their structural complexity but also on the quantity, quality, and connectivity of the surrounding natural vegetation, factors that help mitigate the effects of habitat fragmentation and promote biodiversity persistence in productive landscapes (Higuera-Mora *et al.* 2026)

Conclusions

Cacao agroforestry systems in the municipalities of San Vicente de Chucurí and Zapatoca, Santander, northeastern Colombia, harbor a diversity of 17 species of medium- and large-sized mammals, with a marked number of common and dominant species within the assemblage. Activity patterns showed a predominance of nocturnal and crepuscular habits, with five nocturnal–crepuscular species (*A. rufinus*, *D. fenestratus*, *D. marsupialis*, *M. myosuros*, *P. cancrivorus*), two strictly nocturnal species (*C. centralis*, *C. paca*), and two diurnal–crepuscular species (*D. punctata*, *S. granatensis*), in addition to human activity concentrated during morning hours. Activity pattern analyses revealed different levels of temporal overlap, reflecting reduced temporal coincidence of *D. punctata* and greater temporal coincidence of *S. granatensis* with human presence. Based on taxonomic group and trophic guild, greater overlap was observed among ecologically similar species such as *D. marsupialis*–*M. myosuros*, and stronger temporal segregation among species with different strategies such as *C. centralis*–*D. fenestratus* and *C. paca*–*D. punctata*. These results indicate that the variety of resources provided by cacao agroforestry systems, such as water, food, and shelter, can be utilized by a community of medium- and large-sized terrestrial mammals, highlighting their potential contribution to biodiversity conservation and landscape connectivity in productive landscapes.

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Declaration of artificial intelligence use

During the preparation of this manuscript, the authors used GPT-5.3 to improve grammar and obtain a preliminary translation of the text. This tool was not used for the creation of figures or tables, data generation, statistical analysis, or the scientific interpretation of the results. The authors critically reviewed and edited all AI-assisted content and hold full responsibility for the originality, integrity, and conclusions presented in this work.

Author contributions

Sergio A. García-Mieles and Giovany Díaz-Peñaloza conceived and designed the study. Both authors conducted fieldwork, collected and curated the data, performed data processing and analyses, interpreted the results, and prepared figures and tables. Sergio A. García-Mieles and Giovany Díaz-Peñaloza also wrote the first draft of the manuscript, critically revised subsequent versions, and approved the final version for publication. Carlos H. Cáceres-Martínez and Diana V. Caballero-Aldana contributed logistical support, institutional agreements, and financial resources that enabled the execution of field activities and data collection in the study localities. They also reviewed the manuscript and approved its final version.

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