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DIVERSITY OF BATS (CHIROPTERA) IN VARIOUS HABITATS IN BUALEMO SUB-DISTRICT, CENTRAL SULAWESI, INDONESIA

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ABSTRACT

Bats play an important role in ecosystems as pollinators, seed dispersers, and insect pest controllers. Indonesia has the highest bat diversity in Southeast Asia, with Sulawesi as a global endemicity hotspot. However, data from Central Sulawesi remain limited, particularly amid threats of habitat degradation and hunting toward bats. This study aims to assess the diversity and habitat preferences of Yangochiroptera and Yinpterochiroptera in Bualemo sub-district, Central Sulawesi. Data were collected for 31 nights in June and July 2024 using mist nets and harp traps across plantations near cave, plantations, secondary forests, and rivers. A total of 474 individuals from 5 families and 23 species were identified. Yangochiroptera consisted of 113 individuals from 4 families and 13 species. Meanwhile, Yinpterochiroptera consisted of 361 individuals from one family and 10 species, with *Cynopterus luzoniensis* and *Rousettus amplexicaudatus* as the most frequently found species. The Shannon-Wiener diversity index (H' = 1.534-2.210), indicating moderate diversity, while the evenness index (E = 0.489-0.705), suggesting more balanced distribution in vegetated habitats. Yinpterochiroptera were mainly found in plantations rich in food sources, such as *Ficus* trees, while *Dobsonia exoleta* and *Harpyionycteris celebensis* were restricted to secondary forests. Yangochiroptera displayed distinct habitat preferences. *Rhinolophus* sp.a dominated plantations near cave, whereas *Rhinolophus* sp.b occurred only in secondary forests. These preferences were influenced by food availability, vegetation structure, and environmental conditions such as rainfall and moon phase. These findings emphasize the importance of conserving various habitat types to maintain the diversity and stability of bat populations, while raising public awareness of their ecological role.

Key words: bat diversity, conservation, habitat preference, Sulawesi

INTRODUCTION

Bats (order Chiroptera) are flying mammals comprising 1,500 species globally (Simmons & Cirranello, 2025). Their order name derived from the Greek words *cheir* (hand) and *pteron* (wing), referring to their distinctive wing structure (Simmons, 2005; Fenton & Simmons, 2015). Order *Chiroptera* is currently divided into two suborders: *Yinpterochiroptera* and *Yangochiroptera* based on molecular and genetic evidence (Teeling et al., 2005; Franz-Odendaal, 2013).

Indonesia has the highest bat diversity in Southeast Asia, with 239 identified species. Of these, 158 species are insectivorous bats and 81 species are phytophagous bats (Maryanto et al., 2019). Yangochiroptera are further divided based on the maxillary bone of the upper jaw (premaxilla) which functions for echolocation. Yinochiroptera have movable or absent premaxillaries, while Yangochiroptera have fused premaxillaries (Jones & Teeling, 2006; Anderson et al., 2020). Globally, Southeast Asia contains approximately 320 species of bats, representing nearly 30 percent of the world's total bat species (Simmons, 2005; Kingston, 2008). Sulawesi, as part of the Wallacea biogeographic zone, has a high level of endemicity, particularly for mammals, including bats (Whitten et al., 2002; Wirdhana et al., 2023). Of the 207 mammal species recorded in Sulawesi, 43% are endemic, including bats (Musser, 1987). A total of 72 bat species has been recorded in Sulawesi, of which 18 species are considered endemic (Bergmans & Rozendaal, 1988; Suyanto, 2001; Simmons, 2005). Recent pollination studies have demonstrated that bats are effective pollinators of durian (*Durio zibethinus*), contributing measurable livelihood benefits to local communities in Sulawesi (Sheherazade et al., 2019).

Among the phytophagous bats, ten species are confirmed as endemic to Sulawesi based on the recent *Checklist of the Mammals of Indonesia* (Maryanto et al., 2019): *Acerodon celebensis*, *Dobsonia exoleta*, *Thoopterus suhaniahae, Thoopterus nigrescens, Harpyionycteris celebensis*, *Styloctenium wallacei*, *Rousettus linduensis*, *Rousettus tangkokoensis*, *Boneia bidens*, and *Chironax tumulus*. These taxa are of particular conservation interest due to their restricted distribution. Sulawesi also hosts several endemic insectivorous bats, they are *Hipposideros boeadii, Hipposideros inexpectatus*, and *Rhinolophus tatar*, each exhibiting highly restricted geographic ranges confined to the island. Collectively, these species demonstrate the high chiropteran endemism of Sulawesi and highlight the importance of continued research and conservation in the region.

Bats provide critical ecosystem services across tropical landscapes, reinforcing the conservation importance of Sulawesi's distinctive Chiropteran fauna. Insectivorous bats serve as natural pest control agents that can reduce agricultural insect populations and reduce the use of chemical pesticides (Williams-Guillén et al., 2008; Puig-Montserrat et al., 2015). Meanwhile, phytophagous bats act as pollinators and seed dispersers for around 300 tropical plants, including high economic value plants such as durian (*Durio zibethinus*), aren (*Arenga* sp.), petai (*Parkia speciosa*), and coconut (*Cocos nucifera*) (Suyanto, 2003; Sheherazade et al., 2019). It is estimated that about 95% of forest regeneration in the tropics depends on phytophagous bats (Satyadharma, 2007), with higher seed germination rates than natural dispersal (Quesada et al., 2004). In Thailand, for example, *Mops plicatus* can prevent rice yield losses of up to 2,900 tonnes per year, with an economic value of more than USD 1.2 million (Wanger et al., 2014). These services have both ecological and local economic value in Indonesia and throughout Southeast Asia. Despite their ecological importance, bat assemblages of Sulawesi remain incompletely understood. A few studies on bat diversity in Sulawesi have documented new species and updated species distributions. Maryanto et al. (2019) recorded 16 species of phytophagous bats in Lore Lindu National Park and described a new species, *Rousettus linduensis*. In the same study, *Thoopterus suhaniahae* was also described as a new species from the same region. Donnelly et al., (2020) reported *Hipposideros galeritus* as a new species records for Sulawesi from Buton Island, providing important insights into the biogeography of Sulawesi bats. In the lowlands of Southeast Sulawesi, Wiantoro et al. (2016) recorded 22 bat species, representing nearly one-third of all bat species known from Sulawesi, indicating a high level of local diversity. Their study also highlighted several unresolved taxonomic issues, particularly among morphologically similar and poorly known taxa. Notably, *Myotis* cf. *ridleyi* was reported as a new distributional record for Sulawesi and was suggested to potentially represent an undescribed species pending further investigation, while morphological variation in *Chironax melanocephalus tumulus* raised questions regarding its subspecific or species-level status.

Bats diversity and their distribution in Central Sulawesi remain poorly studied. Bualemo sub-district, Banggai district, has diverse ecosystems, including plantations near cave, secondary forests, plantations, and riverine ecosystems, which hypothetically support high bat diversity. The abundance of fruit trees and roosting sites make this area a potential habitat for phytophagous and insectivorous bats, yet baseline data are lacking. Here, we investigate bat species diversity and their habitat associations in Bualemo sub-district, Central Sulawesi, to provide essential baseline data that will support future research and conservation planning for Sulawesi's Chiropteran fauna.

MATERIALS AND METHODS

This study was conducted in Bualemo Sub-district, Banggai District, Central Sulawesi, Indonesia, from June to July 2024 (Fig. 1). Bualemo sub-district is located in the eastern part of Central Sulawesi province, with diverse ecosystems including plantations near cave, secondary forests, plantations, and riverine areas.

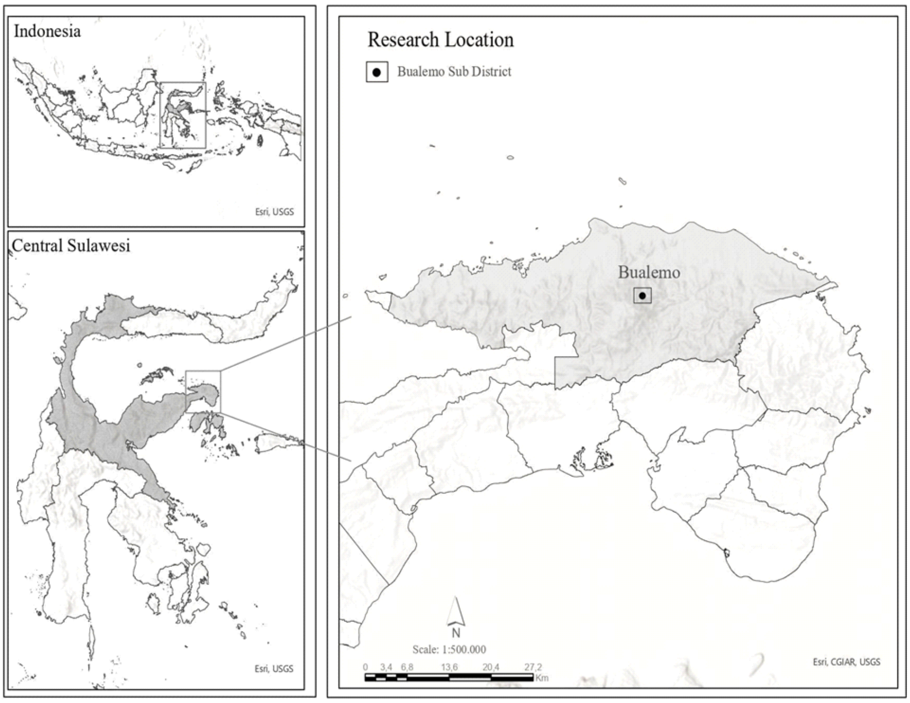


Figure 1. The map shows the research location in Bualemo sub-district.

Sampling was conducted at five sites representing a variety of habitat types, including natural habitats (secondary forest and riverine areas) and artificial or human-modified habitats (plantations and agricultural areas) (Table 1). The study sites were located in human-modified landscapes dominated by polyculture plantations rather than monocultures. Vegetation surrounding the sites consisted of mixed tree crops such as coconut (*Cocos nucifera*), clove (*Syzygium aromaticum*), jackfruit (*Artocarpus heterophyllus*), sugar palm (*Arenga pinnata*), fig trees (*Ficus* spp.), citrus (*Citrus* spp.), bamboo, and various shrubs, including *Lantana camara*. These mixed-vegetation systems form a heterogeneous habitat structure typical of smallholder-managed landscapes.

Bat Sampling

Mist Netting

Bat sampling was conducted using a total of five mist nets deployed each night at each study site: two measuring 2.6 × 6 m, one measuring 2.6 × 9 m, and two measuring 2.6 × 12 m. All standard mist nets were made of 75 denier/2 ply material with a mesh size of 38 mm and consisted of four shelves. In addition, several Ultra Thin Series mist nets (Ecotone and Avinet) were used, with mesh sizes of 20 mm and 38 mm. The nets were installed at heights of 2–3 meters above ground level using 5-meter extension poles of Krisbow and positioned along presumed bat flyway, including near fruiting and flowering trees, beneath the tree canopy, and over river corridors.

Table 1. Description of sampling sites in Bualemo Subdistrict, Banggai District, Central Sulawesi

No	Habitat Types	Elevation	Description
1	Plantations near cave	13 m asl	The plantations near cave area are surrounded by polyculture plantations, which provide natural roosting sites and food sources from the surrounding vegetation. The dominant vegetation includes coconut trees, bamboo, johar (*Senna siamea*), and shrubs.
2	Plantation near river	6 m asl	The plantation is located adjacent to a river and is characterized by a polyculture plantation system. The surrounding vegetation consists of coconut trees, jackfruit (*Artocarpus heterophyllus*), fig trees (*Ficus* spp.), bamboo, and shrubs. This mixed vegetation provides diverse food resources for bats, particularly insects and fruits.
3	Mixed plantation	7 m asl	Plantation is a polyculture plantation, characterized by mixed vegetation including coconut, sugar palm (*Arenga pinnata*), bamboo, petai (*Parkia speciosa*), and shrubs such as *Lantana camara*.
4	Riverine plantation	22 m asl	The riverine plantation is characterized as a riverine polyculture system located along a river. The area is densely vegetated with coconut, kapuk, citrus (*Citrus* spp.), fig trees (*Ficus* spp.), bamboo, and shrubs. This riparian vegetation functions as an important flyway for bats moving between roosting and feeding areas.
5	Secondary forest	158 m asl	Secondary forest with a river; offers dense and diverse vegetation as a suitable habitat for various bat species, providing shelter and abundant food resources.

Nets were checked every 20 minutes from 6:00 pm to 11:00 pm (Central Indonesia Time, CIT), for a total of 5 hours each evening, starting shortly after sunset to ensure capture efficiency and minimize stress on the bats. Captured individuals were placed in bat holding bag for subsequent identification.

Harp Trapping

Five four-bank harp traps were used to capture insectivorous bats. Each harp trap consisted of an aluminium frame fitted with four banks of nylon (damyl) strings with a tensile strength of 20 lbs, forming the capture lines that guided bats into a collecting bag at the base of the trap. Harp traps were placed along understory flyways and other presumed bat flight paths, including plantations near cave entrances, narrow alleys, and over river surfaces, where insectivorous bats are commonly active. To minimize trap avoidance by echolocating bats, harp trap locations were changed daily throughout the study period. Traps were deployed before sunset and inspected regularly from 6:00 pm to 6:00 am (Central Indonesia Time, CIT). They were checked every 30 to 60 minutes until midnight to minimize mortality or escape, and were left in place until morning at 6:00 am. All captured bats were placed in bat holding bags for subsequent identification.

Bats Identification

Bat identification was conducted based on morphological characteristics following standard references, including Suyanto (2001), Prasetyo et al. (2011), Huang et al. (2016), Patterson et al. (2017), Maryanto et al. (2019), and Donnelly et al. (2020). Each bat was identified to the species level using external morphological measurements, and information on sex, age class, and reproductive status was also recorded. External morphology measurements, as part of the identification process, were taken using a stainless digital caliper (precision in millimeters) following standard protocols described by Wiantoro et al. (2015, 2016). The measured parameters included forearm length (FA), from the outer side of the elbow to the outer side of the wrist along the curved wing; head and body length (HB), from the tip of the snout to the anus; thumb length (TH); ear length (E), from the outer exposed base to the tip of the ear; tibia length (TIB), from the knee to the ankle; and hindfoot length (HF), from the heel to the tip of the longest toe, excluding the claw. Additionally, body mass (BM) was measured in grams (g) using a 100 g PESOLA scale (PESOLA).

Sex, Age Categories and Reproduction Status

Male and female bats were differentiated by observing their external reproductive organs, with the presence of the penis and testes in males, and the vagina and mammary glands in females (Racey, 1988). Age categories were divided into infant, juvenile, subadult, and adult. Infants were identified based on external developmental characteristics, such as very small body size, incomplete fur development, and dependence on the mother (Brunet-Rossini & Wilkinson, 2009; Oliveira, 2020). Juveniles and subadults were distinguished by examining the degree of epiphyseal–diaphyseal fusion in the forearm. Juveniles exhibited an unfused or partially fused epiphyseal gap with paler, more translucent cartilaginous joints when backlit, whereas subadults showed an epiphyseal gap that was nearly fused and firmer forearm bones, but not yet as robust as adults. Adults were identified by complete epiphyseal–diaphyseal fusion in the forearm, with fully ossified joints and a robust forearm structure, indicating skeletal maturity (Racey, 1988; Suyanto, 2001; Dietz & von Helversen, 2004). Female conditions were divided into four categories, (1) reproductive (R) referring to females in adult age that were sexually mature and showed signs of active reproduction, but were neither pregnant nor lactating, (2) nulliparous (NR) was a female individual that had not yet shown evidence of reproductive activity, (3) pregnant (P) indicated female individuals exhibiting clear signs of pregnancy, (4) lactating (L) were lactating females, indicated by the presence of nursing young or milk secretion from the mammary gland. Pregnancy in females could be observed with full and enlarged size in abdomen. Lactating females could be observed by enlarged nipples, which when gently massaged, would produce milk. The reproductive condition of male bats was assessed by examining the position and size of the testes. Males with descended and enlarged testes were considered reproductively active, whereas males with abdominal or small testes were considered non-reproductive, following standard field guidelines (Racey, 1988).

Environmental factor

Environmental factors such as rainfall, moon phase and vegetation structure were recorded across five study sites, as these variables are known to influence bat activity and capture success. Weather conditions, especially heavy rainfall and strong winds, often reduced bat flight activity and significantly lowered the number of individuals captured in mist nets and harp traps. Bats generally avoid foraging during poor weather due to increased energetic costs and reduced prey availability. Moon phase also played a critical role in bat behaviour. Bats were more frequently captured during darker lunar phases such as the new moon, and were less active during full moon nights, likely due to a behavioural response aimed at avoiding predation under brighter conditions. Moon phase data for each sampling night were obtained from the website www.moonphasesconnection.com.

Detailed descriptions of the vegetation and habitat characteristics were recorded at each trap location. Mist nets and harp traps were placed strategically along natural bat flyways such as forest trails, river margins and canopy openings, where bat movement was concentrated. The type of surrounding habitat, including primary forest, secondary regrowth, agroforest and open farmland, was recorded together with structural attributes like canopy closure and understorey density. Sites with close proximity to water sources and diverse vegetation tended to yield a greater number of species. These environmental data provided essential context for interpreting bat diversity and patterns of occurrence across the Bualemo landscape.

Data Analysis

Species diversity was analysed using the Shannon–Wiener diversity index (H') and evenness index (E), which provide insight into both species richness and relative abundance within a community (Magurran, 2004). Habitat preference was determined based on the frequency of species occurrence across five habitat types, assuming that higher occurrence indicates greater habitat association (Krebs, 1999).

Species accumulation curves were generated using EstimateS software to evaluate sampling adequacy and to examine the relationship between sampling effort and observed species richness. The cumulative number of species detected (Sobs mean) and 95% confidence intervals were plotted against sampling effort to assess whether the sampling effort was sufficient to represent the bat community (Colwell, 2013). To understand more complex species relative abundance patterns, a Principal Component Analysis (PCA) was performed. This is a statistical technique that reduces the dimensionality of multivariate data by identifying combinations of variables that explain the greatest variance (Jolliffe, 2016). The PCA helped to identify the relationships between bat species and environmental factors, and to visualize community patterns more clearly. Thus, the use of PAST in this research allowed for a comprehensive analysis of bat species diversity, habitat preferences, and relative abundance patterns in Bualemo District.

RESULTS

Bat Composition and Relative Abundance

A total of 474 individuals representing 23 bat species from 5 families were recorded across all sampling sites in Bualemo Sub-district (Table 2). The composition of bats species captured for 31 nights included *Rhinolophus* sp.a (63 individuals; 13.29%), *Rhinolophus celebensis* (9 individuals; 1.89%), *Rhinolophus* sp.b (1 individual; 0.21%), *Rhinolophus euryotis* (5 individuals; 1.05%), *Miniopterus* sp. (7 individuals; 1.47%), *Kerivoula papillosa* (2 individuals; 0.42%), *Kerivoula hardwickii* (2 individuals; 0.42%), *Alionoctula* sp. a (1 individual; 0.21%), *Alionoctula* sp. b (2 individuals; 0.42%), *Myotis* sp. (1 individual; 0.21%), *Megaderma spasma* (14 individuals; 2.95%), *Hipposideros galeritus* (1 individual; 0.21%), *Hipposideros diadema* (3 individuals; 0.63%), *Cynopterus luzoniensis* (39 individuals; 8.22%), *Cynopterus minutus* (115 individuals; 24.26%), *Dobsonia crenulata* (1 individual; 0.21%), *Dobsonia exoleta* (1 individual; 0.21%), *Harpyionycteris celebensis* (7 individuals; 1.47%), *Macroglossus minimus* (30 individuals; 6.32%), *Nyctimene cephalotes* (16 individuals; 3.37%), *Pilonycteris celebensis* (93 individuals; 19.62%), *Rousettus amplexicaudatus* (55 individuals; 11.60%), and *Thoopterus nigrescens* (4 individuals; 0.84%) (Table 2; Fig. 2; Fig. 3).

The assemblage comprised both insectivorous and phytophagous species, reflecting the ecological diversity of habitats surveyed. Distinctive characteristics were observed in the unidentified bat species. *Rhinolophus* sp.a exhibited a complex nose-leaf with the anterior leaf pointing upward, a triangular posterior part with pointed edges, and parallel lancet and sella slightly narrowing; fur was dark brown with a lighter ventral side, and ears were large, oval, and notched with an antitragus. *Miniopterus* sp. had a slender body with short, inconspicuous ears, a simple nose, and fur ranging from light greyish-brown to dark brown. *Alionoctula* sp. a displayed large oval ears with a rounded, relatively long tragus, a short snout, and fur varying from light brown to dark brown or yellowish. *Alionoctula* sp. b showed small oval ears with long, rounded tragus, dark brown fur, and blackish wing membranes attached at the base of the toes. *Myotis* sp. was characterized by long ears, a wide prominent snout, reddish-brown to greyish fur, and blackish wing membranes attached at the base of the toes.

Several individuals could not be identified to the species level due to limitations in the identification process. Specifically, these individuals exhibit strong morphological similarities and overlapping diagnostic characters with closely related species, particularly within the families Rhinolophidae and Vespertilionidae, making reliable identification based on morphology alone difficult. These species are not considered new species and were conservatively classified only at the genus level to minimize the risk of misidentification in the absence of molecular confirmation. The percentage represents the relative abundance of each species, calculated as the number of individuals per species divided by the total number of captured individuals and multiplied by 100.

Figure 2. Phytophagous bats and insectivorous bats species found in Bualemo: a) *Nyctimene cephalotes,* b) *Harpyionycteris celebensis*, c) *Dobsonia exoleta*, d) *Rhinolophus euryotis*, e) *Rhinolophus celebensis,* f) *Alionoctula* sp.b.

Table 2. List of insectivorous and phytophagous bat species found in Bualemo sub-district

Sub Order	Family	*Genus*	*Species*	Total Individuals
Yangochiroptera	Rhinolophidae	*Rhinolophus*	*Rhinolophus* sp.a	63
			Rhinolophus celebensi	9
			Rhinolophus sp.	1
			Rhinolophus euryotis	5
	Vespertilionidae	*Miniopterus*	*Miniopterus* sp.	7
		Kerivoula	*Kerivoula papillosa*	2
			Kerivoula hardwickii	2
		Alionoctula	*Alionoctula* sp. a	1
			Alionoctula sp. b	4
		Myotis	*Myotis* sp.	1
	Megadermatidae	*Megaderma*	*Megaderma spasma*	14
	Hipposideridae	*Hipposideros*	*Hipposideros galeritus*	1
			Hipposideros diadema	3
Yinpterochiroptera	Pteropodidae	*Cynopterus*	*Cynopterus luzoniensis*	39
			Cynopterus minutus	115
		Dobsonia	*Dobsonia crenulata*	1
			Dobsonia exoleta	1
		Harpyionycteris	*Harpyionycteris celebensis*	7
		Macroglossus	*Macroglossus minimus*	30
		Nyctimene	*Nyctimene cephalotes*	16
		Pilonycteris	*Pilonycteris celebensis*	93
		Rousettus	*Rousettus amplexicaudatus*	55
		Thoopterus	*Thoopterus nigrescens*	4

Species Accumulation Curve

The species accumulation curve shows a rapid increase in observed species richness (Sobs Mean) at low levels of sampling effort, indicating that a large proportion of the common bat species was detected during the initial sampling nights. As sampling effort increased, the rate of species accumulation gradually decreased and the curve began to level off. This pattern suggests that additional sampling contributed fewer new species, indicating diminishing returns with increased effort. The tendency toward an asymptote implies that the sampling effort was sufficient to capture most of the detectable species present in the study area, particularly the common and moderately abundant species.

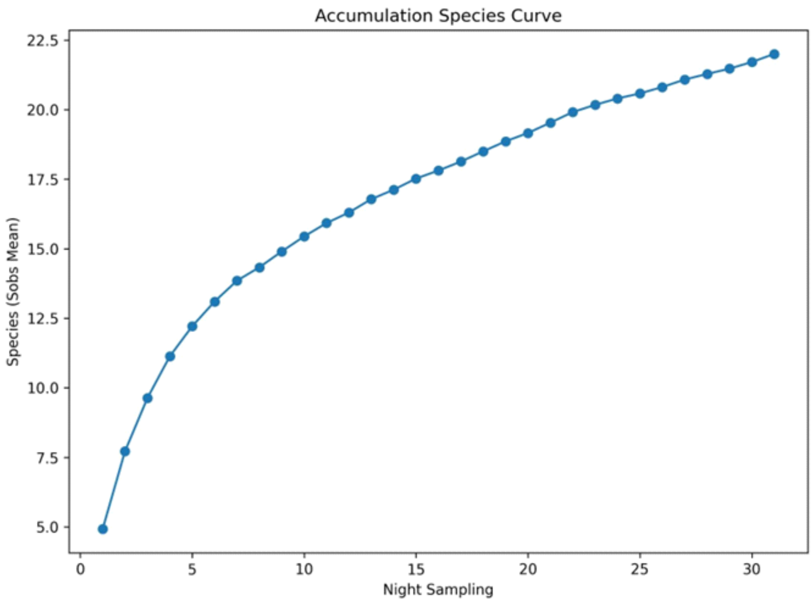


Figure 3. Species accumulation curve showing the relationship between sampling effort and observed species richness (Sobs Mean).

Bats Diversity and Evenness Index

The Shannon–Wiener diversity index (H') ranged from 1.534 at riverine plantation (22 m asl) to 2.210 at secondary forest with river (158 m asl), indicating a moderate diversity level across sites (Table 3). The highest diversity at secondary forest with river indicated the influence of dense and heterogeneous vegetation in supporting a wide variety of bat species, while the lowest diversity at riverine plantation suggested limited habitat complexity and dominance by a few adaptable species. The Evenness index (E) ranged from 0.489 (riverine plantation) to 0.705 (secondary forest), where higher values indicated a more balanced distribution of individuals among species, and lower values showed that certain species dominate the community. These variations in diversity and evenness were closely linked to habitat structure, vegetation complexity, and resource availability, with more complex habitats supporting greater species richness and more even communities.

1. Habitat Preferences

Bat species data were first grouped for Principal Component Analysis (PCA). In this step, each species was assigned an abbreviation for use in the PCA ordination (Table 4), including *Rhinolophus* sp.a (Rsa), *Rhinolophus celebensis* (Rc), *Rhinolophus* b. (Rsb), *R. euryotis* (Re), *Miniopterus* sp. (Ms), *Kerivoula papillosa* (Kp), *K. hardwickii* (Kh), *Alionoctula* sp. a (Asa), *Alionoctula* sp. b (Asb), *Myotis* sp. (My), *Megaderma spasma* (Msp), *Hipposideros galeritus* (Hg), *H. diadema* (Hd), *Cynopterus luzoniensis* (Cl), *C. minutus* (Cm), *Dobsonia crenulata* (Dc), *D. exoleta* (De), *Harpyionycteris celebensis* (Hc), *Macroglossus minimus* (Mm), *Nyctimene cephalotes* (Nc), *Pilenycteris celebensis* (Pc), *Rousettus amplexicaudatus* (Ram), and *Thoopterus nigrescens* (Tn). PCA was used to visualize the correlation between bat species and habitat types. The PCA results showed that the first three principal components (PC1, PC2, and PC3) explained 99.73% of the total variance, with PC1 accounting for 80.44%, PC2 for 16.51%, and PC3 for 2.77% of the variance, indicating strong correlations between bat species and habitat types (Fig. 4).

This step provided abbreviations for each species that were used in the PCA ordination. PCA helped to visualize the correlation between bat species and habitat types. The PCA analysis revealed a clear separation in bat species composition among habitat types. Result of PCA revealed that PC1, PC, and PC3 for 99,73% of the total variance, accounted for 80,44%, (PC1), 16,51% (PC2), and 2,77% (PC3), explaining the correlation between at species and habitats (Fig. 4).

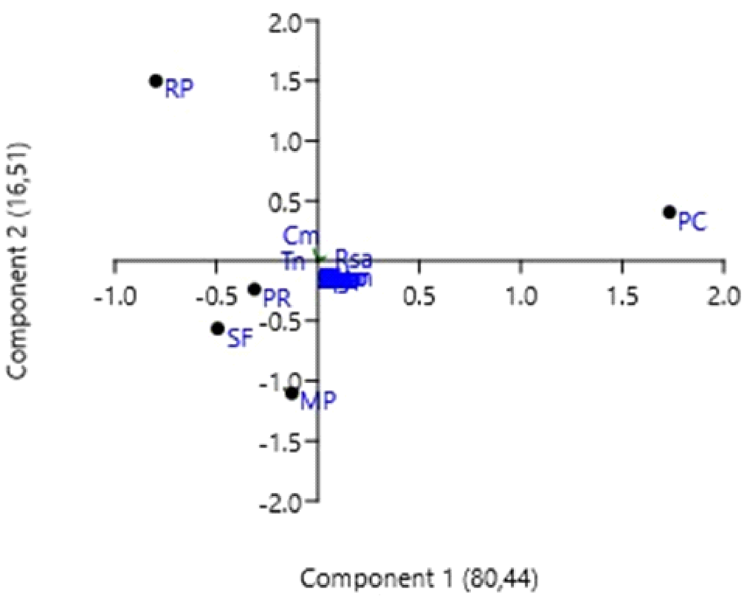
Table 3. List of insectivorous and phytophagous bat species found in Bualemo sub-district

Species	Number of Individuals				
	PC 12 m asl	**PR 6 m asl**	**MP 7 m asl**	**RP 22 m asl**	**SF 158 m asl**
Miniopterus sp.	0	0	0	0	7
Kerivoula papillosa	0	0	0	1	1
Kerivoula hardwickii	0	1	0	0	1
Alionoctula sp. a	0	0	0	0	1
Alionoctula sp. b	0	0	0	0	4
Myotis sp.	0	1	0	0	0
Megaderma spasma	14	0	0	0	0
Hipposideros galeritus	0	0	0	0	1
Hipposideros diadema	0	0	1	1	1
Cynopterus luzoniensis	5	8	4	14	8
Cynopterus minutus	2	24	9	56	24
Dobsonia crenulata	1	0	0	0	0
Dobsonia exoleta	0	0	0	0	1
Harpyionycteris celebensis	0	0	0	0	7
Macroglossus minimus	7	8	5	9	1
Nyctimene cephalotes	1	6	5	4	0
Pilonycteris celebensis	33	15	17	19	9
Rousettus amplexicaudatus	43	4	7	1	0
Thoopterus nigrescens	0	0	0	2	2
Number of individuals	**170**	**71**	**49**	**110**	**74**
Number of species	**10**	**9**	**8**	**10**	**16**
Shannon-Wiener Index (H')	**1.704**	**1.840**	**1.785**	**1.534**	**2.210**
Evenness Index (E)	**0.543**	**0.586**	**0.569**	**0.489**	**0.705**

Abbreviations of habitat: PC = Plantations near cave; PR = Plantation near rivers; MP = Mixed plantation; RP = Riverine plantation; SF = Secondary forest with river.

Table 4. List of bat species abbreviations used in the PCA analysis.

Abbreviation	Full species name	PC	PR	MP	RP	SF
Rsa	*Rhinolophus* sp.a	58	4	1	0	0
Rc	*Rhinolophus celebensis*	6	0	0	3	0
Rsb	*Rhinolophus* sp.b	0	0	0	0	1
Re	*Rhinolophus euryotis*	0	0	0	0	5
Ms	*Miniopterus* sp.	0	0	0	0	7
Kp	*Kerivoula papillosa*	0	0	0	1	1
Kh	*Kerivoula hardwickii*	0	1	0	0	1
Asa	*Alionoctula* sp. a	0	0	0	0	1
Asb	*Alionoctula* sp. b	0	0	0	0	4
My	*Myotis* sp.	0	1	0	0	0
Msp	*Megaderma spasma*	14	0	0	0	0
Hg	*Hipposideros galeritus*	0	0	0	0	1
Hd	*Hipposideros diadema*	0	0	1	1	1
Cl	*Cynopterus luzoniensis*	5	8	4	14	8
Cm	*Cynopterus minutus*	2	24	9	56	24
Dc	*Dobsonia crenulata*	1	0	0	0	0
De	*Dobsonia exoleta*	0	0	0	0	1
Hc	*Harpyionycteris celebensis*	0	0	0	0	7
Mm	*Macroglossus minimus*	7	8	5	9	1
Nc	*Nyctimene cephalotes*	1	6	5	4	0
Pc	*Pilonycteris celebensis*	33	15	17	19	9
Ram	*Rousettus amplexicaudatus*	43	4	7	1	0
Tn	*Thoopterus nigrescens*	0	0	0	2	2



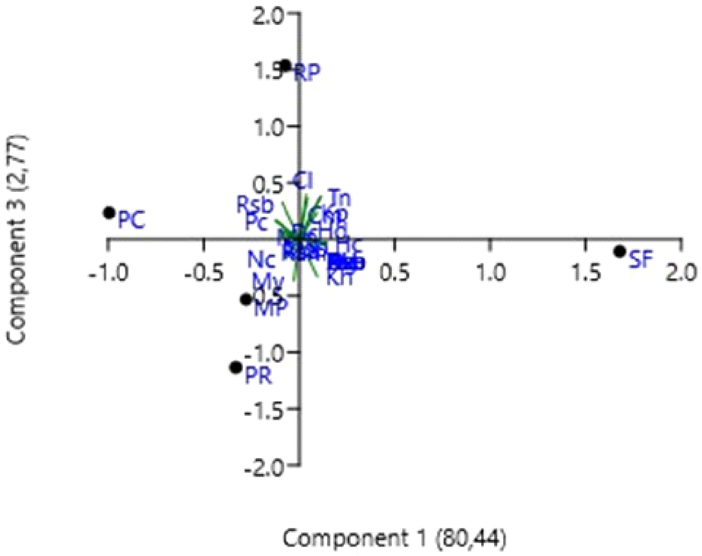


Figure 4. Principal component analysis (PC1, PC 2, and PC3) accounted for 99,73% of the correlation between bat spesies and habitat. Species abbreviations correspond to those listed in Table 4.

Insectivorous species, such as *Rhinolophus celebensis* and *Hipposideros diadema*, were strongly associated with secondary forest habitats characterized by dense canopy cover and high insect availability. Conversely, phytophagous species were more closely related to agroforests and settlements, which were dominated by fruiting trees and open vegetation.

2. Environmental factor

Environmental factors such as rainfall, moon phase, and vegetation structure were recorded and observed at all five study sites. Moon phase data for each sampling night were obtained from Moonconnection.com (Southern Hemisphere). Rainfall occurred at the secondary forest site on 10 July 2024 during the observation period (5:34 pm–8:15 pm), during which no insectivorous bats were captured. This aligns with studies by Voigt et al. (2011) and Appel et al. (2019), which demonstrated that rainfall reduces bat foraging activity due to increased energetic costs, disruption of echolocation efficiency, and decreased insect prey availability. These findings suggested that bats may reduce or suspend foraging flights during rain to conserve energy and avoid inefficient foraging conditions.

Lunar phase also appeared to affect bat activity throughout the sampling period. The highest number of individuals was recorded during the waxing crescent moon phase (150 individuals), followed by the waning gibbous (130 individuals) and first quarter (64 individuals) (Fig. 5). Fewer bats were captured during the full moon (55 individuals), third quarter (31 individuals), and waning crescent (21 individuals). The lowest numbers were recorded during the axing gibbous (12 individuals) and new moon (11 individuals). Vegetation structure also differed between sites. The secondary forest supported dense and heterogeneous vegetation, including fruiting trees and understorey plants, which provided a rich variety of roosting and foraging resources. In contrast, the plantation and mixed agroforestry sites (sites 1–4) featured more open canopies and simpler plant compositions.

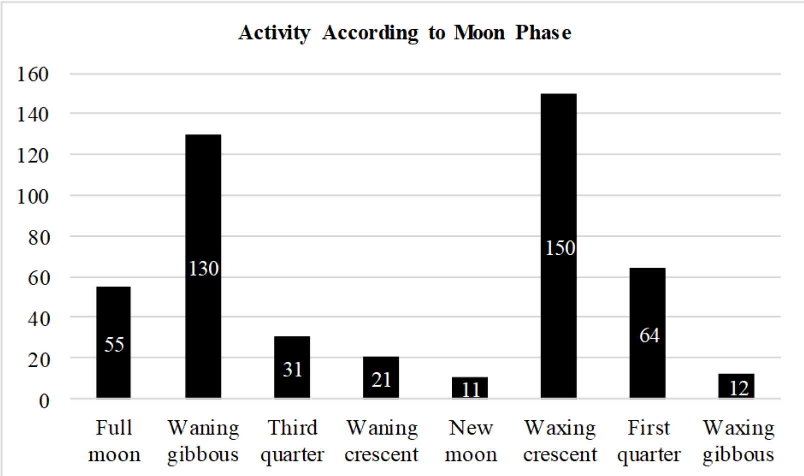


Figure 5. Number of bats captured during different moon phases in the Bualemo Sub-district.

DISCUSSION

1. Bat Composition and Distribution

The insectivorous bats recorded in this study consisted of thirteen species, with a total of 113 individuals. *Rhinolophus* sp.a was the most dominant, representing 63 individuals and found consistently across all sites except the secondary forest. Its widespread occurrence across different habitat types demonstrates ecological flexibility and tolerance to environmental change, in line with Kingston's findings (2013) on generalist bat species in Southeast Asia. *Hipposideros diadema* was also detected at more than one location, although in smaller numbers, suggesting a preference for more specific microhabitats while still showing some degree of adaptability (Francis, 2008).

Other insectivorous species such as *Rhinolophus* sp.b, *Rhinolophus euryotis*, *Miniopterus* sp., *Alionoctula* spp., *Kerivoula* spp., Myotis sp., *Megaderma spasma*, and *Hipposideros galeritus* were found only at a single site, mostly the secondary forest, and were recorded in low numbers. The occurrence of *R. euryotis* (Fig. 2), a species distributed across Sulawesi, the

Maluku Islands, and Papua (Maryanto et al., 2019) and also known under the taxonomic synonym *Rhinolophus tatar* in global conservation assessments (Patrick & Ruedas, 2017), together with *R. celebensis* (Fig. 2), which has a wide distribution across Sumatra (Krakatau), Java, Bali, the Lesser Sundas, and Sulawesi (Maryanto et al., 2019), reflects the importance of forested habitats in supporting both regionally distributed and widespread insectivorous bat species.

In addition, the presence of *Alionoctula* sp.b (Fig. 2) is noteworthy, as members of this genus were previously classified under *Pipistrellus* and have only recently been reassigned following taxonomic revisions (Simmons & Cirranello, 2025). The restricted occurrence of these species suggests that they are likely habitat specialists, dependent on specific environmental features such as tree cavities, dense understorey vegetation, and closed canopy conditions. Similar patterns have been reported from forest ecosystems in Lore Lindu and Southeast Sulawesi (Wiantoro et al., 2016; Maryanto et al., 2019), supporting the conclusion by Stein et al. (2014) that vegetation complexity is a key factor in maintaining forest-dependent bat species richness.

Sites 1 and 2, which consist of plantation vegetation adjacent to natural areas, supported a higher number of insectivorous bat species and individuals. This may be attributed to greater habitat heterogeneity and the availability of nocturnal insects, particularly along ecotones and transitional zones, as reported in tropical agroecosystems by Fenton & Simmons (2015).

Phytophagous bats in this study were represented by ten species and a total of 361 individuals. *Cynopterus minutus* was the most abundant, followed by *Pilonycteris celebensis*. Both species were found across all sampling sites. Their widespread occurrence reflects a strong tolerance to habitat variation and the ability to utilise a variety of fruit sources from both wild and cultivated plants. This pattern aligns with the findings of Sheherazade et al. (2019), who identified *Cynopterus* and *Pilonycteris* as key pollinators and seed dispersers in both natural and disturbed landscapes. Other phytophagous species such as *Cynopterus luzoniensis*, *Macroglossus minimus*, and *Rousettus amplexicaudatus* were observed at several sites, indicating moderate ecological flexibility. In contrast, *Dobsonia exoleta*, *Dobsonia crenulata*, and *Thoopterus nigrescens* were recorded at only one or two locations and in low numbers. These species are considered sensitive to habitat degradation and are commonly associated with more intact forest environments. This is consistent with observations by Bergmans & Rozendaal (1988) and Donnelly et al. (2021), who noted the dependence of these bats on undisturbed vegetation for feeding and roosting. Their limited occurrence in Bualemo may reflect the scarcity of suitable forest habitat or low population densities in the area. Sites 2 and 5 recorded the highest abundance of phytophagous bats. These sites offer a combination of fruiting trees, dense canopy structure, and access to water, which are recognised as important factors influencing bat diversity and foraging behaviour. This is supported by studies from Kunz et al. (2011) and Voigt & Kingston (2016). Overall, the distribution and abundance patterns observed in this study indicate that food resources, vegetation structure, and roosting opportunities strongly influence the composition of bat communities. Species with broad ecological tolerance tend to occur in a wide range of habitats, while those with narrow habitat requirements are confined to more specific environments. These findings highlight the importance of preserving diverse and structurally complex habitats in order to conserve bat biodiversity in Sulawesi and other regions of Indonesia.

Several distinctive phytophagous bat species documented in this study are illustrated in Fig. 2. *Nyctimene cephalotes* is a morphologically distinctive species characterised by spotted wings and facial markings, with a distribution across Sulawesi, the Maluku Islands, and Timor-Leste (Tsang, 2016). *Harpyionycteris celebensis* is an endemic species restricted to Sulawesi and Buton Island and is closely associated with forested habitats (Sheherazade & Waldien, 2021). Meanwhile, *Dobsonia exoleta*, a Sulawesi-restricted species, was recorded in low numbers, reflecting its strong association with relatively intact forest environments (Hutson et al., 2019).

2. Bat Diversity and Evenness Index

The Shannon–Wiener diversity index (H') varied across habitats, ranging from 1.534 in Site 4 (riverine plantation) to 2.210 in Site 5 (secondary forest), indicating a moderate level of diversity (Magurran, 1988). The higher diversity in secondary forest was likely influenced by its structurally complex vegetation, which provides more roosting opportunities and stable food resources for both insectivorous and phytophagous species. In contrast, the riverine plantation showed the lowest diversity, possibly due to its more homogeneous vegetation dominated by cultivated trees, which tends to support fewer specialist taxa. The evenness index (E = 0.489–0.705) further indicated that species were more evenly distributed in vegetated habitats such as mixed plantation and secondary forest compared to plantations near cave-adjacent areas, where a few dominant species (e.g., *Rhinolophus* sp.a) comprised a large proportion of captures.

These patterns align with the habitat preference analysis, where phytophagous species such as *Cynopterus minutus* and *Pilonycteris celebensis* were more frequently associated with fruit-rich plantations, while forest-dependent species like *Dobsonia exoleta* and *Harpyionycteris* *celebensis* occurred almost exclusively in secondary forests. Meanwhile, insectivorous taxa showed distinct microhabitat preferences, with *Rhinolophus* sp.a dominating plantations near cave and *Rhinolophus* sp.b occurring only in secondary forest. Together, the diversity index and habitat preference analyses demonstrate that habitat heterogeneity strongly influences species composition and community structure in Bualemo.

3. Habitat Preferences

Bat diversity index values varied across the five study sites, reflecting differences in habitat structure and vegetation composition. Site 5, characterised by secondary forest with dense and diverse vegetation, exhibited the highest diversity index (2.210). This richness is supported by the presence of various plant species, including clove (*Syzygium aromaticum*), bamboo (*Bambusoideae*), fig trees (*Ficus* spp.), and pitcher plants (*Nepenthes* spp.), which together provide essential food sources, shelter, and roosting opportunities for many forest-dependent bat species (Kunz & Fenton, 2003). Several species were recorded exclusively in this site, indicating a strong preference for structurally complex forest habitats. In contrast, Site 4, a plantation area near a river, recorded the lowest diversity index (1.534). This area was dominated by relatively homogeneous vegetation, such as coconut (*Cocos nucifera*) and kapuk (*Ceiba pentandra*), offering limited resources and canopy complexity. The species present in Site 4 were mostly those known to tolerate open or disturbed habitats, consistent with patterns observed in anthropogenic landscapes (Meyer & Kalko, 2008). The remaining sites, Sites 1, 2, and 3, showed intermediate diversity index values ranging from 1.704 to 1.840. These areas represented mixed plantations with moderate vegetation variety, which appeared to support species capable of surviving in semi-open and transitional environments. Thus, each habitat type played an important role in maintaining bat diversity across the Bualemo landscape.

This pattern supports earlier research indicating that bat diversity is strongly influenced by vegetation complexity. Structurally rich habitats are more likely to accommodate a greater range of ecological niches and therefore support a wider variety of species (Kingston, 2013). Moreover, this study highlights the critical role of habitat conservation in sustaining bat populations. Sites with higher diversity and evenness values tend to reflect more stable ecosystems, whereas lower values may indicate environmental stress due to factors such as habitat fragmentation and land use changes (Frick et al., 2020). Conservation efforts should prioritize the protection of natural and semi-natural habitats, particularly those with high vegetation heterogeneity, to preserve the ecological roles of bats in seed dispersal, pollination, and insect population control (Kunz et al., 2011; Voigt & Kingston, 2016).

Species-specific habitat associations observed in this study further highlight the importance of habitat diversity, as certain bat species showed strong preferences for particular habitat types (Kingston, 2008). For example, *Harpyionycteris celebensis* was recorded exclusively in secondary forest, such as the availability of fruiting trees and proximity to riparian or coastal features, which are similar to habitats where the species has previously been recorded, including coconut plantations, areas near rivers, and coastal areas (Sheherazade & Waldien, 2021). *Rhinolophus* sp.a was detected across multiple sites, suggesting broad ecological tolerance. In contrast, species such as *Rhinolophus* sp.b, *Dobsonia exoleta*, and *Harpyionycteris celebensis* were only found in the secondary forest, indicating a strong dependence on intact forest conditions. Phytophagous bats such as *Cynopterus minutus* and *Pilonycteris celebensis* were present in all five sites, reflecting their adaptability to human-modified environments, provided that fruit resources are available (Ramadhan & Winarni, 2015; Wiantoro et al., 2020). Meanwhile, insectivorous species such as *Hipposideros diadema* and *Miniopterus sp.* exhibited more restricted distributions, likely due to their reliance on specific roosting sites and prey availability. These findings suggest that habitat heterogeneity plays a fundamental role in shaping bat community composition and that the conservation of a mosaic of habitat types is essential to support the full spectrum of bat biodiversity.

4. Environmental factor

The results of this study indicate that environmental factors such as rainfall, moon phase, and vegetation structure play a critical role in shaping bat activity and distribution. The absence of insectivorous bat captures during rainfall in the secondary forest on 10 July 2024 supports earlier findings that bats reduce flight activity under poor weather conditions to conserve energy and avoid inefficient foraging. This behaviour is particularly relevant for insectivorous species, which rely on acoustic prey detection that can be disrupted by heavy rain and wind (Voigt et al., 2011; Appel et al., 2019). Moon phase variation also influenced bat activity. The highest number of individuals was recorded during the crescent moon phase, with 150 individuals captured. Notably the new moon phase in our sampling occurred only for one night, which may explain the particularly low capture rate compared to other phases that spanned several nights. These findings suggest that moderate moonlight may provide optimal conditions for foraging, offering a balance between visibility and reduced predation risk, particularly for phytophagous species foraging in semi-open habitats. In contrast, extreme brightness during a full moon or total darkness during a new moon may suppress bat activity. This interpretation aligns with studies by Lang et al. (2006), Rydell (1992), and Eriksson and colleagues, who documented species-specific responses to lunar illumination depending on habitat type and foraging strategy. Ciechanowski et al. (2007) and Gannon & Willig (1997) also showed that species such as *Desmodus rotundus* and *Artibeus jamaicensis* exhibit changes in activity levels according to lunar illumination.

Thirteen species of insectivorous bats were recorded in this study, totalling 113 individuals. *Rhinolophus* sp.a was the most abundant and was found in all sites except the secondary forest, suggesting high ecological tolerance and the ability to persist in modified habitats. *Hipposideros diadema* was also detected in more than one location, although in lower numbers, indicating a degree of flexibility with a tendency to prefer habitats with more structural complexity (Francis, 2008).

Other species, including *Rhinolophus* sp.b*, Rhinolophus euryotis, Miniopterus* sp., *Alionoctula* sp. a, *Alionoctula* sp. b, *Kerivoula papillosa, Kerivoula hardwickii, Myotis* sp., *Megaderma spasma*, and *Hipposideros galeritus*, were each restricted to the secondary forest and found in very low numbers. This suggests that they are more specialised and reliant on dense forest features such as tree cavities, thick understorey, and closed canopy conditions. Similar distribution patterns have been documented in other parts of Sulawesi, including Lore Lindu and Buton Island, where forest-dependent insectivorous bats are known to avoid open or disturbed areas (Wiantoro et al., 2016; Maryanto et al., 2019).

Sites 1 and 2 had higher numbers of insectivorous species and individuals compared to the other sites. These areas featured mixed vegetation with elements of both natural and plantation habitats, offering transitional zones that combine open foraging space with nearby roosting opportunities. Fenton & Simmons (2015) reported similar responses in tropical agroforestry systems, where ecotones play a vital role in supporting bat diversity.

Phytophagous bats were more numerous overall, comprising ten species and 361 individuals. *Cynopterus minutus* and *Pilonycteris celebensis* were the most common, recorded at all sites. Their wide distribution reflects their ability to adapt to varied environments and take advantage of fruit sources from both wild and cultivated plants. These species have been recognized as important pollinators and seed dispersers in disturbed landscapes (Sheherazade et al., 2019). Other phytophagous bats, including *Cynopterus luzoniensis, Macroglossus minimus*, and *Rousettus amplexicaudatus,* were found at multiple sites, suggesting moderate ecological flexibility. These species are known for their broad ecological tolerance and ability to utilize a variety of roosts and food sources, allowing them to thrive in both natural and modified environments.

In contrast, *Dobsonia exoleta, Dobsonia crenulata*, and *Thoopterus nigrescens* were only recorded at one or two sites, and in small numbers. These species are typically more sensitive to disturbance and tend to depend on intact forest for their foraging and roosting needs. This pattern is consistent with studies by Bergmans & Rozendaal (1988) and Donnelly et al. (2021), which described their limited distribution in relation to habitat integrity. Sites 2 and 5 recorded the highest numbers of phytophagous bats. These sites contained fruiting trees, denser canopy layers, and water sources, all of which are recognised as key drivers of bat activity and diversity in tropical landscapes (Kunz et al., 2011; Voigt & Kingston, 2016).

Overall, this study highlights that bat community structure in Bualemo is closely shaped by environmental conditions, particularly rainfall, lunar cycle, and vegetation complexity. Maintaining diverse and connected habitats is therefore essential to support the ecological roles of bats in both natural and human-altered ecosystems.

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