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CHAPTER 12

A century of small mammal research in Borneo: Diversity trends, conservation status, and future directions

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Abstract: Borneo is recognised as a global biodiversity hotspot, hosting a remarkable diversity of small mammals, including bats, rodents, shrews, and tree-dwelling insectivores. Despite their ecological importance in pollination, seed dispersal, and insect population control, these species remain understudied and often overlooked in conservation planning. This chapter examines the past and present diversity of Borneo's small mammals, synthesising knowledge from historical field surveys, taxonomic collections, and contemporary molecular and ecological studies. By integrating data from species inventories, phylogenetic analyses, and metagenomic approaches, the chapter explores patterns of species distribution, evolutionary adaptation, and biogeographic history across the island. This chapter also reviews the conservation trends, highlighting how anthropogenic effect have impacted population stability and species survival over time. The findings emphasise the dynamic interplay between evolutionary processes and human-driven environmental change, providing a clearer understanding of small mammal biodiversity in Borneo with an emphasise on Sarawak and Sabah. By combining traditional and modern research methods, this work underscores the critical role of small mammals in tropical forest ecosystems and the urgent need to integrate them into conservation strategies.

INTRODUCTION

Small mammals are typically defined as mammals weighing less than 5 kg and serves as a threshold that distinguishes them from medium and large-sized mammals (Merritt 2010). This group includes terrestrial members such as rodents (Order: Rodentia), treeshrews (Order: Scandentia) and shrews (Order: Eulipotyphla). In addition, volant mammals such as bats (Order: Chiroptera) are also categorised as small mammals. Collectively, these mammals play important roles in natural ecosystems by contributing to seed dispersal, predator–prey interactions and forest regeneration (Wells *et al*. 2009; Lacher *et al.* 2019). The study of these mammals is important because they serve as indicators of ecosystem health, as evidenced by the long history of research on these taxa spanning more than a century (Figure 1).

In the early 1900s, studies mainly relied on museum specimens and focused on describing and classifying species (Banks 1931). By the mid-20th century, researchers began conducting more intensive field surveys, which provided better understanding of where species occur and how they live in their natural environments (Banks 1952; Kobayashi and Hotta 1978). From the 1990s onwards, attention increasingly turned to how human activities such as logging and agricultural expansion affect small mammal communities

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(Brooks *et al.* 1999). In recent years, studies have also incorporated molecular approaches and conservation-focused perspectives, allowing researchers to better understand species relationships and population structure through genetics (Hinckley *et al.* 2022; Khan *et al.* 2025b). This progression reflects how advances in research methods and growing environmental concerns have gradually shaped the direction of small mammal studies.

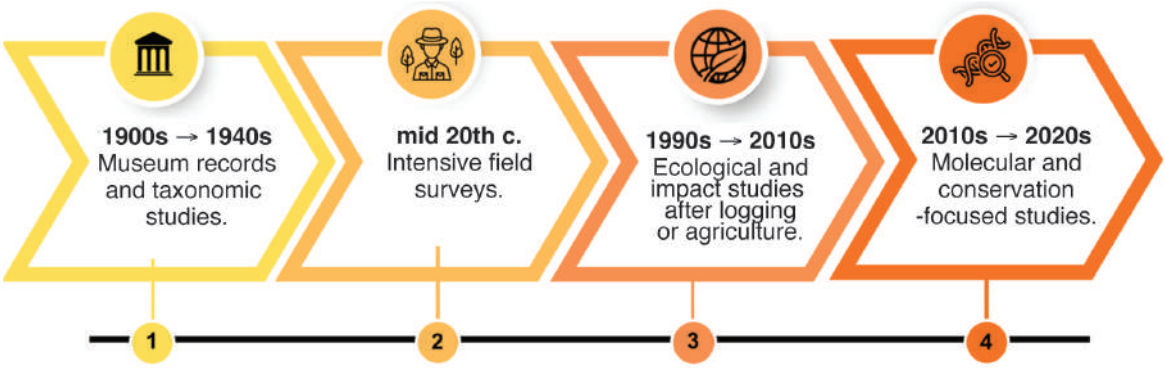

Figure 1. Conceptual timeline summarising the progression of small mammal research in Borneo, from early museum-based taxonomy to modern molecular and conservation studies.

Terrestrial small mammals in Borneo are represented by several families belonging to three main orders, each with distinct ecological roles (Phillipps and Phillipps 2018) (Figure 2). Shrews (Order: Eulipotyphla) are represented by the families Soricidae (true shrews) and Erinaceidae (gymnures), which are primarily insect-eating mammals that help regulate invertebrate populations. Treeshrews (Order: Scandentia) belong to the family Tupaiidae and are commonly found in undisturbed forested habitats. Rodents (Order: Rodentia) form the most diverse group and include the families Sciuridae (squirrels), Muridae (rats and mice) and Hystricidae (porcupines). Over time, the documented number of terrestrial small mammal species in Borneo has gradually increased, from 75 species in the early 1900s to 87 species by 2025 (Phillipps and Phillipps 2018; Mammal Diversity Database 2025) (Figure 3). While most of the families show relatively stable numbers, the number of Muridae species has increased as new species were described or recorded through continued field surveys and taxonomic work.

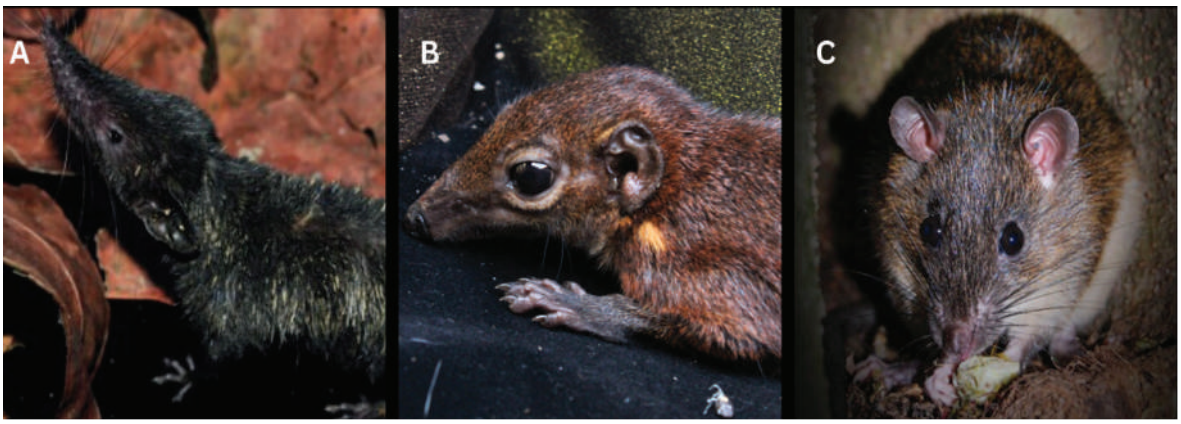

Figure 2. Representative terrestrial small mammal species from the three orders recorded in Borneo: **A.** Eulipotyphla, **B.** Scandentia, and **C.** Rodentia.

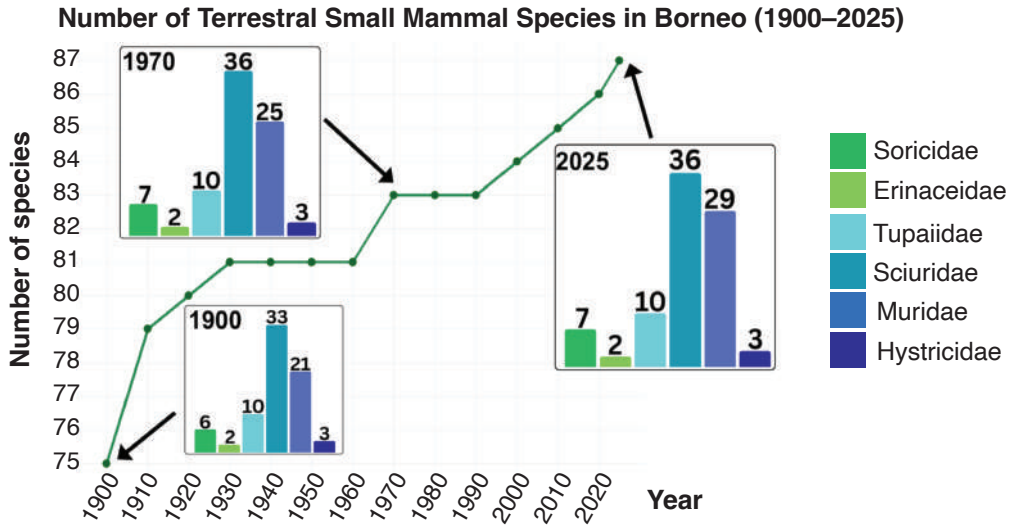

Figure 3. Changes in the recorded number of terrestrial small mammal species in Borneo between 1900 and 2025, illustrating the contribution of major taxonomic families.

Bats (Order: Chiroptera) represent the most diverse group of small mammals in Borneo and are classified into several families (Phillipps and Phillipps 2018) (Figure 4). Fruit bats in the family Pteropodidae, commonly known as flying foxes and fruit bats, play important roles in pollination and seed dispersal. In contrast, most other bat families are insect-eating species that help control insect populations. These include Rhinolophidae (horseshoe bats), Hipposideridae (leaf-nosed bats), Miniopteridae (bent-winged bats), Megadermatidae (false vampire bats), Nycteridae (slit-faced bats), Vespertilionidae (evening bats), Emballonuridae (sheath-tailed bats) and Molossidae (free-tailed bats). Similar to terrestrial small mammals, the recorded number of bat species in Borneo has increased over time, rising from 72 species in the early 1900s to 100 species by 2025 (Phillipps and Phillipps 2018; Mammal Diversity Database 2025) (Figure 5). This increase largely reflects continued exploration and the use of improved sampling methods, such as mist nets and harp traps, which have enabled researchers to detect bat species that were previously unrecorded.

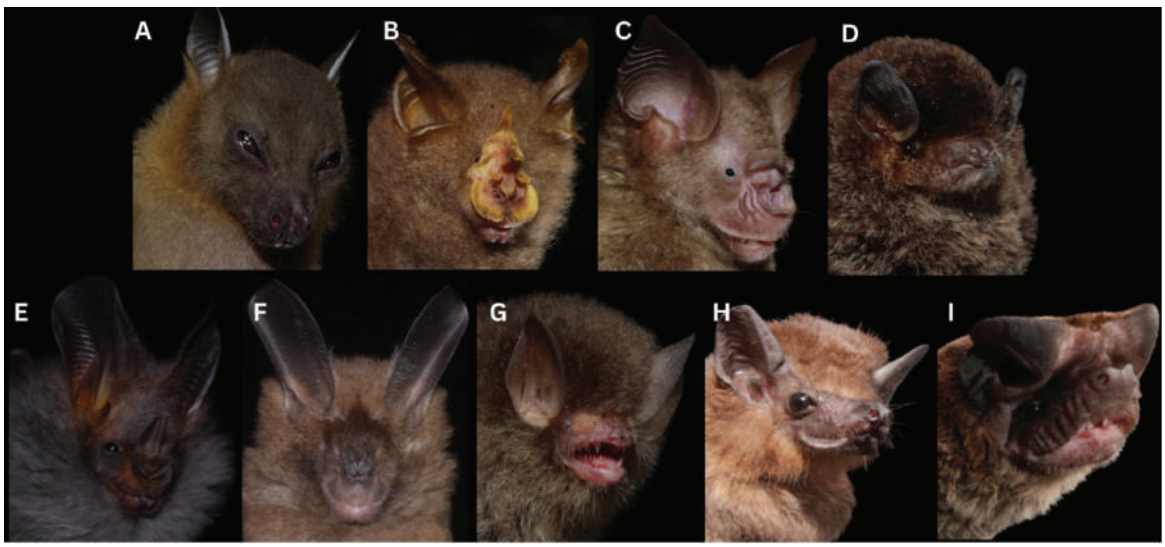

Figure 4. Representative bat species from the nine bat families recorded in Borneo (Order: Chiroptera): **A)** Pteropodidae, **B)** Rhinolophidae, **C)** Hipposideridae, **D)** Miniopteridae, **E)** Megadermatidae, **F)** Nycteridae, **G)** Vespertilionidae, **H)** Emballonuridae, and **I)** Mollosidae.

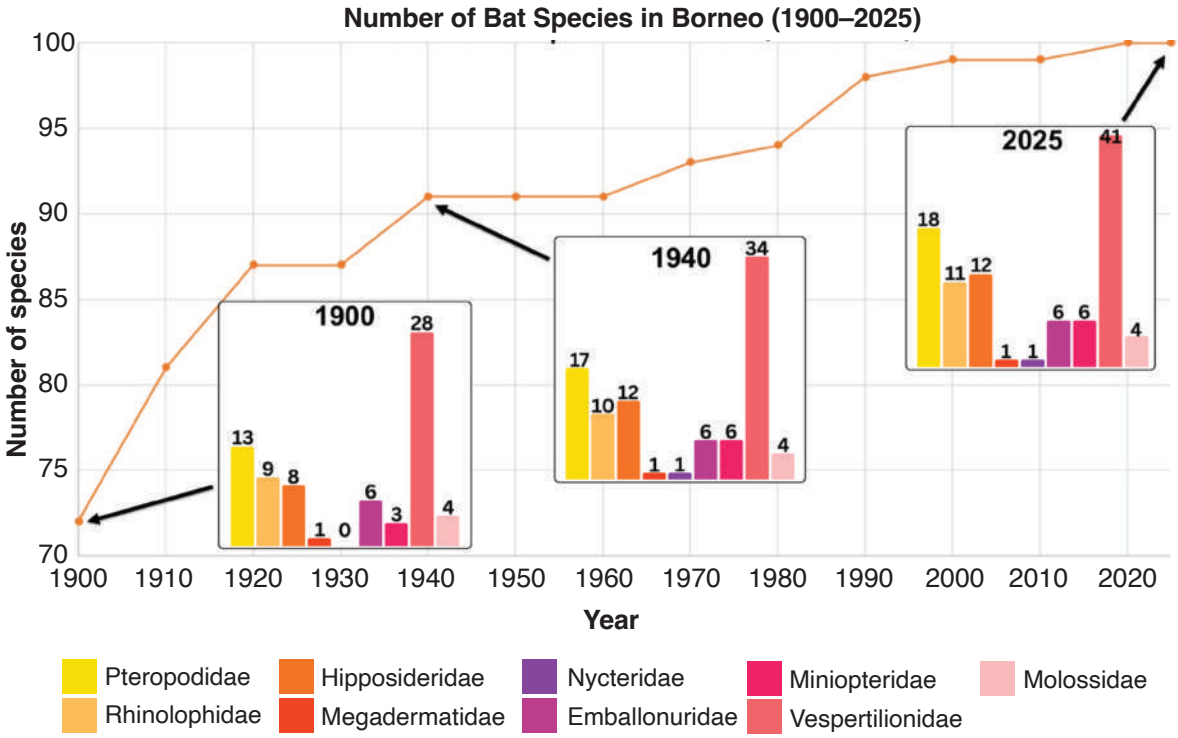

Figure 5. Historical increase in the number of bat species recorded in Borneo from 1900 to 2025, with family-level contributions highlighted for selected periods.

Conservation status of small mammal in Borneo

In terms of conservation status, the majority of terrestrial small mammal species in Borneo are currently classified as 'Least Concern' under the International Union for Conservation of Nature (IUCN) Red List (Figure 6). However, approximately 20% of species are listed as 'Data Deficient' in 2025, meaning that there is insufficient information to properly assess their risk of extinction. Notably, flying squirrels and tree mice within the rodent order make up about half of this category. This highlights an important research gap, particularly among flying squirrels, as several species within this group are already recognised as 'Vulnerable' or 'Endangered'. Improved ecological and population studies are therefore needed to better understand their conservation status and potential threats.

While terrestrial small mammals generally remain well represented in the lower-risk categories, the conservation outlook for bats in Borneo shows a slightly different pattern. Over the assessment period between 1996 and 2025, the proportion of bat species classified as 'Near Threatened', 'Vulnerable' or 'Endangered' has gradually increased, rising from about 15% in 1996 to around 25% in 2025 (Figure 7). Although most species are still considered 'Least Concern', this increase suggests that a growing number of Bornean bats face heightened risks of population decline and extinction. Factors such as habitat loss, disturbance of roosting sites and environmental change may contribute to these increasing conservation concerns.

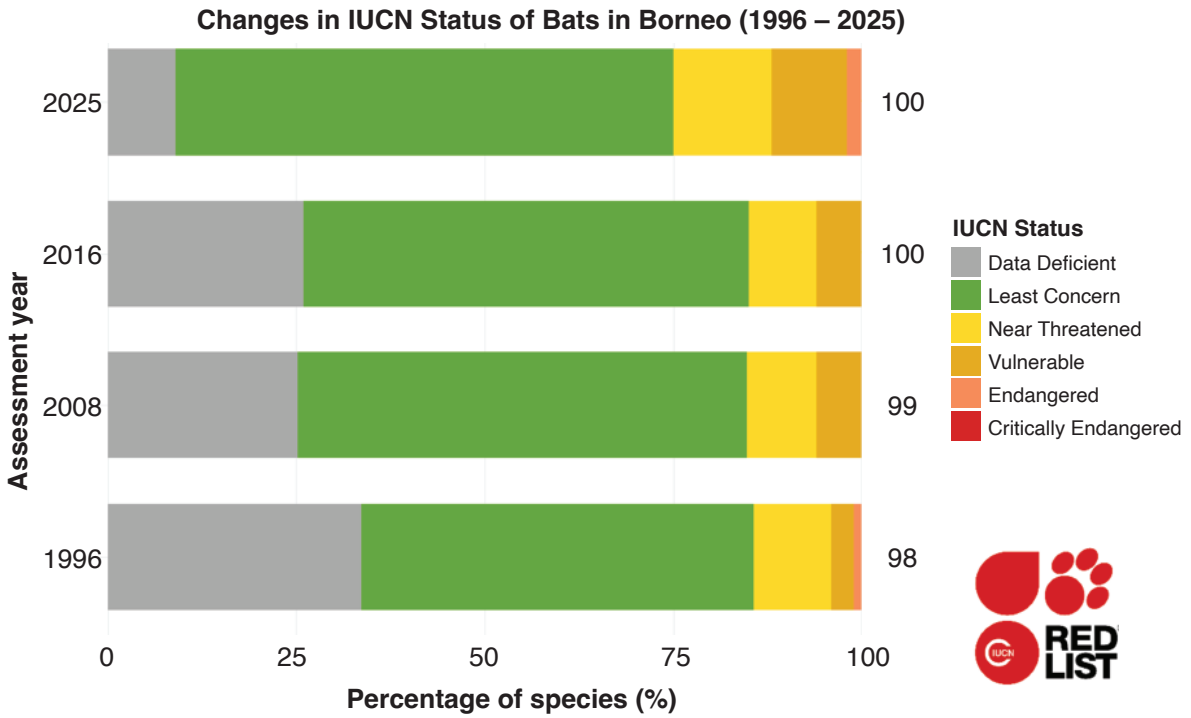

Figure 6. Conservation status of terrestrial small mammal species recorded in Borneo according to the IUCN Red List categories from 1996 to 2025, showing the proportion of species within each conservation status

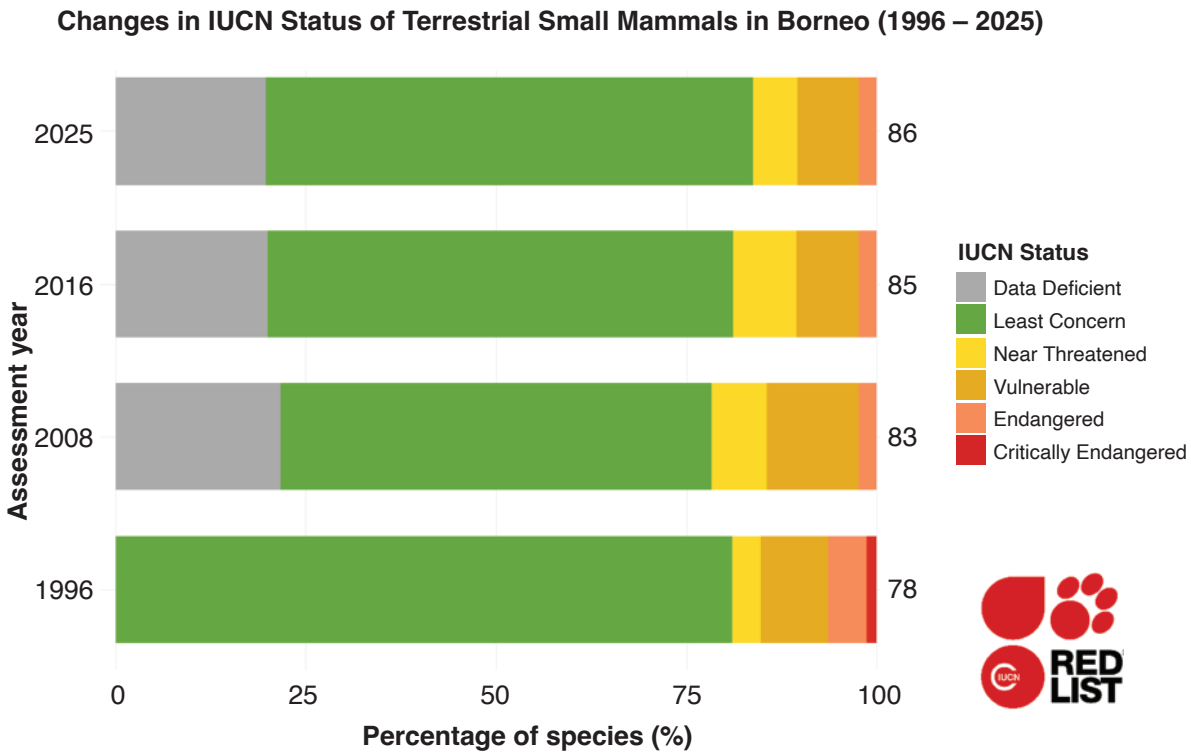

Figure 7. Conservation status of bat species recorded in Borneo based on the IUCN Red List categories from 1996 to 2025, illustrating proportion of species within each conservation status.

Trends in small mammal research in Borneo

The development of research on terrestrial small mammals in Borneo has followed a gradual trajectory, with early studies receiving limited scientific attention. These early contributions were instrumental in establishing the taxonomic framework for many Bornean taxa and provided the first systematic inventories of terrestrial small mammal fauna across different regions of the island (Figure 8). Nevertheless, many of these studies were constrained by limited sampling coverage and relied predominantly on morphological identification.

In recent decades, research on terrestrial small mammals has expanded significantly with the integration of modern ecological and molecular methodologies. Field-based studies have increasingly addressed patterns of species richness, community composition and habitat specialisation across different forest types, including lowland dipterocarp, montane and disturbed habitats (Kaicheen *et al.* 2025; Voon *et al.* 2025). Molecular phylogenetic analyses and DNA-based approaches have further revealed substantial cryptic diversity within several groups, leading to taxonomic revisions (Nations *et al*. 2022; Giarla *et al*. 2025). Additionally, rodents have gained attention in studies of disease ecology, highlighting their potential roles as reservoirs for zoonotic pathogens (Frederick *et al*. 2022; Widayati *et al*. 2022; Azmi *et al*. 2025). These developments highlight the growing recognition of terrestrial small mammals as key components of Borneo's biodiversity and as important indicators of environmental change.

The progression of bat research in Borneo reflects the broader development of mammalogy and tropical biodiversity studies in Southeast Asia. Early scientific investigations, primarily conducted during the late nineteenth and early twentieth centuries, were largely taxonomic and descriptive (Figure 9). These studies focused on specimen collection, morphological characterisation and the documentation of species distributions, often based on material deposited in major natural history museums (Banks 1931). Such foundational work was critical for establishing baseline knowledge of Bornean chiropteran diversity and for describing numerous species and subspecies within the region. However, research during this period was geographically limited and largely centered on accessible localities and major expeditions.

From the latter half of the 20th century onward, bat research in Borneo expanded substantially in both scope and methodological approaches. Ecological studies began to investigate community structure, habitat associations and trophic interactions, particularly within lowland dipterocarp forests and cave ecosystems (Kofron 1997; Khan *et al*. 2007; Shazali *et al*. 2017; Mc Arthur *et al*. 2024). Advances in bioacoustics, molecular phylogenetics and integrative taxonomy have also enabled researchers to identify cryptic species, reconstruct evolutionary relationships and refine species boundaries within several bat lineages (Khan *et al*. 2010; Ith *et al.* 2016). The incorporation of conservation biology has also become increasingly prominent, particularly in response to accelerating habitat loss and land-use change across Borneo. Collectively, these developments highlight a transition from primarily descriptive studies toward multidisciplinary research that integrates ecology, systematics, genetics and conservation science.

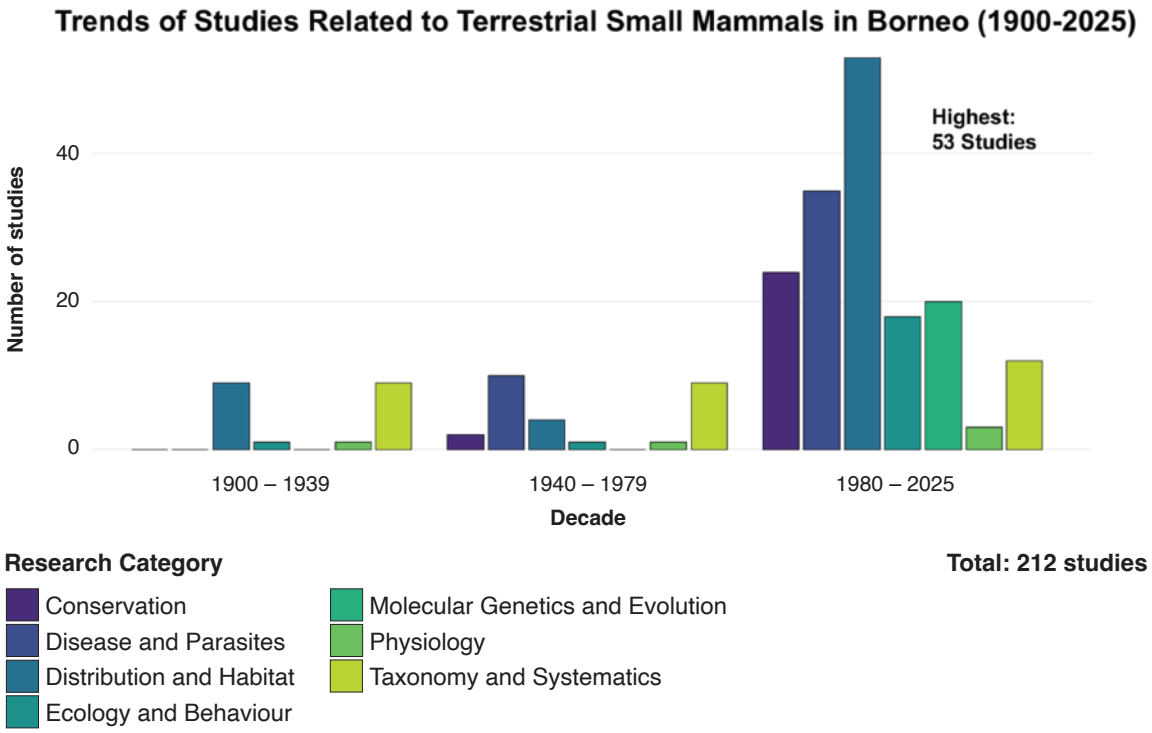

Figure 8. Trends in terrestrial small mammal research in Borneo based on research category from 1900 to 2025.

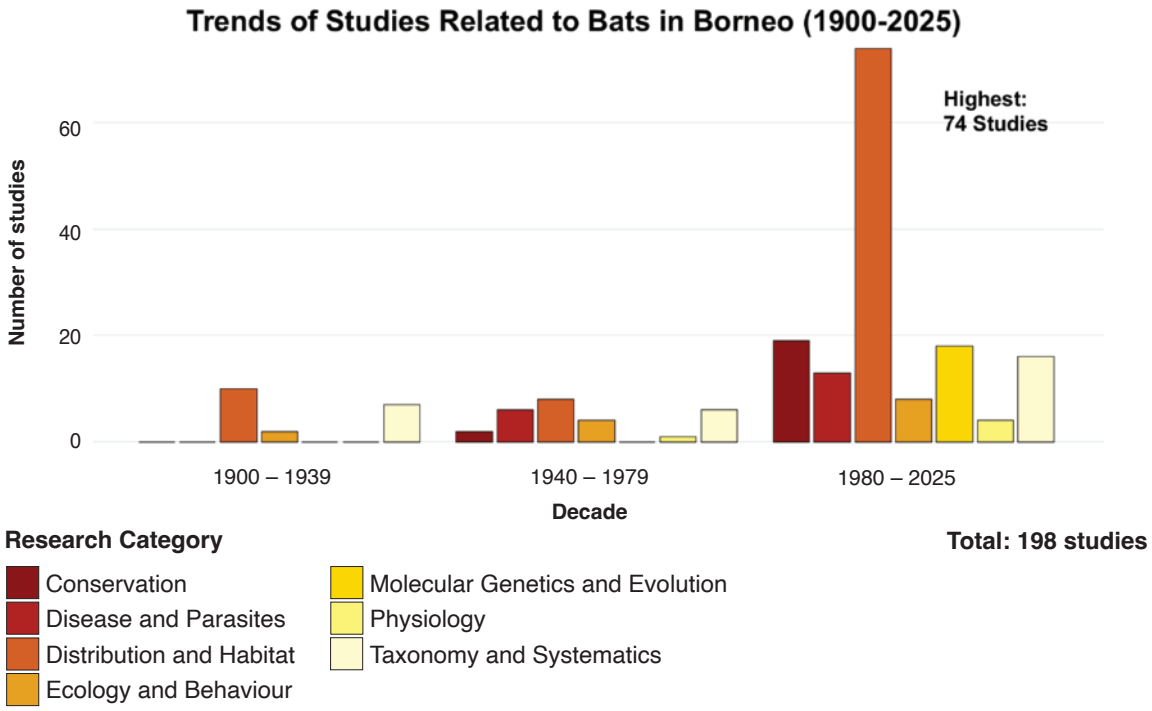

Figure 9. Trends in bats studies in Borneo according to research category from 1900 to 2025.

Distribution of small mammal research in Borneo

Studies on small mammals in Borneo are predominantly concentrated in northern Borneo, particularly in Sarawak, Sabah and Brunei, while relatively few investigations have been conducted in Kalimantan despite its extensive land area (Figure 10). In northern Borneo, research encompasses a wide range of themes, with distributional surveys, zoonotic disease investigations and conservation studies being particularly prevalent. Urbanised regions, especially around Kuching, have facilitated pathogen-related studies associated with synanthropic small mammals (Perison *et al.* 2022), whereas forested areas have supported distribution and conservation research on native species (Laneng *et al*. 2021; Khan *et al.* 2025a). In contrast, studies in Kalimantan remain sparse and are largely limited to conservation and genetic research. Although recent taxonomic discoveries from Kalimantan highlight its importance for uncovering undocumented diversity (Achmadi and Maryanto 2012; Dwijayanti *et al.* 2025), the region remains substantially underexplored.

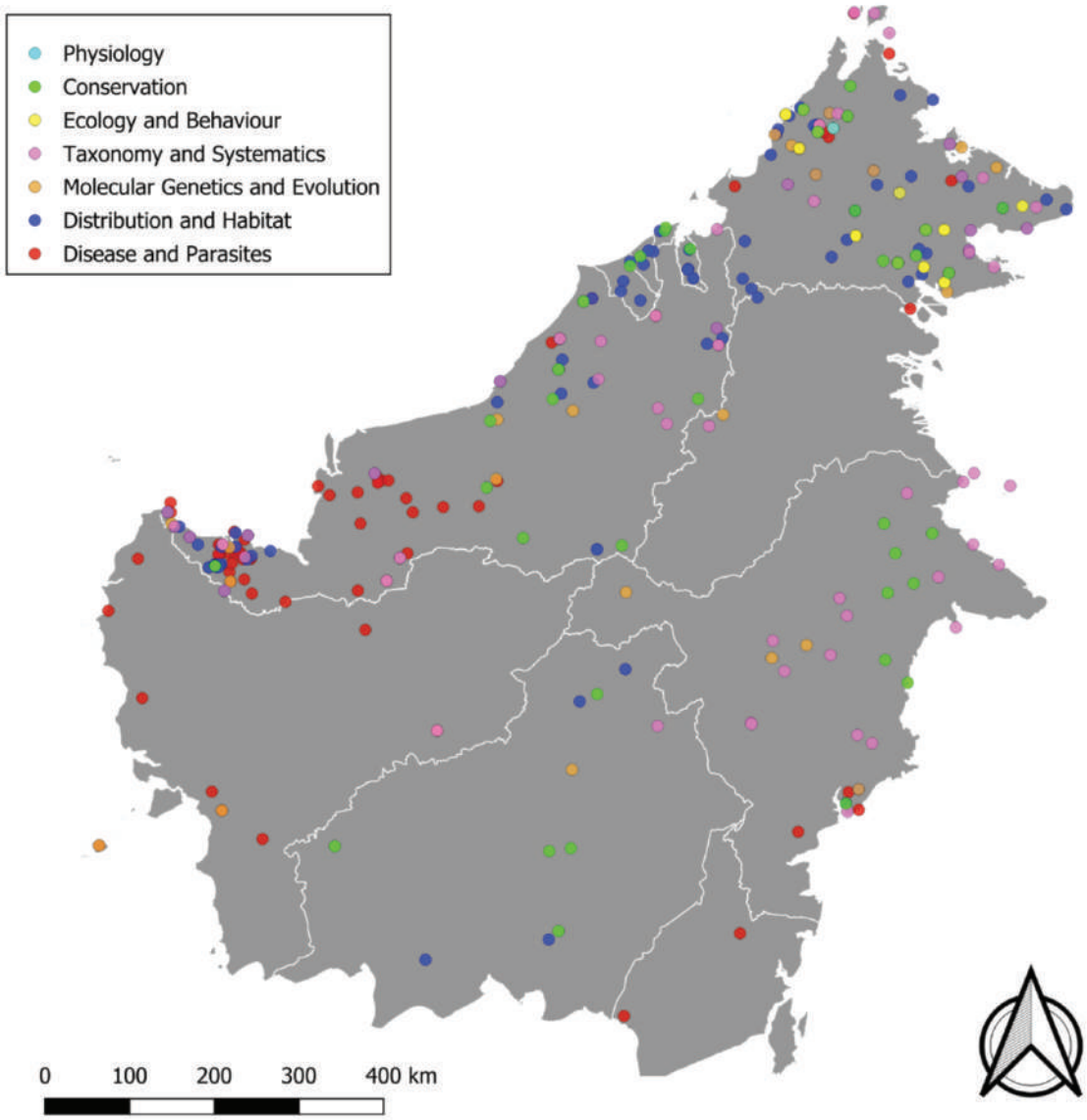

Figure 10. Distribution of research sites across Borneo compiled from published studies on small mammals, showing geographical coverage and research focus across the island.

Overall, small mammal research in Borneo has expanded considerably over the past century, evolving from early descriptive and distributional accounts to increasingly diverse and integrative research approaches. Early taxonomic and faunal surveys established the foundation for understanding species diversity and endemism on the island, while subsequent studies have broadened to include ecological, conservation and disease-related investigations. Collectively, these studies highlight the ecological significance of terrestrial small mammals in Bornean ecosystems and emphasise their importance for biodiversity assessments, conservation planning and public health research.

Despite these advances, substantial knowledge gaps remain. Research effort across the island is geographically uneven, with studies heavily concentrated in northern Borneo, particularly in Sarawak and Sabah, whereas Kalimantan remains comparatively under-represented despite comprising the largest portion of the island. In addition, physiological and functional studies on terrestrial small mammals remain relatively scarce compared with work on larger mammals. Expanding research in under-surveyed regions and incorporating emerging approaches such as next-generation sequencing will be essential going forward. Addressing these gaps will support more effective conservation and management strategies in the face of ongoing environmental change. Ultimately, continued research will be crucial for revealing the complete diversity and ecological significance of Borneo's terrestrial small mammals, the island's often overlooked yet vital "tiny titans."

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