A review of research on artiodactyla-habitat relationships in Indonesia, with a comparison to Malaysian Borneo

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Abstract:
Artiodactyla is among the most species-rich mammalian order in Indonesia, a country known for its high level of biodiversity. However, Indonesia is also experiencing a high rate of deforestation, threatening its biodiversity, including 20 Artiodactyla species distributed throughout the country. Our goal here is to assess the status of knowledge on Artiodactyla in Indonesia to identify knowledge gaps and major biases and propose a research prospectus to stimulate new research paths and approaches. To achieve our goal, we reviewed and summarized 110 field-based research articles published between 1988 and 2022 covering Artiodactyla species throughout Indonesia and, as a comparison, Malaysian Borneo, aiming to identify biases in Artiodactyla research in the region. We found three sources of bias: 1) geographical bias, with most studies being conducted in the western part of the country and Malaysian Borneo; 2) taxonomic bias, with the number of papers covering the three most studied species equivalent to the number of papers covering the rest of the species combined; and 3) bias in research approaches, whereby few studies measured habitat selection and quality. Through our review, we provide recommendations for future research priorities, including: 1) improving research on nine understudied species, which will simultaneously add to the amount of research in less studied regions; 2) collecting basic data such as distribution and abundance for most Artiodactyla species throughout the country; and 3) integrating habitat selection assessment in designing research.

Keywords: conservation, habitat selection, geographical bias, taxonomic bias, research priority.

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Review of research on Artiodactyla in Indonesia

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INTRODUCTION

Understanding wildlife-habitat relationships is critical for conservation, particularly in a country such as Indonesia, which despite being a biodiversity hotspot (Mittermeier, 1997), is facing among the highest deforestation rates globally (Margono et al., 2014). The ability of wildlife to survive in modified landscapes depends on critical habitats that can support viable populations in the long term (Morrison et al., 2006). Identifying critical habitats is a fundamental step towards integrating wildlife conservation into development plans (Cook et al., 2012). For instance, recognizing areas that contain essential habitat features for a species would ensure the effectiveness of areas allocated to conserve it (e.g., national parks), as well as predicting the consequences of landscape management (Sanderson et al., 2002), e.g., whether the species would persist if its habitat were managed for timber production.

Despite the importance of understanding wildlife-habitat relationships, the order Artiodactyla in Indonesia is often overlooked by researchers, especially if compared to other mammalian taxa (Albert et al., 2018). Whereas comprising 20 species, Artiodactyla is among Indonesia's most diverse order of large mammals (IUCN, 2021; Francis and Barrett, 2008). This group also includes the primary game species and prey items for large carnivores, emphasizing its critical roles in ecosystem (Ripple et al., 2016; Hayward et al., 2012; Bennett and Robinson, 1999). The IUCN Red List of Threatened Species currently categorize 12 species as threatened by extinction (IUCN, 2021), but it is likely the conservation of Artiodactyla is not at its optimum because most species of this group are considered less charismatic than other large mammals in Indonesia, such as the Sumatran tiger, the Sumatran elephant, or the orangutans (Sibarani et al., 2019). Typically, less popular species receive lower public awareness, which leads to less funding for conserving them (Bellon, 2019; Colléony et al., 2017). Furthermore, this low recognition also lowers research interest towards them, regardless of their conservation status (Fleming and Bateman, 2016). As an example, the National Conservation Strategies and Action Plans for six Artiodactyla species were developed from a small number of studies, leaving uncertainty in the program's effectiveness.

Despite the general acceptance that habitat loss and degradation negatively affect Artiodactyla (Costa et al., 2021), interpretations of their responses are often inconsistent among studies (Jati et al., 2018). For instance, *Sus barbatus* was reported to be negatively affected by logging in some studies (Jati et al., 2018; Wilson and Johns, 1982) but also documented as not showing significant response in other studies (Granados et al., 2016; Brodie et al., 2015; Samejima et al., 2012). This discrepancy can be attributed to research bias (Buxton et al., 2021), as shown by Broto and Mortelliti (2019), who found that mammal research in Sulawesi, Indonesia, is biased toward specific taxa, geographical areas, and topics; a similar pattern likely exists throughout Indonesia. Taxonomic bias resulted in insufficient studies on some species, making it challenging to interpret their responses accurately (Troudet et al., 2017). Furthermore, geographical bias skews research distribution across regions, limiting the generalizability of findings (Martin et al., 2012). Lastly, limited focus on habitat selection and quality in wildlife research may overlook critical habitat components of a species. Our goals here are to contribute to filling these critical knowledge gaps by identifying biases in research (including taxonomic, geographic, and methodological biases) and developing a prospectus for future research to reduce the aforementioned biases.

In this article, we reviewed field research papers covering Artiodactyla species in Indonesia and Malaysian Borneo to evaluate the status of knowledge on Artiodactyla-habitat relationship studies in these regions. First, we synthesized existing publications to provide an overview of Artiodactyla-habitat relationships. Second, we investigated the geographical distribution of research, examining whether research is disproportionally distributed throughout the regions. Third, we explored the taxonomic bias inherent in research across the archipelago, pinpointing the most and least studied species. Fourth, we reviewed research approaches in each article, particularly in data collection techniques, sampling approaches, and research topics. Finally, we discuss potential future research priorities to address the biases and enhance our comprehension of Artiodactyla-habitat relationships in Indonesia.

METHODS

Taxonomic and geographic scope

We reviewed all Artiodactyla species, both native and introduced, excluding feral species, i.e., *Bubalus bubalis* (Table 1), present within the Indonesian and Malaysian Borneo territory (here, we refer to these areas as the Malay Archipelago; Fig. 1). Although our focus was Indonesia, we included publications from Malaysian Borneo (i.e., Sabah and Sarawak States) because species and ecosystem are the same as in the Indonesian part of the Borneo Island, therefore, can be used as a comparison. This archipelago lies within three biogeographical realms (Brodie et al., 2018): Asiatic, where its fauna communities highly resemble fauna from the Asian mainland (Artiodactyla is associated with this realm and is highly diverse); Australian, which is characterized by fauna communities that resemble Australian fauna (Artiodactyla is not Australian fauna, and all species in this realm are introduced); and Wallacea, which is the transition zone between the two realms (Fig. 1).

We followed the species' taxonomic status adopted by the IUCN Red List of Threatened Species (https://iucnredlist.org; IUCN hereafter). If a new species was proposed, but the IUCN still used the previous taxonomy, we followed the IUCN classification. For example, *Sus verrucosus blouchi* was proposed to be *Sus blouchi*, but the IUCN considers the species *Sus verrucosus*; in this case, we considered all publications of *Sus blouchi* as *Sus verrucosus*. Likewise, if the taxonomic status has changed and the IUCN has adopted the new one, we adopted the current species name. For example, *Tragulus javanicus* from Sumatra and Borneo is now *Tragulus kanchil*, but *Tragulus javanicus* from Java remains the same.

Literature search

We conducted the literature search between April-June 2021 and updated it in July-August 2023 using Google Scholar with combinations of the following keywords: species scientific or local name, 'mammals', 'wildlife', 'Indonesia', geographic location in Indonesia (e.g., island's name or national parks), 'Sabah', and 'Sarawak' (Malaysian Borneo). We only selected peer-reviewed field-based

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research articles published before 2023. Research that only used data from captive individuals, simulated data, or did not involve data from wild populations was excluded from the literature list. Interview-based research was included as long as the subject was a wild population. We collected articles on various topics, including habitat use, habitat selection, population, inventory studies, and hunting investigation (i.e., studies focusing on hunting practices by local communities), as long as information about species-habitat relationships could be obtained. For example, Luskin et al. (2014) investigated hunting practices in Sumatra, but because the habitat where the Artiodactyla were hunted was provided (i.e., oil palm plantation), we know that the species was present there. If several publications used the same datasets, we only included articles that provide new information about species-habitat relationships. For example, we found four papers covering *Axis kuhlii* based on the same dataset (i.e., Rahman and Mardiastuti 2021; Rahman et al., 2017a, b, 2016), we only included the one most relevant to our purpose (Rahman et al., 2017b). We included articles published in English or Indonesian and noted if the articles were indexed in either Scopus or ISI Web of Science.

Synthesizing Artiodactyla-habitat relationships

We modified the categorization by Pfeifer et al. (2017) to group the species into four habitat-response type categories. Specifically, the groups considered were 1) *forest core*: species highly associated with intact or non-degraded forest; 2) *forest edge*: species that depend on forest but are highly associated with forest edge or degraded habitat; 3) *forest-no preference*: species that inhabit forest and use intact and edge or degraded areas equally; 4) *generalist*: species that uses multiple habitat types, such as forest, grassland, and plantations.

We grouped each species based on a pattern supported by most papers. For example, if the majority of articles described a particular species was more abundant in intact forests, we categorized this species in the forest core group, regardless of findings from the other articles. We did not assign a category to a species if there was no clear pattern among publications, i.e., the number of articles supporting one category rivals the number of articles suggesting a different one, or all studies of the

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species were not habitat selection or habitat quality studies (see issues below concerning research topics).

Geographical and taxonomic bias

We evaluated the geographical bias of research distribution based on eight island groups: *Sumatra, Java, Kalimantan, Malaysian Borneo, Sulawesi, Lesser Sunda, Maluku*, and *Papua* (Fig. 1). We grouped them following their administrative boundaries, e.g., satellite islands under the administration of Sumatra's provinces are part of the Sumatra group. Bali Island, although it is spatially part of Lesser Sunda Islands, is grouped with Java due to its similar biogeographical realm (i.e., part of the Asiatic realm). We estimated the centre coordinate of each article's study sites and used ArcGIS Pro's Kernel Density Estimation to create a heat map of research distribution across the archipelago. We compared the number of articles to the number of Artiodactyla species in each island group. We also compared the number of articles relative to the island groups' area size. An article that covered more than one island group was counted once for each group. We also assessed the geographical bias of each species by comparing the number of papers within the species distribution range. For example, *Muntiacus muntjac* is present in Sumatra, Java, Kalimantan, and Malaysian Borneo, so we examined research distribution for this species in those areas.

To examine taxonomic bias, i.e., the most studied and least studied species, we counted and compared the number of articles among species. If an article assessed multiple species, it was counted once for each species. For example, Rode-Margono et al. (2020) assessed *Axis kuhlii* and *Sus verrucosus*, so this article contributed to the number of articles for both species.

Bias from research approaches

We summarized how Artiodactyla were studied among different publications. In particular, we focused on the data collection, taxonomic level, sampling approach, and research topic. We grouped the data collection techniques into the following categories: *direct survey* (sampling techniques that require direct sighting of the animals), *indirect survey* (the occurrence of the animals was recorded based on traces left by the animals, such as footprints or dung), *camera trapping* (camera traps were used to record the animals), and *interview survey* (data was collected by interviewing local communities). We evaluated how these different data collection approaches might introduce bias in surveying Artiodactyla, given their elusive nature. We also recorded whether the study sampled single or multiple habitat types. For the taxonomic level, we noted which species were mainly studied at the genus level.

For research topics, we were specifically interested in identifying the proportion of true *habitat selection* (rather than use) and *habitat quality studies* because these studies allow researchers to identify critical habitat components of a species. We categorized a paper into a habitat selection study when the article included an evaluation of resources used and their availability (Manly et al., 2004; Johnson, 1980). We classified a paper into a habitat quality study if it evaluated demographic performances (i.e., abundance differences) or animals' body conditions among habitats (Mortelliti et al., 2010). If a paper did not meet the criteria for those two categories, we classified it into one or more of the following categories: *inventory, behaviour, demographic*, and *habitat use studies*. A study that only provided information on the species occurrence was categorized as an inventory study. We included hunting investigations in this category because they provide information on where the species was found. The behavioural studies include prey-predator relationships, activity patterns, and daily activities or time budgets. The demographic studies include papers assessing population abundance, group structure, and sex ratio. The difference between demographic and habitat quality studies is that a demographic study does not evaluate how habitat conditions affect the demographic parameters. We included an article in a habitat use study if it assessed how a species used resources but did not evaluate the selection process or did not consider habitat availability. For example, Maiwald et al. (2021) reported the occupancy estimates of six Artiodactyla species but did not analyse how the habitat types influence their occupancy.

RESULTS

Publications reviewed

We reviewed 110 articles published between 1988 and 2022, with the number of articles per year generally increasing (Fig. 2; Appendix S1). Twenty-four papers were single-species assessments, and 86 were multi-species assessments (not limited to Artiodactyla). Seventy-three articles were indexed in either Scopus or ISI Web of Science. Ninety articles were published in English, while 20 were in Indonesian. All papers published in Indonesian were not indexed. Table 2 shows the number of papers by species by island group.

Synthesis of Artiodactyla-habitat relationships

We categorized Artiodactyla species into the following groups: '**forest core species'** include *Capricornis sumatraensis* and *Muntiacus atherodes*; '**forest edge species'** include *Sus verrucosus*, *Bos javanicus* in Borneo, and *Axis kuhlii*; '**forest-no preference'** includes *Muntiacus muntjac* and *Rusa unicolor*; and '**generalist'** includes *Babyrousa togeanensis*, *Bos javanicus* in Java, *Rusa timorensis*, *Sus barbatus*, and *Sus scrofa*. For the other species, we did not find consensus or sufficient information to categorize them. For example, the number of papers that report a high association of *Tragulus napu* and *Tragulus kanchil* with intact forests was comparable to papers that report their tolerance to degraded forests.

Some species were consistently reported to have similar habitat relationships among different islands, while others were found to display different patterns on different islands. For example, *Rusa timorensis* in Java, Lesser Sunda, and Papua were reported to use a variety of habitats, and *Rusa unicolor* in Sumatra and Borneo were reported as a forest species but showed no preference in the forest condition. Conversely, *Bos javanicus* in Borneo was reported as a forest edge species, but in Java the species showed more generalist habits, such as using grassland, but showed greater sensitivity to human disturbance. We provide our summary of each species-habitat relationships in Appendix S2.

Taxonomic bias

We found that the numbers of papers were disproportionally distributed among species, with the three most studied species (*Rusa unicolor*, *Sus barbatus*, and *Muntiacus muntjak*) equalling 138 papers, which is comparable in number to the 143 papers concerning the remaining 17 species (Fig. 3; note that the sum of publications exceeds 110 since many papers were counted once for each species covered). The most studied species include *Rusa unicolor* (48), *Sus barbatus* (47), *Muntiacus muntjac* (43), *Sus scrofa* (31), *Tragulus kanchil* (22), and *Tragulus napu* (19). While the least studied species include *Babyrousa babyrussa* (0)*, Bubalus quarlesi* (0)*, Muntiacus montanus* (0)*, Babyrousa togeanensis* (1)*, Babyrousa celebensis* (2)*, Axis kuhlii* (2)*, Bubalus depressicornis* (3), and *Tragulus javanicus* (3). Numbers in parentheses report the number of papers.

Geographical bias

Research on Artiodactyla was unevenly distributed across the archipelago, with a concentration in the western regions (Asiatic realm), as illustrated in Fig. 1. Within the Indonesian territory, the number of publications was proportional to the number of Artiodactyla species present, specifically, there were more publications from island groups with more species (Fig. 4A excluding Malaysian Borneo, and Fig. 4B). The number of publications from Malaysian Borneo (including Malaysian territory) was the highest among island groups (Fig. 4A and 4B). The number of publications was not related to the size of the island groups (Fig. 4A and 4C).

For species present on multiple islands, the number of publications per island was not proportional to island size. For example, about 70% of publications of *Sus barbatus* and *Rusa unicolor* (distributed in Sumatra and Borneo) were from Borneo. Within Borneo itself, more than 70% of the publications were from Malaysia. For *Sus scrofa* (present in the islands of Sumatra, Java, Papua, and Lesser Sunda), more than 60% of publications were from Sumatra. For *Sus celebensis* (native to Sulawesi, introduced to Sumatra, Lesser Sunda, and Maluku), there was no study from the islands where it was introduced.

Within each island, some species were only studied at a few sites. For example, *Babyrousa celebensis*, distributed throughout Sulawesi, was only studied at two sites in North Sulawesi. In Java, all studies of *Rusa timorensis* were from one national park in East Java, and one study from Yogyakarta was on an experimental introduced population. Throughout Java, *Tragulus javanicus* was only studied at two sites in West Java and one on an offshore island in East Java. *Bos javanicus* in Java was also mainly studied in two national parks in East Java.

Bias from research approaches

Data collection and sampling approaches

Different data collection methods were employed to survey Artiodactyla species. All studies on *Sus verrucosus* in mainland Java and *Babyrousa togeanensis* relied on interview surveys to collect the data. All studies on *Babyrousa celebensis*, *Tragulus javanicus*, and most on *Bubalus spp.* and *Sus celebensis*, relied on direct and indirect observations. For the following species, most studies utilized camera traps to collect data: *Tragulus napu*, *Tragulus kanchil*, *Sus scrofa*, *Sus barbatus*, *Rusa unicolor*, *Muntiacus muntjac*, *Muntiacus atherodes*, *Bos javanicus*, and *Axis kuhlii*.

More than half of the publications only sampled one habitat type, typically natural forest (90% of cases). Articles that covered more than one habitat type included two or more of the following in their sample: natural forest, forest plantation (i.e., acacia), and oil palm plantation.

Taxonomic precision

Thirty-three studies (more than 40% of publications of the respective species) analysed sympatric species only at the genus level. Specifically, 27 papers from Sumatra and Borneo combined *Tragulus napu* and *Tragulus kanchil* in their analysis, 15 papers combined *Muntiacus muntjac* and *Muntiacus atherodes* in Borneo, and three papers combined *Bubalus depressicornis* and *Bubalus quarlesi* in Sulawesi (See Table 2 to compare with the number of publications analysing those species separately).

Research topic

Except for *Axis kuhlii*, *Bos javanicus*, *Rusa timorensis*, and *Sus verrucosus,* more than 60% of the studies were not designed to assess habitat selection or quality. For example, out of 43 studies on *Muntiacus muntjac*, 34 were not designed to assess habitat selection or quality (i.e., mostly habitat use or inventory studies). Particularly for *Babyrousa celebensis, Babyrousa togeanensis, Bubalus depressicornis,* and *Tragulus javanicus*, all available studies were not habitat selection or habitat quality studies. In general, there were 49 inventory studies, 42 habitat selection studies, 11 habitat use studies, 10 behavioural studies, nine demography studies, and four habitat quality studies (note that the total number is greater than the total number of papers reviewed because there were papers with more than one topic).

DISCUSSION

We reviewed and summarized 110 publications covering the order Artiodactyla throughout Indonesia and Malaysian Borneo to identify potential bias in our knowledge of the species-habitat relationships. In this review, we discuss Indonesia's Artiodactyla in its entirety, not every species individually, although some species were highlighted as examples. For each species, we provide our summaries in Appendix S2. Through our review, we were able to identify three major sources of bias: 1) *geographical bias*, with most studies taking place in western Indonesia and Malaysian Borneo; 2) *taxonomic bias*, with the number of publications covering the three most studied species equivalent to the number of publications of the rest of the other species combined; 3) *bias in research approaches,* whereby a small proportion of studies quantified habitat selection or quality.

Synthesis of Artiodactyla-habitat relationships and management implications

Our summaries categorized Artiodactyla species into four groups, each with characteristics requiring different management strategies. We grouped *Capricornis sumatraensis* and *Muntiacus atherodes* as forest core species, suggesting that these species may severely decline if a substantial amount of undisturbed habitat disappears. This emphasizes the significance of protected areas in preserving or at least in slowing down the disappearance of intact habitats for conserving these animals (Gaveau et al., 2009). This finding also underscores the importance of allocating areas of intact forests in a landscape assigned for production (i.e., High Conservation Value Forest in forest concessions or plantations) to facilitate coexistence between production activities and forest core species (van Kuijk et al., 2009).

Managing forest edge species (i.e., *Sus verrucosus*, *Bos javanicus*, and *Axis kuhlii*) and forest-no preference species (i.e., *Muntiacus muntjac* and *Rusa unicolor*) might allow a higher degree of flexibility because they can persist in degraded forests, allowing multi-purpose land uses for both wildlife conservation and production, such as in logged forests. However, despite being able to persist in recovering habitats, they still depend on the existence of forested landscapes, which emphasizes the value of logged forests over non-forested land-uses (Kitayama, 2013; Meijaard and Sheil, 2007). Supporting timber companies that can perform sustainable forest management (i.e., Reduced Impact Logging/ RIL) may encourage these companies to continue this practice (Gullison, 2003). Currently, RIL is not mandatory in Indonesia, and such support may also promote the adoption of this practice by other companies.

Generalist species require careful management, particularly those that can exploit human-modified habitats (e.g., *Sus scrofa* and *Babyrousa togeanensis*). These species are often considered pests if found foraging in agricultural areas, leading to human-wildlife conflicts. Besides increasing mortality risk, human-wildlife conflict could also diminish public support for conserving the species (Gemeda and Meles, 2018). Therefore, landscape management should also integrate human-wildlife conflict mitigation strategies (Nyhus, 2016).

We emphasize that the management strategies we discussed above are conceptual. We understand that integrating conservation is not as simple as fitting knowledge of the Artiodactyla-habitat relationships into the spatial development plan. High-conservation-value regions in Indonesia frequently overlap with areas of significant economic importance, which serve as a crucial source of national income (Carwardine et al., 2008), not to mention socio-cultural diversity, which will require more local and multidisciplinary approaches (Laurance et al., 2012). Nevertheless, we show that understanding species-habitat relationships could guide the integration of conservation strategies into development plans, and our focus here is addressing potential biases from the existing literature that could undermine this knowledge.

Our review indicates that existing research publications were still limited in understanding Artiodactyla-habitat relationships. Notably, we could not adequately summarize the habitat relationships for nine Artiodactyla species. Also, our summaries may differ from general knowledge about the nature of the species or are probably even inaccurate. For example, *Babyrousa celebensis* was assumed to be a forest core species (Macdonald, 2017), but we did not find sufficient evidence to support this claim. This limitation happened for several reasons. First, the number of studies for some species was too low (including three species with no field-based study ever published). Second, there was no consensus among studies on species-habitat relationships. For example, about half of publications on *Tragulus napu* and *Tragulus kanchil* suggested that they depend on the availability of intact forests (i.e., forest core species), whereas the other half suggested they can also use degraded forests equally (i.e., forest-no preference). Third, many studies were not designed to assess habitat selection or quality, so we could not find a clear pattern of the species' responses to the changing habitat. We will discuss these sources of bias in more detail in the following sections.

Geographical and taxonomic bias

Geographical bias

Artiodactyla research in Indonesia was mainly conducted in the western part of the archipelago, corresponded to the number of species present, regardless of the size of the area (Fig. 1; Fig. 4). The amount of research in western Indonesia, the Asiatic realm, was expected to be higher than in the eastern parts because the number of species present is also higher. In the Malay Archipelago, island size is not correlated with the Artiodactyla species richness. For example, West Papua is almost as large as Sumatra but has the lowest number of Artiodactyla species, and all species are introduced. Because of the biogeographic characteristics of this archipelago, the species richness of Artiodactyla is higher in the Asiatic realm, and then declines towards the east (Lohman et al., 2011).

Besides this biogeographical characteristic, the average travel time to large cities (i.e., access from airports or other major transportation systems) is higher in eastern Indonesia, resulting in higher operational costs (Weiss et al., 2018). Therefore, a limited research budget in the country (Rochmyaningsih, 2018b; Carwardine et al., 2008) also limits the ability to perform research in eastern Indonesia. Higher operational costs may also explain the fewer studies on minor islands (e.g., no study on Sumatra's satellite islands), which are typically less developed.

The more intensive research activity that we recorded for Artiodactyla in western Indonesia, particularly in Sumatra and Borneo, could also be affected by the presence of highly charismatic fauna, such as the Sumatran tiger, the Sumatran elephant, the Sumatran rhinoceros, and the orangutans, which attracted more research investment, including the establishment of research stations by several NGOs (e.g., Frankfurt Zoological Society, Wildlife Conservation Society, and World Wildlife Fund). Although it is not their primary focus, data on Artiodactyla were often collected as by-catch, i.e., through camera trapping. Also, these NGOs may attract more research by providing basecamps, team support, and even student internships. About 25% of the research publications we reviewed were supported by local NGOs in some ways, such as data sharing, field support, or funding. The deforestation issue, more prevalent in Sumatra and Borneo (Margono et al., 2014), was another reason for more research taking place in these regions, as indicated by the 40% of publications there were related to deforestation or fragmentation.

In Malaysian Borneo, the number of publications was higher than any other Indonesian island group despite sharing the same species and being less than half the size of Kalimantan (Fig. 4). This pattern may have several causes. First, research spending is correlated with the number of publications produced (Meo et al., 2013). From 2000 to 2020, Malaysia allocated about 0.95% of its gross domestic product annually for research, compared to Indonesia, which allocated only about 0.17% (UNESCO Institute for Statistics, 2023). Second, obtaining research permits in Indonesia is challenging, particularly for foreign researchers, which may potentially limit international collaborations (Rochmyaningsih, 2021, 2019, 2018a).

The general geographical bias described above also correlated with the geographical bias of each species. For example, the high research density in Malaysian Borneo also caused most *Sus barbatus* and *Rusa unicolor* studies to be from this region. Similarly, less research in Wallacea resulted in studies of *Babyrousa celebensis* and *Bubalus depressicornis* only within a small part of their distribution range. A species could have different habitat relationships in different areas (see *Bos javanicus* and *Muntiacus muntjac* in Appendix S2); therefore, the poor spatial coverage of research could lead to improper generalization of the species-habitat relationships (Martin et al., 2012).

Taxonomic bias

Geographical bias contributed to taxonomic bias. The most studied species (i.e., *Sus barbatus*, *Rusa unicolor*, *Muntiacus muntjac*, *Tragulus kanchil*, and *Tragulus napu*) are distributed in Sumatra and Borneo, which were also the two most studied islands. Most papers covering Sumatra and Borneo were multi-species assessments, with more than 80% using camera traps to collect data (more discussion about the usage of camera traps below). Therefore, one paper could contribute research on multiple species, including those species we listed as the most studied. Similarly, most of the least studied species are distributed in eastern Indonesia, i.e., all babirusas (*Babyrousa spp*.) and all anoas (*Bubalus spp.*), where the number of publications is also limited. This is contrary to the assumption that charismatic species tend to get more attention since babirusas and anoas are known as Sulawesi's or Wallacea's flagship species, suggesting that Artiodactyla are considered less charismatic than other megafauna in Indonesia (Burton et al., 2005; Caldecott et al., 1993). The new taxonomic classification might also affect the number of publications by creating new research attention and opportunities, i.e., most conservation grants are targeting species level research. Three allopatric babirusas were previously considered a single species (Meijaard and Groves, 2002); should the three species be recognized earlier, it could potentially attract more research for each species.

Among the least studied species, the taxonomic status of *Muntiacus montanus* and *Bubalus quarlesi* is uncertain. The classification of *Muntiacus montanus* as a distinct species from *Muntiacus muntjac* is unclear, given that it is listed as a species in the IUCN (Timmins et al., 2016) but not in the Mammal Diversity Database (Mammal Diversity Database, 2023). Also, whether *Bubalus quarlesi* is a distinct species from *Bubalus depressicornis* is doubtful (Burton et al., 2005). Currently, there is no field-based ecological study on *Muntiacus montanus* and *Bubalus quarlesi*, and this taxonomic uncertainty raises questions about whether investing research efforts for them as independent species units will contribute to the conservation of the species (Mace, 2004).

Bias from research approach

Data collection and sampling approaches

Camera trapping is probably the most advantageous method to study Artiodactyla, particularly for its ability to record multiple species in a single survey (Trolliet et al., 2014; O'Connell and Nichols, 2011). This method has been employed frequently in western Indonesia and Malaysian Borneo, contributing to the large amount of research for the most studied species, i.e., most studied species were from those regions. Also, although animals could change their behaviour around camera traps (Meek et al., 2014; Séquin et al., 2003), the absence of humans enables camera traps to record animals that will generally flee from humans.

Direct and indirect observations were still favoured methods to study *Babyrousa celebensis*, *Bubalus spp.*, *Sus celebensis*, and *Tragulus javanicus,* probably because they did not require substantial financial investment like camera trapping. However, such methods are more susceptible to false absences because animals may avoid researchers during the survey (Elenga et al., 2020; Fragoso et al., 2016). In many places, Artiodactyla are the primary target for bushmeat hunting (Bennett and Robinson, 1999), and they have developed behaviour to avoid humans. Combined with dense vegetation that limits the surveyors' field of view, direct observation becomes challenging to survey terrestrial Artiodactyla (Aguiar and Moro-Rios, 2009). Moreover, without proper training, field surveyors are prone to misidentify species (Fragoso et al., 2016).

Some studies relied on interview surveys to collect data, although this method is probably less reliable for ecological studies. First, local people were not trained to observe wildlife for scientific purposes, hence, they may provide inaccurate information. Second, sightings by locals may not represent the spatial distribution of the animals because locals did not spend a proportional amount of time in wildlife habitats. For example, locals likely spend more time in agriculture fields than in the forests so that they may observe more animals around their fields. Third, they may hide or deliberately provide false information because they fear prosecution (Meissner et al., 2012), for example if they have hunted protected species. Nevertheless, because of their spatial and long-term connection with their environment, local knowledge may provide valuable information that can be overlooked by field surveys (Predavec et al., 2016).

About half of the studies only sampled one habitat type, predominantly natural forest. When budget and timeline are restricted, surveying one habitat type is probably the most practical option when organizing research. Also, different habitat types are usually managed by different agencies, such as a protected forest which is typically managed by a national park agency, a logged forest by a timber company, and a plantation by a plantation company. Therefore, designing a study spanning multiple land covers may involve complex administrative procedures besides being financially more costly. However, focusing on one habitat type may potentially overlook the habitat use of a species among different habitats. A species assumed to be a forest species may turn out to be more of a generalist than previously thought because of this sampling limitation.

Taxonomic precision

We found that closely related sympatric species were often analysed at the genus level. Ideally, two or more sympatric species should be examined at a species level, but their similar appearance made species identification difficult. For example, in two studies, anoas (*Bubalus depressicornis* and *Bubalus quarlesi*) were studied by surveying their dungs or footprints, which made it almost impossible to distinguish between the two species, not to mention the taxonomic uncertainty (see above) which added more complexity in species identification. Even for sympatric species with an established classification and distinct morphological characteristics, i.e., *Muntiacus atherodes* vs. *Muntiacus muntjac* and *Tragulus napu* vs. *Tragulus kanchil*, identification was still challenging, although pictures or videos of the animals were recorded, i.e., most studies analysing them at the genus level used camera traps.

Analysing sympatric species at the genus level could introduce bias, especially if each species has different traits. Our summaries of papers analysing them at the species level show that *Muntiacus muntjac* appeared more tolerant to habitat degradation than *Muntiacus atherodes*, and either *Tragulus kanchil* or *Tragulus napu* was more tolerant than the other. This shows that combining data from two sympatric species could potentially overlook important species-habitat relationships. Admittedly, identifying sympatric species is challenging, and compromising the data is often unavoidable, either by excluding observations that could not be identified to the species level or accepting that genus-level analysis is the best option.

Research topic

Habitat selection and habitat quality studies should be available to infer species-habitat relationships, especially when wildlife conservation and management become a concern. These studies, if properly done, will inform us of the key habitat requirements and conditions that support the greatest fitness of a species (Tellería, 2016). Such information is valuable as guidance to planning conservation strategies, such as evaluating the current design of a protected area (Jati et al., 2024), planning and segregating human structures from essential habitats (Rio-Maior et al., 2019), and managing corridors to maintain habitat connectivity (Killeen et al., 2014).

However, the majority of studies on Artiodactyla species in Indonesia were not designed to provide such information. Solely relying on studies that did not address habitat selection or quality could be misleading. For example, if a species was detected in several habitat types, including human-modified ones, we may assume that the species is a generalist. However, whether the species can perform well in various habitats or depends on particular resources is unclear. Animals may also be present in a sub-optimal habitat because their preferred habitat is not available, they are unable to immediately move or respond to disturbance (Kuussaari et al., 2009), or they avoid competition with more dominant individuals (Amarasekare, 2003).

The lack of habitat selection or habitat quality studies (less than 20% of studies on the respective species) has made us unable to adequately classify six Artiodactyla species (not including three species without published field research) into one of the four habitat response types. Particularly for *Babyrousa celebensis, Bubalus depressicornis*, and *Tragulus javanicus*, none of the available studies provide a clear pattern of habitat characteristics that can support these species. Even for species we managed to categorize, we still need to be cautious in interpreting their habitat relationships, considering that many available studies did not assess habitat selection or quality. For example, *Babyrousa togeanensis* was categorized as a generalist species primarily from a single interview-based paper that reported its lack of association with forested habitats, as it was predominantly observed in agricultural and coastal areas. However, the study mainly evaluated habitat use in areas where locals saw the animal, so the influence of habitat availability on the species' habitat use was unclear. A recent habitat selection study (Jati et al., 2024, not part of the literature list) shows that the availability of forests highly influenced the habitat selection of this babirusa.

It was expected that basic studies, such as inventory studies, would be the dominant topic among publications because assessing biodiversity is among the first steps in conservation (Boulinier et al., 1998), particularly in the Malay Archipelago where many areas lack such information (Collen et al., 2008). Also, habitat selection or habitat quality studies are typically more expensive due to the large sample size requirements and sampling techniques, e.g., radio telemetry (Manly et al., 2004), adding

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limitations to researchers with limited budgets. Regardless, basic data such as species occurrence across the archipelago is also essential for developing conservation strategies, such as mapping and evaluating the species distribution range (Ke and Luskin, 2019; Merow et al., 2017)

However, even such basic information is lacking for many Artiodactyla species. For example, *Babyrousa celebensis* is distributed across the Sulawesi Mainland (Macdonald, 2017), but the only two field-based studies of the species were in North Sulawesi, so a precise estimate of the current species range is unavailable. This is primarily true for the least studied species since their spatial research coverage was minimal. Introduced populations, such as *Rusa timorensis* and *Sus scrofa* in eastern Indonesia, as well as introduced *Sus celebensis*, are also less explored. Although introduced populations are arguably less prioritized, managing them without knowing where they are will be problematic.

Publication approach

About one-third of the publications we reviewed were not indexed in either Scopus or ISI Web of Science, including all papers written in Indonesian. Non-indexed papers are less visible (Allen and Weber, 2015), making them less likely to contribute to developing knowledge of a topic, in this case, Artiodactyla-habitat relationships. Moreover, papers written in Indonesian further lower their visibility because they are mostly unseen by international readers. Non-indexed articles also have higher bias potential because they usually undergo a poor peer-review process (Clements et al., 2018). However, although we need to be more cautious, non-indexed papers, including articles written in Indonesian, are also important source materials to develop our knowledge, especially for rarely studied species or regions (Konno et al., 2020). For example, all publications on *Tragulus javanicus* were not indexed.

Limitations of our study

We acknowledge that despite our intensive effort to gather research publications under our criteria, some papers might be missed from our explorations. Also, there might be publications written in languages other than English or Indonesian that we could not review. Nevertheless, we are confident that we have covered a significant number of papers to adequately summarize and examine research bias in the Artiodactyla-habitat relationships in Indonesia.

Priorities for future research

Our review demonstrates significant biases in the publications covering Artiodactyla in Indonesia. We showed that most studies took place in the western part of the archipelago and significantly less coverage of species from eastern regions. We also showed potential bias caused by researchers' approaches in studying Artiodactyla. In the following paragraphs, we provide suggestions for future research priorities to develop knowledge on Artiodactyla-habitat relationships in Indonesia.

Improving research on less studied species

We encourage researchers to conduct studies on poorly known Artiodactyla species, specifically 1.) species lacking field-based studies focusing on them, including *Babyrousa babyrussa* (Vu), *Bubalus quarlesi* (En), and *Muntiacus montanus* (DD); and 2.) species covered in few studies with inadequate research approaches and poor geographical coverage, including *Babyrousa celebensis* (Vu), *Babyrussa togeanensis* (En), *Bubalus depressicornis* (En), *Sus celebensis* (NT), *Sus verrucosus* (specifically in Java mainland; En), and *Tragulus javanicus* (DD). Abbreviations in the parentheses are IUCN Red List categories (please refer to Table 1). In the case of *Bubalus quarlesi* and *Muntiacus montanus*, we endorse further taxonomic evaluation of these species to clarify whether they should be managed or studied as independent species units. Most species distributed in eastern Indonesia are also listed above, so improving the study on those species will also improve research in those regions. Almost all of those species are also listed by IUCN as threatened or Data Deficient, so they are eligible subjects for numerous small conservation research grant schemes, which is an excellent opportunity for researchers, especially Indonesian nationals, to raise research funding.

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Improving basic research

Our review indicates that basic information for many species, such as species distribution and abundance (i.e., a range of possible densities reached by the species), is still lacking. We encourage studies to improve basic information such as distribution (i.e., area of occupancy) and abundance (i.e., population or abundance indices), particularly but not limited to the least studied species. It is also important to develop a standard monitoring protocol for species of conservation concern (i.e., protected or endangered) to evaluate the effectiveness of conservation strategies in place over time.

Camera trapping is an advantageous option to collect such basic data. First, all Artiodactyla species are terrestrial and relatively large; therefore, they are suitable targets for camera trapping (Ancrenaz et al., 2012). Second, camera traps can record multiple species in a single survey. Even if Artiodactyla is not the primary target, Artiodactyla data can still be collected. We encourage that basic habitat data and spatial information (i.e., coordinates) of the camera trapping sites also be recorded for habitat selection analysis (see below). Third, abundance indices (i.e., relative abundance index or occupancy probability) and even true abundance can be estimated through camera trapping (Nakashima et al., 2017; Chandler and Andrew Royle, 2013). Fourth, having each observation documented as a picture or video makes species identification more reliable, although still challenging for some species, i.e., sympatric species. Lastly, camera traps are currently more affordable than in previous decades, therefore a single small research grant can cover a reasonable number of cameras to perform a study. Many institutions (i.e., universities, NGOs, and conservation agencies) also own camera traps, making collaboration or equipment sharing possible. However, it should be noted that camera trapping is not the perfect tool for all situations, and it should not discourage researchers with no access to camera traps from conducting research.

Increasing the number of studies assessing habitat selection rather than use

Our understanding of species-habitat relationships for about half of the Artiodactyla species is highly assumptive because few studies investigated habitat selection. This is understandable since basic data for many species is still limited. However, when resources allow, we encourage researchers to integrate habitat selection analysis into their studies, allowing a more in-depth investigation into species-habitat relationships. Indeed, performing a habitat selection study will require more effort than, for example, an inventory study because habitat characteristics and availability need to be assessed. However, with the availability of free-access satellite imagery (i.e., Landsat and Sentinel imagery) and open-source platforms (i.e., Google Earth Engine and QGIS), remote sensing can become a cost-effective option to evaluate habitat conditions on a landscape scale. We also encourage studies on how hunting practices affect Artiodactyla habitat selection, since hunting is also among the most serious threats to these taxa (Bennett and Robinson, 1999).

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Table 1. Distribution of Artiodactyla species in Indonesia’s island groups and Malaysian Borneo (refer to Fig. 1 for the island-group arrays). The species are arranged by their family (printed in bold). The abbreviation shown after the species name is the IUCN Red List Categories and Criteria: DD/ Data Deficient, LC/ Least Concern, NT/ Near Threatened, VU/ Vulnerable, EN/ Endangered, CR/ Critically Endangered. *: native, **: introduced.

Species	Sumatra	Borneo	Java	Lesser Sunda	Maluku	Sulawesi	Papua
Bovidae							
Bos javanicus (EN)		*	*				
Bubalus depressicornis (EN)						*	
Bubalus quarlesi (EN)						*	
Capricornis sumatraensis (VU)	*						
Cervidae							
Axis kuhlii (CR)			*				
Muntiacus atherodes (NT)		*					
Muntiacus montanus (DD)	*						
Muntiacus muntjac (LC)	*	*	*				
Rusa timorensis (VU)			*	**	**	**	**
Rusa unicolor (VU)	*	*					
Suidae							
Babyrousa babyrussa (VU)					*		
Babyrousa celebensis (VU)						*	
Babyrousa togeanensis (EN)						*	
Sus barbatus (VU)	*	*					
Sus celebensis (NT)	**			**	**	*	
Sus scrofa (LC)	*		*	**			**
Sus verrucosus (EN)			*				
Tragulidae							
Tragulus javanicus (DD)			*				
Tragulus kanchil (LC)	*	*					
Tragulus napu (LC)	*	*					

Table 2. Number of publications per species per island group. The species list is arranged by the total number of publications. Shaded cells indicate island groups where the species is not present. It should be noted that total papers per species and island group are greater than the actual number of reviewed articles because some papers were counted more than once.

Species	Borneo		Sumatra	Java	Sulawesi	Lesser Sunda	West Papua	Maluku	total per species
	Malaysian Borneo	Kalimantan							
Babyrousa babyrussa								0	0
Bubalus quarlesi					0				0
Muntiacus montanus			0						0
Babyrousa togeanensis					1				1
Axis kuhlii				2					2
Babyrousa celebensis					2				2
Bubalus depressicornis					3				3
Bubalus spp.[1]					3				3
Tragulus javanicus				3					3
Sus verrucosus				4					4
Sus celebensis			0		7	0		0	7
Capricornis sumatraensis			9						9
Rusa timorensis				3	2	3	2	0	10
Muntiacus atherodes	10	3							13
Muntiacus spp.[2]	11	4							15
Bos javanicus	11	2		5					17
Tragulus napu	9	5	5						19
Tragulus kanchil	8	3	11						22
Tragulus spp.[3]	15	4	8						27
Sus scrofa			23	6		1	1		31
Muntiacus muntjac	7	4	22	10					43
Sus barbatus	30	10	8						47
Rusa unicolor	23	9	16						48
Total per island group	39	11	27	20	12	2	2	0	110

[1]*Bubalus depressicornis* and *B. quarlesi*

[2]*Muntiacus atherodes* and *M. muntjac* in Borneo

[3]*Tragulus napu* and *T. kanchil*

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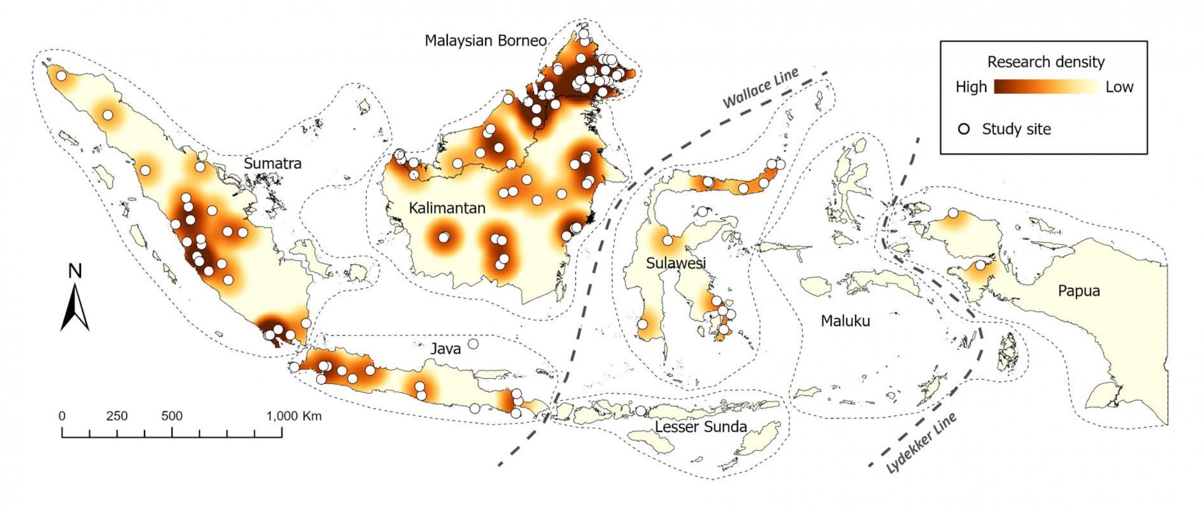

Fig. 1. Artiodactyla research hotspots across the Malay Archipelago (Indonesia and Malaysian Borneo). Colour gradients represent research density, with darker colours indicating areas where more research took place. The hotspot map was created using ArcGIS Pro's Kernel Density Estimation based on the study site's locations (white dots) estimated from the reviewed publications. Thin dashes show the island-group arrays but do not necessarily represent administrative boundaries. Thick dash lines are Wallace and Lydekker Lines, separating the archipelago into three biogeography realms: Asiatic realm (the west side of Wallace Line), Wallacea (between Wallace and Lydekker Lines), and Australian realm (the east side of Lydekker Line).

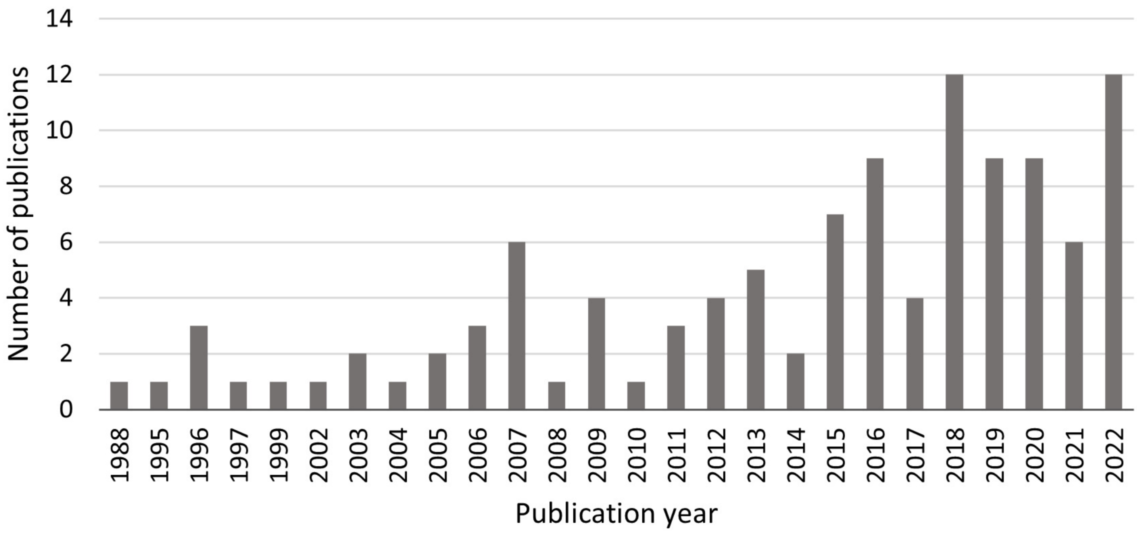

Fig. 2. Number of publications per year. The X-axis shows only the years with publications.

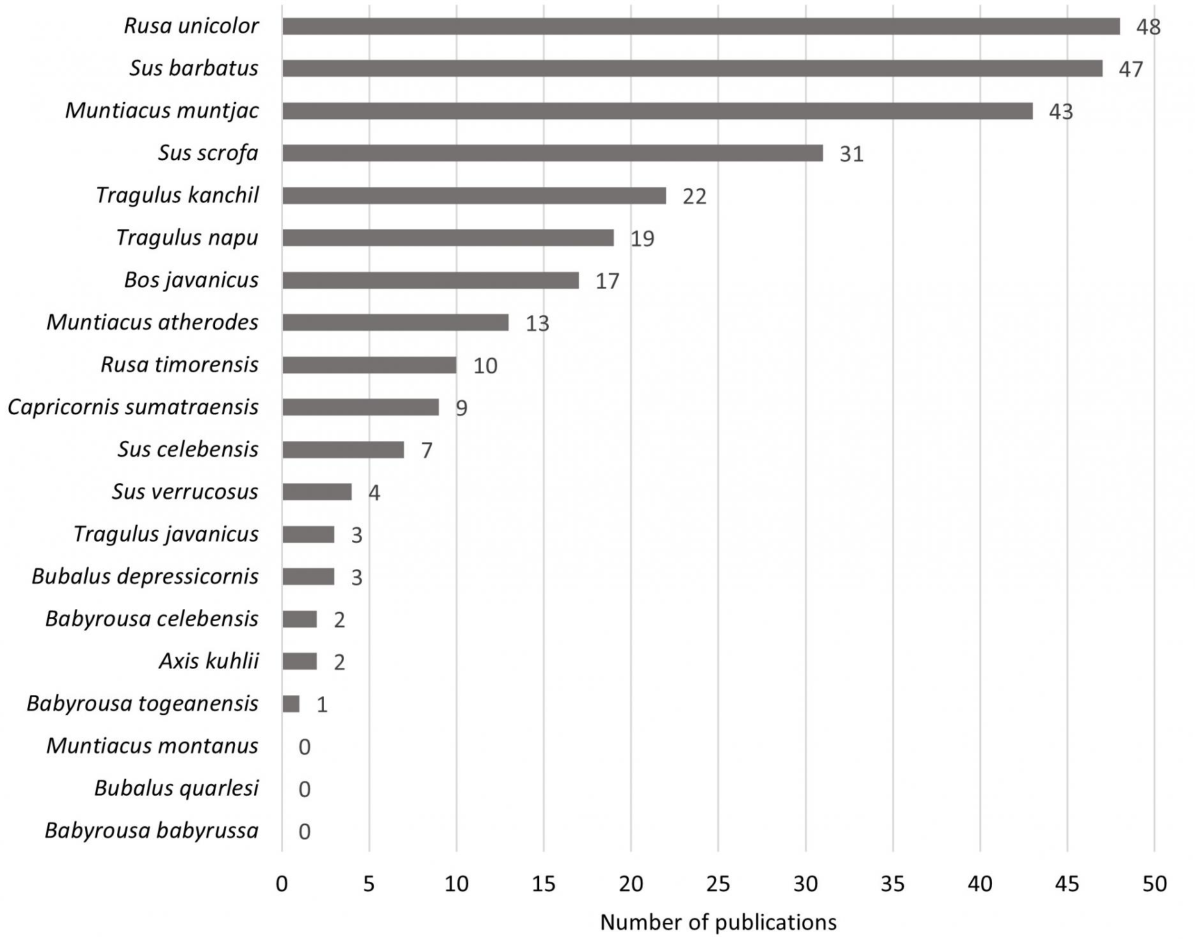

Fig. 3. Number of publications per species. Species are arranged from the least studied to the most studied. Numbers above the bars show the number of papers covering each species. These graphs were summarized from 110 research publications covering Artiodactyla species-habitat relationships in Indonesia and Malaysian Borneo published between 1988-2022. The sum of publications exceeds 110 since many papers cover multiple species.

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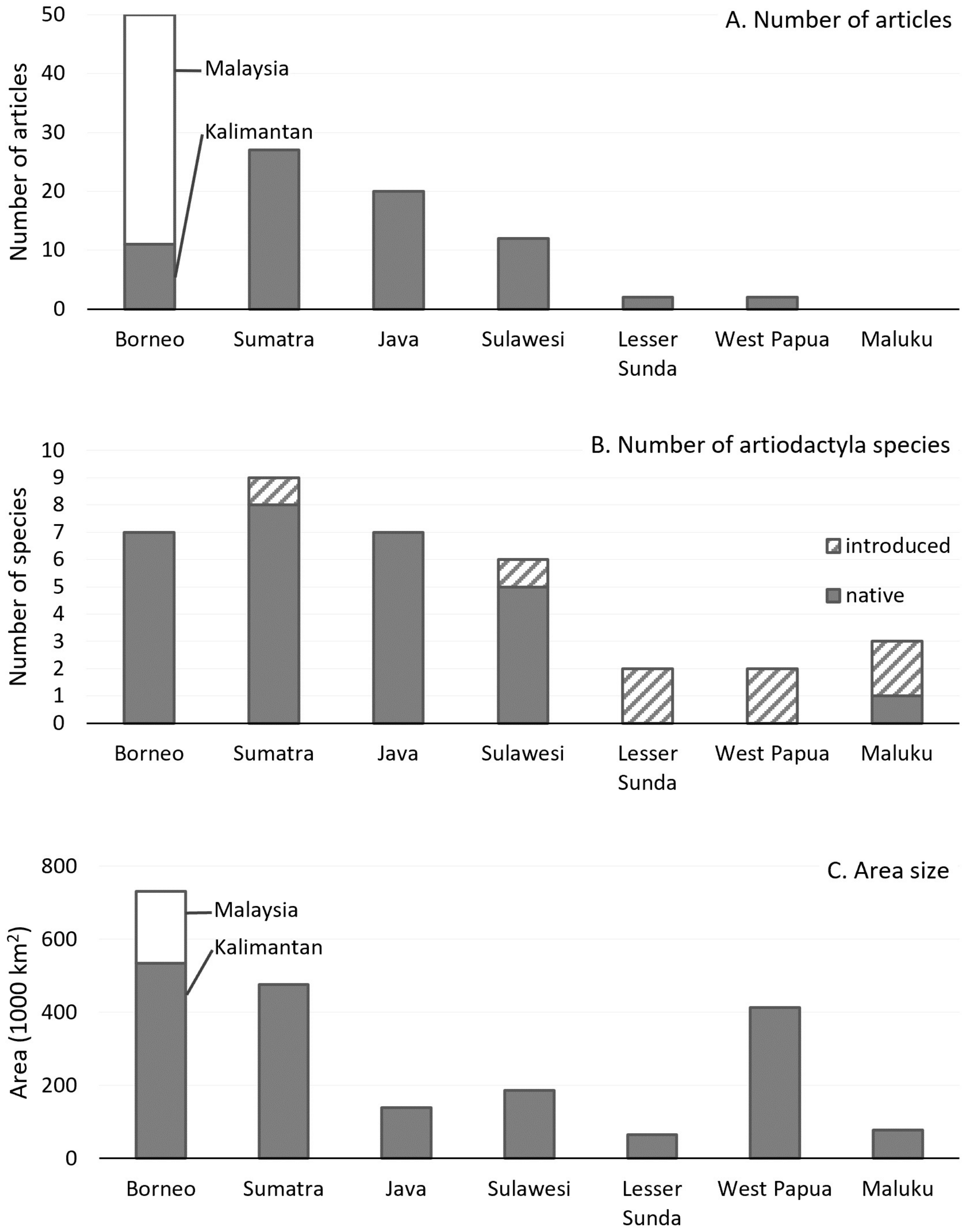

Fig. 4. Number of publications per island group, compared to number of species and area size. A: Number of papers per island group. B: Number of Artiodactyla species per island group, including native and introduced species. C: Area size of island groups. Island groups in all panels are arranged following the number of papers. These graphs were summarized from 110 research publications covering Artiodactyla species-habitat relationships in Indonesia and Malaysian Borneo published between 1988-2022.

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Tables

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Table 1 and Table 2 (revised)

Figures

Figure 1 - Download source file (1.01 MB)
Fig. 1. Artiodactyla research hotspots across the Malay Archipelago (Indonesia and Malaysian Borneo). Colour gradients represent research density, with darker colours indicating areas where more research took place. The hotspot map was created using ArcGIS Pro's Kernel Density Estimation based on the study site's locations (white dots) estimated from the reviewed publications. Thin dashes show the island-group arrays but do not necessarily represent administrative boundaries. Thick dash lines are Wallace and Lydekker Lines, separating the archipelago into three biogeography realms: Asiatic realm (the west side of Wallace Line), Wallacea (between Wallace and Lydekker Lines), and Australian realm (the east side of Lydekker Line).

Figure 2 - Download source file (36.34 kB)
Fig. 2. Number of publications per year. The X-axis shows only the years with publications.

Figure 3 - Download source file (75.21 kB)
Fig. 3. Number of publications per species. Species are arranged from the least studied to the most studied. Numbers above the bars show the number of papers covering each species. These graphs were summarized from 110 research publications covering Artiodactyla species-habitat relationships in Indonesia and Malaysian Borneo published between 1988-2022. The sum of publications exceeds 110 since many papers cover multiple species.

Figure 4 - Download source file (109.42 kB)
Fig. 4. Number of publications per island group, compared to number of species and area size. A: Number of papers per island group. B: Number of Artiodactyla species per island group, including native and introduced species. C: Area size of island groups. Island groups in all panels are arranged following the number of papers. These graphs were summarized from 110 research publications covering Artiodactyla species-habitat relationships in Indonesia and Malaysian Borneo published between 1988-2022.

Supplementary Online Material

File 1 - Download source file (35.68 kB)
Appendix S1 contains list of publications being reviewed in this study and their brief summary.

File 2 - Download source file (1.2 MB)
Appendix S2 provides summary of Artiodactyla species-habitat relationships in Indonesia, developed from 110 field-based research papers