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The last supper: Conservation implications of Sumatran rhinos selective foraging ecology

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ABSTRACT

Centuries of overhunting and habitat loss have driven Sumatran rhinos (*Dicerorhinus sumatrensis*) to the brink of extinction, with the IUCN Red List estimating fewer than 30 mature individuals in the wild and only 11 in captivity. The scarcity of ecological research and the challenges of studying this critically endangered forest megaherbivore limit the effectiveness of conservation efforts. We conducted 28 h of focal observations on four Sumatran rhinos at the Sumatran Rhino Sanctuary in Way Kambas National Park to quantify their diet composition, feeding preferences, and foraging impacts in old-growth forest. Using a functional heterogeneity framework, we classified food resources into optimal, staple, buffer, and reserve categories based on preference ratios and availability. Sumatran rhinos were highly specialized browsers, feeding almost exclusively on the apical buds of dicot saplings. Of the 179 plant species from 45 families consumed, most belonged to optimal or staple categories, with limited use of buffer and reserve resources. Foraging impacts were less destructive than those of sympatric Asian elephants (*Elephas maximus*), with an estimated annual damage of ~7300 stem breakages—about one-fifth of the damage caused by an Asian elephant under similar conditions—and ~80,000 apical bud removals per rhino. These results emphasize the need to maintain diverse, structurally complex plant communities rich in optimal and staple resources when designing in-range captive breeding facilities and selecting post-breeding release sites. They also highlight the complementary ecological roles of Sumatran rhinos and other critically endangered Southeast Asian megaherbivores in sustaining forest ecosystem structure and function.

1. Introduction

The ongoing decline of megaherbivores, particularly in Southeast Asia, has reached critical levels, contributing to a biodiversity crisis with profound and lasting ecological consequences (Ripple et al., 2016, 2017). These large-bodied animals are key to ecosystem functioning (Malhi et al., 2016), and their loss triggers cascading disruptions (Dirzo et al., 2014). They influence seed dispersal, forest regeneration, and nutrient cycling (Campos-Arceiz and Blake, 2011; Malhi et al., 2016; Terborgh et al., 2025). Understanding such biotic interactions—particularly diet, food preferences, and foraging impacts—is essential for conserving threatened megaherbivores and the ecological roles they

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support.

Sumatran rhinos (*Dicerorhinus sumatrensis*), the last surviving members of the subtribe Dicerorhinina (Fischer von Waldheim, 1814; Groves, 2016), are solitary, elusive, forest-dwelling, and the smallest of the five extant rhinoceros' species, distinguished by two horns, hairy red-gray skin, and a prehensile upper lip (Hubback, 1939; Nardelli et al., 2025). Historically ranging from the Himalayan foothills to Indonesia (Corbett and Hill, 1992; Mahmood et al., 2021), their numbers collapsed due to intensive hunting (van Strien, 1975; Nardelli, 2014; KLHK, 2014) and habitat loss in the latter half of the 20th century (Vigne et al., 2025). Following their extirpation in Malaysia (in the wild in 2015 and in captivity in 2019; Gilchrist, 2019; Lam et al., 2020), they now survive only in a few remote landscapes in Sumatra and Kalimantan, Indonesia (Pusparini et al., 2015).

Conservation efforts both in situ and in distant ex situ facilities have largely failed (Rabinowitz, 1995; Rookmaaker, 2019). Current conservation strategies focus on capturing wild individuals and managing them in fenced breeding facilities within their native range (Zafir et al., 2011; Ahmad et al., 2013), an approach already anticipated by Hubback in 1939 (Hubback, 1939; van Strien, 2001). The Sumatran Rhino Sanctuary in Way Kambas National Park (SRS-WKNP), established in 1996, is the largest and most important such facility, providing extensive natural forest to support breeding.

As of August 2025, SRS-WKNP housed ten individuals—about 90 % of the global captive population—including three wild-born females, two males born at Cincinnati Zoo, and five rhinos born there since 2011. No deaths have occurred since 2011, a turning point in the program's success, in contrast with other programs, which recorded numerous deaths without a single birth (Rookmaaker, 2019). Plans are underway to expand SRS-WKNP and replicate its model in northern Sumatra (SRS Aceh Timur; Hanafiah, 2021) and Borneo (SRS Kelian Kalimantan; Gokkon, 2020). Understanding factors behind SRS-WKNP's success—particularly rhino diet and habitat relationships—is critical for identifying suitable locations for new breeding facilities and potential post-breeding release sites.

Sumatran rhinos feed on a variety of plants by biting saplings, cutting shoots, or stripping leaves with their prehensile lips (van Strien, 1985; Flynn, 1983; Nardelli et al., 2025). They are known to consume leaves from ~150 species (Strickland, 1967; van Strien, 1985; Flynn, 1983), with occasional stem consumption (Flynn, 1983; Borner, 1979), rarely eat herbaceous plants, and obtain most of their diet from closed-canopy forests (Flynn, 1983). However, much of this knowledge is based on indirect observations from decades ago.

Like other megaherbivores, rhinos play key roles in ecosystem functioning (Owen-Smith, 1988; Hyvarinen et al., 2021; Wielgus et al., 2023). For example, white rhinos (*Ceratotherium simum*) in South Africa maintain short grass swards used by other grazers (Waldram et al., 2008); black rhinos (*Diceros bicornis*) affect the survival of their preferred food plant, *Euphorbia bothae* (Luske et al., 2009); and greater one-horned rhinos (*Rhinoceros unicornis*) in Nepal enhance plant growth via nutrient-rich latrines (Awasthi et al., 2024).

Despite such evidence for other rhino species, the ecological roles of Sumatran rhinos remain largely undocumented (but see McConkey et al., 2022 on seed dispersal). With wild populations nearing extinction, their foraging impacts—and the ecological functions they support—may vanish before being understood. This gap has direct conservation relevance: without knowledge of the plant taxa, size classes, and structural features they rely on, and how they modify vegetation, habitat management in breeding facilities and release sites may fail to meet both nutritional needs and potential ecosystem functions. Documenting these interactions now is critical for integrating ecological requirements into recovery planning and anticipating the broader consequences of their loss from Southeast Asian forests.

Drawing on Owen-Smith's model of functional heterogeneity (Owen-Smith, 2002, 2004), we hypothesized that Sumatran rhinos would concentrate foraging on a narrow subset of optimal and staple resources—those most preferred and/or abundant—while also consuming a broader range of buffer and reserve species when available, reflecting some dietary flexibility. We predicted that, despite this flexibility, their foraging impacts on vegetation structure would be lower in magnitude but broadly comparable in type to those of sympatric Asian elephants (*Elephas maximus*; see Ong et al., 2023, Terborgh et al., 2025), with greater emphasis on selective browsing and less on destructive behaviors such as uprooting or breaking large stems. SRS-WKNP provides a unique opportunity to test these ideas through direct observation in a semi-natural forest environment. Our objectives were to: (1) quantify diet composition, (2) assess food preferences relative to resource availability, and (3) characterize the extent and nature of foraging impacts on the plant community. These findings aim to inform habitat management (e.g., breeding facility design, ecosystem restoration) and the selection of post-breeding release sites, while contributing to a broader understanding of the species' ecological role.

2. Methods

2.1. Study site

This study was conducted at SRS-WKNP, North Lampung, Sumatra, Indonesia (Fig. 1A). Way Kambas National Park (WKNP) covers an area of 1300 km^2 at altitudes of 0–60 m asl, with annual rainfall of 2000–3500 mm, and average daily temperatures of 27–30 °C (BPS Lampung Utara, 2024). The park's vegetation is dominated by lowland dipterocarp forests, swamps, and Imperata grasslands, and supports one of the last wild Sumatran rhino populations along with Sumatran elephants (*E. maximus sumatranus*), tigers (*Panthera tigris sumatrae*), and Malayan tapirs (*Tapirus indicus*). Javan rhinos (*Rhinoceros sondaicus*) were once present but the last individual was killed in 1961 (Wind et al., 1979).

SRS-WKNP is located inside WKNP. Despite its name, it should be classified as an 'in-range paddock captive breeding facility', not as a 'sanctuary' (see Leader-Williams et al., 1997 for a classification of rhinos' conservation areas). SRS-WKNP is managed by Yayasan Badak Indonesia (YABI). YABI is a working partner of Way Kambas National Park, Directorate General of Natural Resources and Ecosystem Conservation, Ministry of Forestry. It occupies ~200 ha of fenced old growth forest divided into individual 25-ha paddocks. Each rhino has two paddocks, and individuals are rotated every six months to allow for vegetation recovery.

SRS-WKNP' vegetation is characterized by large dipterocarps (*Shorea* spp., *Dipterocarpus* spp.), with a ground layer dominated by *Rubiaceae* shrubs and palms, especially *Salacca* spp. and *Pholidocarpus sumatranus* (Fig. 1B). The enclosures are frequently visited by other wildlife such as sambar (*Rusa unicolor*), muntjac (*Muntiacus muntjak*), and siamang (*Symphalangus syndactylus*).

In addition to naturally available forage, each rhino is offered ~100 kg per day of supplementary browse (branches with leaves) from nearby forests, mainly from Moraceae (*Artocarpus* spp.), Rubiaceae (*Uncaria* spp.), Convolvulaceae (*Decalobanthus peltatus*), and Clusiaceae (*Garcinia griffithii*). Rhinos typically consume only about one-third of this supplement (Awaliah, 2018).

2.2. Data collection

Conducting direct observations of Sumatran rhinos in the wild is not feasible due to their extreme rarity and the complexity of Sundaic rainforest vegetation (van Strien, 1985; Flynn, 1983). We therefore observed rhinos within the fenced, natural forest paddocks of SRS-WKNP.

We followed four focal individuals (two males and two females) for ~1 h sessions (one session = one independent observation), recording all plants foraged. Observations took place between 09.00 and 11.00 and 14.00–16.00 from July to September of 2024. For safety, only one

Fig. 1. (A) Map of Way Kambas National Park (WKNP), located in the southeast of the island of Sumatra, Indonesia (red rectangle in the inset map). (B) Habitat condition in one of the Sumatran rhinos' enclosures at the Sumatran Rhinoceros Sanctuary in Way Kambas National Park (SRS-WKNP). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

researcher (TSH) and one trained SRS-WKNP keeper entered the enclosure per session. The researcher focused on the focal rhino's mouth, recording the number of mouthfuls and the plant species and plant parts consumed; the keeper recorded the types of plant damage. We observed from $\leq$10 m using binoculars (Bushnell 10x42mm lens) and a Nikon P950 camera. We conducted one to two observations per day, recording a total of 28 sessions (i.e., ~ 28 h) on two male and two female rhinos ($N = 4$).

Here, we define ecological impact as direct, observable alterations to plants or vegetation structure caused by rhino feeding or handling, including removal of apical buds, stem or branch breakage, uprooting, and debarking. These represent primary pathways by which Sumatran rhinos can influence plant community composition, forest structure, and related processes.

We classified plant damage into five categories: (1) apical decapitation, defined as the removal of the apical meristem or the plant's growing tip; (2) main stem breakage, which occurs when a rhino applies sufficient force pulling the tip of a branch while feeding as to snap the plant's main stem; (3) branch breakage, involving the snapping or detachment of branches and twigs from the main stem; (4) pushing-over, where the plant is forcefully crushed to the ground, leaving it unable to regain its original posture; and (5) debarking, the stripping or removal of bark from the stem, typically by horn rubbing. In some mouthfuls, rhinos consumed multiple apical buds, which we recorded as a single apical decapitation; thus, the total buds consumed may be underestimated. To distinguish between foraging and non-foraging damage, we tagged damaged plants with colored labels, noting whether they were "eaten" or damaged without consumption.

We quantified plant availability using 8-m-radius circular plots (201.1 m^2) placed at the rhino's location at the 10-, 30-, and 50-minute marks of each observation session. Each plot was divided into subplots by plant size classes: a 1-m-radius for seedlings, a 2-m-radius for herbaceous plants, a 4-m-radius for saplings, gingers, and palms, and an 8-m-radius for trees. For saplings and trees, we measured height and stem diameter. In total, we established 84 availability plots. Plants were identified in the field by experienced botanists, and voucher specimens verified at Herbarium ANDA, West Sumatra. For life forms, we classified monocots as gingers, grasses, and palms; and dicots as trees, shrubs, and lianas. We followed Ong et al. (2023) for size categories: seedlings ($<$1 m tall), small saplings ($\geq$ 1 m tall and $<$1 cm dbh), large saplings ($\geq$1 cm dbh and $<$10 cm), and trees (dbh $\geq$10 cm).

2.3. *Data analysis*

We analyzed diet preference at the plant life form, species, and family levels using preference ratios (PR) adapted from Olivier (1978), English et al. (2014), and Ong et al. (2023):

$$\textbf{PR}, \textbf{ preference ratio} = \frac{RU}{RA}$$

where:

$$\textbf{RU, relative use} = \frac{\textit{Nu, number of times a plant type was eaten}}{\textit{Tu, total number of plant types eaten across all plant types}}$$

$$\textbf{RA, relative availability} = \frac{\textit{Na, number of available plants of a given type}}{\textit{Ta, total number of available plants across all types}}$$

A PR = 1 indicates no selection (i.e., the plant is consumed as expected based on its availability); PR >1 indicates preference, and PR < 1 indicates avoidance.

To link dietary patterns with theory, we applied a modified version of Owen-Smith's model of functional heterogeneity, which classifies food items into optimal, staple, buffer, and reserve categories based on nutritional value, growth potential, intake rate, and capacity to retain forage through the lean period (Owen-Smith, 2002). In our case, we adapted the framework and classified food items based on the combination of preference ratios and local availability. We defined (a) optimal resources as preferred (PR > 1) and rare (<35th percentile of availability); (b) staple resources as preferred (PR > 1) and abundant (≥ 65th percentile); (c) buffer resources as avoided (PR < 1) and abundant (≥ 65th percentile); and reserve resources are avoided (PR < 1) and rare (<35th percentile). This classification allowed us to assess both resource selectivity and potential dietary flexibility.

To estimate annual foraging impacts, we extrapolated observed damage rates using the assumption that Sumatran rhinos forage ~10 h per day (data from SRS-WKNP; Suharto et al., 2007), giving 3650 h per year (i.e., 10 h × 365 days). We multiplied observed hourly damage rates by this value, following Ong et al. (2023). We restricted our analysis to woody plants (lianas, shrubs, and trees) and the five defined damage types (apical decapitation, main stem breakage, branch breakage, debarking, and pushing-over).

All the analyses were conducted in R, and visualizations produced with *ggplot2* (Wickham, 2011).

3. Results

3.1. Food availability

In the availability plots, we recorded ~11,500 individual plants representing 80 families and ~ 600 species. Dicots dominated the vegetation, with the most abundant families being Rubiaceae (15 % of stems), Phyllanthaceae (12 %), Dilleniaceae (5 %), Annonaceae (3 %), and Melastomataceae (3 %). Monocots were less prevalent, comprising primarily Arecaceae (6 %), Zingiberaceae (1.4 %), Graminae (0.5 %), and Araceae (0.1 %). Ground cover was predominantly composed of non-vascular plants, particularly Selaginellaceae, which represented 13 % of all the individual plants (Appendix, Table S1).

The plant community was dominated by large saplings (28 %), small saplings (16 %), and non-vascular plants (14 %). At intermediate levels of abundance were shrubs (10 %), lianas (9 %), palms (6 %), grasses (6 %), and trees (5 %). Seedlings, herbs, and gingers, each contributed a minor proportion (2 %) to the overall plant abundance.

3.2. Diet composition

During the feeding observations, the Sumatran rhinos fed at a rate of 44.9 ± 1.2 mouthfuls per hour ($N = 28$ sessions, totaling ~28 h and 1256 mouthfuls). All the mouthfuls involved apical decapitation (details in Section 3.4).

The rhinos consumed plants from 45 families and 179 species, with 70 % of the taxa associated with closed canopy forest (Table S1). The diet was overwhelmingly dominated by dicots, accounting for 99 % of mouthfuls and 95 % of species consumed. In contrast, monocots contributed only 1 % of mouthfuls and 5 % of the species. The most frequently consumed plant families were Rubiaceae (37 % of mouthfuls), Phyllanthaceae (10 %), Lauraceae (6 %), Violaceae (5 %), and Annonaceae (4 %). At the species level, the most frequently consumed were *Lasianthus hirsutus* (16 % of mouthfuls), *Rinorea anguifera* (6 %),

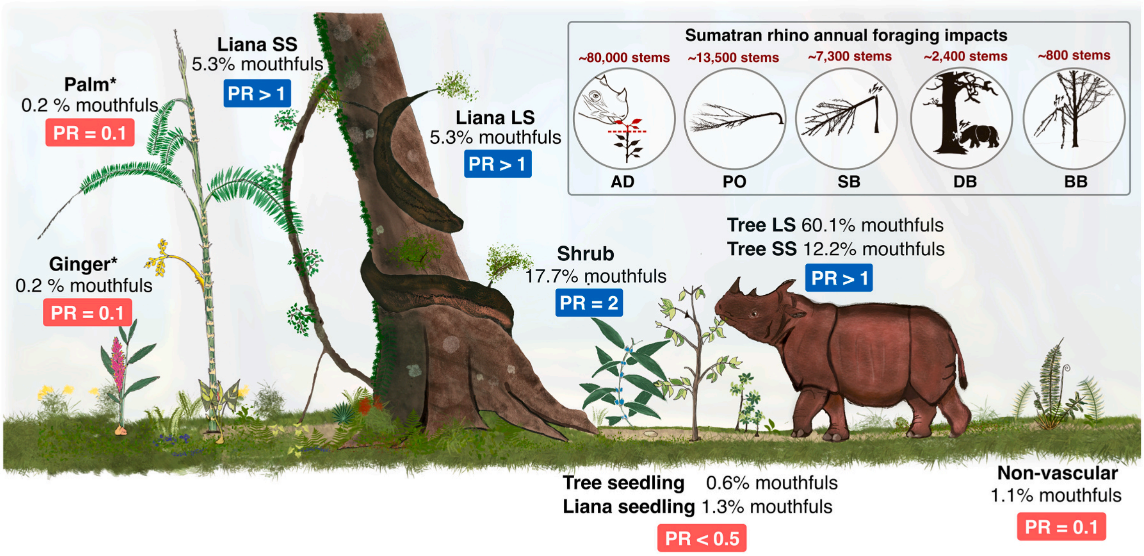

Fig. 2. Ratio representation of mouthfuls, rhino plant handling, apical decapitation, and preference ratio (PR) across plant life forms. Annual foraging impacts: AD, apical decapitation; PO, pushed over; SB, stem breakage; DB, debarked; BB, branch breakage. SS, small sapling; LS, large sapling. Asterisk (*) indicates monocots.

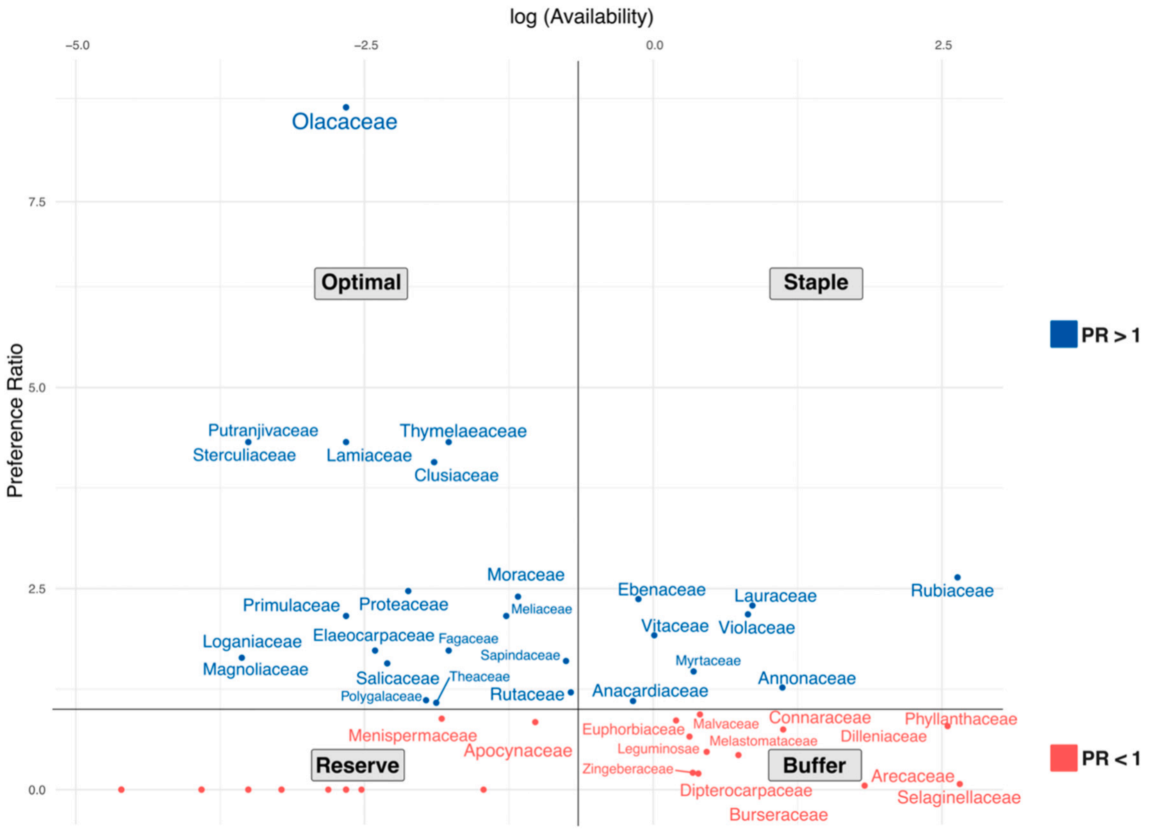

Fig. 3. Sumatran rhino's resource heterogeneity model. Preference ratio >1 indicates preferred plant families.

Fig. 4. Sumatran rhino plant handling behavior. (A) Red rectangle showing the apical decapitation signs. (B) Tree infection caused by debarking. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Neonauclea calycina (5 %), and *Cleistanthus sumatranus* (4 %). Structurally, large tree saplings were the primary food source, making up 60 % of mouthfuls, followed by small tree saplings (12 % of mouthfuls). Large liana saplings and small liana saplings, contributed moderately, at 5 % and 1.4 % respectively. Gingers and palms were consumed in very small quantities, each representing 0.2 % of the total diet (Fig. 2).

3.3. Food preferences and resource use

The rhinos were selective in their feeding behavior. They consumed plants of 25 families at rates higher than their availability, while other plants were eaten less frequently than expected based on their availability (Fig. 3). The most preferred families included Olacaceae (PR = 8.1), Lamiaceae, Putranjivaceae, Sterculiaceae, Thymelaeaceae (all with PR = 4.1), and Clusiaceae (PR = 3.8). By species, rhinos showed strong preference towards *Uncaria callophylla* (PR = 11.5), *Strombosia ceylanica* (PR = 9.2), *Uncaria callophylla* (PR = 8.6), and *Monocarpia maingayi* (PR = 8.6) (Appendix Table S1).

Conversely, rhinos strongly avoided all monocots, including gingers (Zingiberaceae; PR = 0.2) and palms (Arecaceae; PR = 0.1). Notably, only one individual (Harapan, a male) was observed feeding on ginger and palm once, while other individuals never did. None of the rhinoceros ate grasses (Graminae). Similarly, herbaceous plants available on the forest floor—such as star grass (Hypoxidaceae, 51 % of available herbs), pandan (Pandanaceae, 14 % of herbs), arrowroots (Marantaceae, 10 % of herbs)—were not eaten at all. Some abundant plants were scarcely eaten, leading to low PR scores, for example spike mosses (Selaginellaceae, PR = 0.1).

Applying the functional heterogeneity model (Fig. 3), 19 families were classified as optimal food resources (preferred but rare). These included the six most preferred families (Olacaceae, Putranjivaceae, Sterculiaceae, Lamiaceae, Thymelaeaceae, and Clusiaceae). Eight families were classified as staple foods (preferred and abundant), including Rubiaceae, Lauraceae, Ebenaceae, Vitaceae, Violaceae, Myrtaceae, Anacardiaceae, and Annonaceae. Twelve families were classified as buffer resources (abundant but not preferred), including Euphorbiaceae, Leguminosae, Malvaceae, Arecaceae, and Dipterocarpaceae. Just two families were classified as reserve resources (neither preferred nor abundant).

Structurally, the rhinos showed preference for large tree saplings (PR = 2.1), shrubs (PR = 2), small tree saplings (PR = 1.2), and large liana saplings (PR = 1.1); they showed lack of preference for small liana saplings (PR = 0.7) and both liana and tree seedlings (PR $<$ 0.5), and strong avoidance of gingers (PR = 0.2), non-vascular plants (PR = 0.1), and palms (PR = 0.1).

3.4. Plant handling and foraging impacts

The rhinos appeared to use sight and olfaction to identify and select food plants. Once a plant was selected, they used their incisors to bite off the twigs' apical area (terminal bud, leaves, and soft lateral branches; Fig. 4A). If the plants were too high to reach with their mouth, they used their chests or mouths to push down the plants, which sometimes resulted in pushing-over, branch breakage, or main stem breakage impacts. When feeding on a particular plant, the rhinos did not consume all its apical buds. Rather, they consumed a small amount and moved to eat from another plant, leaving many apical buds intact in the first plant. We did not quantify number of apical buds available.

We recorded 788 incidents of plant damage caused by the rhinos. Apical decapitation was the most common type of damage, accounting for 76.8 % of cases, followed by pushing-over (13.1 %), main stem breakage (7.1 %), debarking (2.3 %), and branch breakage (0.76 %). Apical decapitation was mainly recorded in large saplings (48 % of 605 cases), as it did pushing-over (73 %; $n = 103$), main stem breakage (80 %; $n = 56$), and debarking (56 %; $n = 18$). Branch breakage was evenly distributed, affecting large saplings, shrubs, and small saplings (33.3 % each; $n = 6$).

Rhinos were not observed consuming tree bark. However, both male and female rhinos were seen polishing their horns on trunks, resulting in tree debarking ($n = 18$ instances). In some cases (4 out of 18, involving both males and females), rhinos urinated—spraying urine into the debarked area—while scraping the ground soil using one hind leg (Fig. 4B).

The rhinos' feeding behaviors inside the barn paddocks differed from those in their natural habitat. In the barn paddock they consumed most plant parts provided by SRS-WKNP' keepers, including shoots, leaves, and mature twigs of both trees and lianas (Appendix Video 1).

The mean height of eaten plants was 1.65 ± 1.07 m, while damaged but not-consumed plants had a height of 3.03 ± 2.41 m. (Fig. S1). The stem size of eaten plants was 1.86 ± 1.36 cm and that of damaged but not-consumed plants was 3.42 ± 2.62 cm (Fig. S2). The average height of stem breaks was 0.82 ± 0.50 m tall ($n = 52$) composed from large saplings (84.9 %), shrubs (9.4 %), and small saplings (5.6 %).

3.5. Projected annual impacts

Our projections indicated that each individual rhino, foraging in old growth tropical forest, is expected to damage ~104,000 woody plants annually (simulated from $N = 28$ observation sessions). The damage consisted of ~80,000 stems suffering apical decapitation, ~13,500 stems being pushed over, ~7300 main stem breakages, ~2400 stems being debarked, and ~800 plants suffering branch breakage.

4. Discussion

Access to SRS-WKNP presented a unique opportunity to observe Sumatran rhinos, one of the world's most endangered megafauna, in their natural old-growth Sundaic forest habitat. Our findings reveal that, unlike sympatric Asian elephants, Sumatran rhinos are highly specialized browsers, primarily feeding on the apical buds of selected dicot saplings. They show a strong preference for these plants while avoiding monocots and herbaceous species. Contrary to our expectations, the foraging impacts of Sumatran rhinos were relatively mild, with little severe damage to the plant community compared to the more destructive foraging behavior of Asian elephants. This suggests that Sumatran rhinos exert less pronounced foraging impacts, highlighting their specific roles in forest dynamics.

4.1. Sumatran rhino diet and feeding preferences

Our findings provide new information about the feeding ecology of Sumatran rhinos, revealing a highly specialized diet dominated by dicots, particularly Rubiaceae, Phyllanthaceae, and Lauraceae. Apical decapitation was the predominant foraging behavior, present in all observed mouthfuls, with tree saplings constituting 95 % of their diet. Apical buds and young leaves are structurally tender and more nutritious due to early cell development, which requires high nitrogen and water content (Brenes-Arguedas et al., 2006). Compared to mature leaves and stems, younger leaves contain a higher richness of phenolic compounds (Liu et al., 2020), which serve as a defense strategy but are less effective against large mammalian herbivores (e.g., black rhinos; Scogings et al., 2021). Monocots, herbaceous plants, and non-vascular plants were largely avoided, reflecting the rhinos' strict browsing habits and limited dietary flexibility. Their brachydont dentition likely limits graze consumption, as their teeth are better suited to process softer, more tender plant material (Clauss and Dierenfeld, 2008).

Our findings align with previous research identifying Rubiaceae, Moraceae, Lauraceae, Clusiaceae, Anacardiaceae, and Myrtaceae as some of the most frequently consumed families (Strickland, 1967; Flynn, 1978; van Strien, 1985; Borner, 1979). In our study, those plant families were classified as optimal or staple resources under Owen-Smith's functional heterogeneity framework, with consumption exceeding their availability. The genus *Lasianthus* from Rubiaceae family was particularly notable, being among the most consumed species in both our study and previous work in Peninsular Malaysia (Flynn, 1978). In contrast, van Strien (1985) reported exclusive feeding on herbs such as *Elatostema* spp., gingers (Zingiberaceae), and giant taro (*Alocasia* sp.) in the Upper Mamas region of Gunung Leuser National Park (2000 m asl). In our study, herbs mostly fell under the buffer category (abundant but avoided), suggesting that Sumatran rhinos can exploit these resources when optimal and staple foods are scarce.

The avoidance of monocots, grasses, and herbaceous plants—including palms, gingers, and graminoids—suggests that Sumatran rhinos may be highly sensitive to habitat degradation and loss. Unlike Asian elephants, which exhibit greater dietary flexibility and consume significant quantities of monocots such as palms, gingers, and bamboo (Chen et al., 2006; Sitompul et al., 2013; Yamamoto-Ebina et al., 2016; Ong et al., 2023), Sumatran rhinos consistently avoided these plant groups, even when abundant (Appendix Video 2).

This strict dietary selectivity may contribute to their poor performance in captivity and heightened sensitivity to habitat loss. These findings highlight the importance of maintaining diverse, structurally complex plant communities in in-range paddocks and release sites. Providing a mix of optimal and staple food resources—as identified in this study—together with fallback options during periods of scarcity will be critical to maintaining rhino welfare in both captive and post-release contexts.

We acknowledge several limitations: our dataset is based on 28 observation sessions of four individuals, conducted during the dry season, in daytime hours only, within fenced forest areas, and on rhinos receiving supplementary food as part of captive breeding management. These factors may influence foraging behavior and limit generalizability. However, given the extreme rarity of Sumatran rhinos, the relatively mild seasonality in Sumatra, the high plant diversity in the enclosures, and the consistent selectivity patterns observed, we believe our findings are robust and highly relevant for designing and managing in-range facilities and selecting potential release sites.

Addressing these limitations will require further research. Additionally, future studies should investigate the chemical and physical attributes of preferred plants, including the potential role of secondary compounds, to better understand the drivers of foraging decisions.

4.2. Ecological impacts

By ecological impacts we refer to direct, observable changes to plants and vegetation structure resulting from rhino feeding and other plant-handling behaviors. These are primary pathways through which Sumatran rhinos may influence forest composition and structure, but not the only ones (see McConkey et al., 2022 for impacts via seed dispersal).

We recorded four types of foraging impacts (pushing over, apical decapitation, main stem breaking, and branch breaking) and one non-foraging impact (debarking), expanding upon Flynn's (1978) observations in Peninsular Malaysia. Sumatran rhinos showed a clear preference for smaller sapling-size plants (~1.65 ± 1.07 m) and selectively targeted soft, rapidly growing tissue. Large saplings sustained the highest damage rates. Malayan tapirs show similar browsing on young leaves but without exclusively targeting apical buds (Williams and Petrides, 1980; Simpson et al., 2013).

Debarking was not linked to feeding and likely functions in territorial marking (van Strien, 1985; Flynn, 1978). This behavior was often accompanied by urination and ground scraping, potentially leading to fungal or insect infection (Fig. 3) and, over time, tree mortality (Owen-Smith, 1988; Owen-Smith et al., 2019). Both sexes displayed this behavior, echoing previous reports of similar scent-marking habits in males and females (van Strien, 1985).

Compared with sympatric Asian elephants, the foraging impacts of Sumatran rhinos are structurally less destructive. While an elephant in old-growth forest may uproot and break ~39,000 saplings annually in Peninsular Malaysia (Ong et al., 2023), a rhino at SRS-WKNP would break ~7300 stems and decapitate ~80,000 plants per year. Rhinos do not uproot plants—the most destructive form of elephant feeding (Terborgh et al., 2024)— and their dominant impact, apical decapitation, can have neutral and even positive effects in some plant species by enhancing seed mass, fruit production, or branching (Huhta et al., 2000; Rooke and Bergström, 2007; Ward, 2010; Mesa et al., 2019). However, these benefits are likely limited to species with strong apical dominance (Barbier et al., 2017), and may reverse if browsing is too frequent, reducing survival or competitive ability.

By maintaining shorter vegetation through repeated browsing, Sumatran rhinos may create foraging opportunities for other herbivores, such as tapirs and deer. Their preference for closed-canopy dicots contrast with those of the critically endangered Sumatran elephants (Sitompul et al., 2013), suggesting potential for niche complementarity. This selectivity may also promote the persistence of less-preferred, carbon-rich taxa such as *Dipterocarpaceae*, *Leguminosae*, and *Burseraceae*.

As with diet patterns, our dataset is based on a small sample size collected under a limited range of conditions, which might have affected the rhinos' plant handling behaviors and the observed foraging impacts. Future studies should focus on evaluating the consequences of rhino foraging impacts on the plant community's structure, diversity, and composition.

4.3. Conservation management of Sumatran rhinos

Our findings indicate that Sumatran rhinos have specific and stringent habitat and dietary requirements, which likely contributed to the high mortality in past captive breeding programs (e.g., Rabinowitz, 1995; Rookmaaker, 2019). Their strong preference for closed-canopy saplings highlights the need to maintain a rich understory structure associated with old-growth Sundaic forests. Disturbed forests, with open canopies, abundant pioneer saplings, and high monocot density, are unlikely to meet these requirements. Habitat planning for captive breeding facilities should therefore include detailed vegetation surveys to ensure the availability of optimal and staple food resources, as identified in this study. For example, the proposed third Sumatran Rhino Sanctuary (SRS Aceh Timur) is in a disturbed forest adjacent to palm oil plantations, an environment unlikely to meet rhino resource needs (Fig. S2). Such surroundings increase the risk of disease transmission from domestic animals (e.g., Guerrero-Sánchez et al., 2022) and water pollution from pesticide runoff.

Future captive breeding facilities should be located exclusively within old-growth forests, with a minimum of 25 ha of natural forest per paddock, two paddocks per rhino, and flexible rotation schedules based on resource depletion, rather than fixed intervals.

Captive breeding alone will not secure the species' future. Although advanced breeding technologies for Sumatran rhinos hold promise (Nardelli, 2014; Havmøller et al., 2016; Payne et al., 2025; von Houwald et al., 2025), these technologies are not yet ready for widespread application (Roth, 2024). In parallel, Indonesia must strengthen law enforcement in rhino habitats and implement state-of-the-art surveillance systems. Indonesia's relative success in retaining the last populations of Sumatran and Javan rhinos into the 21st century—while these species have disappeared from elsewhere in their former ranges—demonstrates the nation's capacity. The future of both rhino species now depends almost entirely on Indonesia's sustained conservation commitment.

Access to SRS-WKNP provided valuable insights into the dietary and habitat preferences of Sumatran rhinos. Similar studies are urgently needed for the last population of Javan rhinoceros in Ujung Kulon National Park (Campos-Arceiz and Lim, 2019) and for Sumatran tapirs. Recent genetic evidence has identified Sumatran tapirs as a distinct subspecies (Lim et al., 2025); with fewer than 400 wild individuals remaining (Traeholt et al., 2016), the subspecies is likely to be Critically Endangered. Without targeted conservation action, Sumatran tapirs may follow a trajectory similar to that of the rhinos.

5. Conclusions

Our findings demonstrate that Sumatran rhinos are specialized browsers with a narrow range of preferred food plants and specific habitat requirements. They exert less severe impacts on forest structure and composition than other megaherbivores, particularly Asian elephants. These ecological interactions should be integrated into conservation planning. While current Sumatran rhino conservation strategies emphasize expanding captive breeding facilities (known in Indonesia as "sanctuaries"), it is critical to ensure that these areas provide the dietary resources—especially the optimal and staple resources identified in our study—and the structural conditions needed to support rhino health and reproduction.

Assuming continued success in increasing Sumatran rhino numbers at SRS-WKNP and other facilities, identifying suitable release sites will be paramount. These sites must offer strict protection from poaching and other threats and contain forest habitats with rich sapling cover and low monocot dominance. Finally, the unique foraging impacts of Sumatran rhinos—complementary to those of sympatric herbivores such as Sumatran elephants and tapirs—highlight the importance of megafauna community assemblages for maintaining the health and resilience of Sumatra's and Southeast Asia's forest ecosystems.

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CRediT authorship contribution statement

Try Surya Harapan: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nurainas:** Validation, Resources. **Rezi Rahmi Amolia:** Validation, Resources. **Lisa Ong:** Writing – review & editing, Methodology. **Dedy Surya Pahlawan:** Writing – review & editing, Resources, Data curation. **Sukatmoko:** Resources, Project administration. **Rikha Aryanie Surya:** Resources, Project administration. **Ahimsa Campos-Arceiz:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Ethics statement

Ethical review and approval were not required for the animal study. The observations had no direct contact with animals. Field activities inside enclosure followed the standard operating procedure and safety requirements from Sumatran Rhino Sanctuary, Way Kambas National Park, Indonesia.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (model 4o) in order to improve the language and readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

Authors declare no conflict of interest.

Data availability

Data will be made available on request.

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