Ecological and evolutionary significance of bark feeding: implications for mammal and plant

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Abstract

Bark feeding is a widespread but under-reported form of mammalian herbivory that can buffer herbivores against seasonal food shortages while imposing disproportionate damage on woody plants. Despite its ecological significance, the drivers and adaptations underlying bark feeding remain poorly understood. Here we synthesise evidence for the ecological and evolutionary significance of bark feeding for both mammals and plants, and compile a global inventory of bark-feeding mammals to evaluate patterns across body size, dietary guild, biogeographic distribution and biome. We identify 215 bark-feeding mammal species (45 families, 10 orders), nearly half of which are large herbivores (≥ 5 kg), representing up to 20% of large mammals and 21% of woody plant feeders within those clades. Both current richness and estimated pre-human relative prevalence of bark feeders peak in seasonal systems, especially woodlands/shrublands, subtropical deserts and tropical seasonal forests/savannas. Although bark typically contributes a small fraction of annual intake, consumption often increases during resource bottlenecks, consistent with a fallback-resource strategy; available studies also link bark use to improved physiological condition in some herbivores. For plants, bark feeding can girdle stems, cause mortality, alter regeneration and canopy structure, and shift vegetation composition and openness, with consequences that can cascade to community and ecosystem dynamics. Taken together, bark feeding links seasonal scarcity to selection for dietary plasticity and foraging innovation in mammals, with downstream consequences for niche partitioning and community assembly, while recurrent debarking can impose strong selection on stem

traits (e.g., bark structure) and, by filtering recruitment and survival, promote heterogeneous ('mosaic') vegetation structure.

Key words: bark feeding, mammalian herbivory, fallback resource, plant-animal interactions, ecosystem dynamics, seasonal ecosystem, conservation, rewilding.

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I. Introduction

Traditionally, animal feeding behaviours have been classified according to the food items that dominate the diet, with research largely focused on the most frequent resources such as woody plant folivory, frugivory, and grazing (Bodmer & Ward, 2006; Venter, Vermeulen & Brooke, 2019). These behaviours are known to fundamentally shape terrestrial ecosystems, influencing plant population dynamics, vegetation structure, and nutrient cycling (Wardle & Bardgett, 2004; Schmitz, 2008; Sobral et al., 2017; Lacher et al., 2019). While this focus on primary food sources offers a pragmatic, majority-rule perspective, it tends to overlook the ecological significance of fallback resources—items consumed less frequently, but which become disproportionately important when preferred foods are scarce and mammalian fitness is challenged, such as during seasonal shortages, climatic anomalies, or anthropogenic disturbances. These fallback strategies may not optimise performance in typical years—unless harsh seasonal conditions are the norm—but they can be essential for survival during critical periods. As adaptive buffers against ecological bottlenecks, fallback mechanisms may exert outsized influence on community resilience and long-term ecosystem dynamics, especially under growing environmental variability and climate change.

In this review, we examine whether bark feeding (Fig. 1)—a relatively overlooked behaviour involving the removal and ingestion of tree bark—should be recognised as both a key fallback strategy for mammals and a significant driver of vegetation evolution. Though often regarded as marginal or opportunistic, bark feeding may play a critical role during resource bottlenecks by providing essential nutrients and may exert lasting ecological effects through its impact on plant survival and ecosystem structure.

Bark feeding has been documented across diverse mammalian clades and ecosystems (Gill, 1992a, b; Baxter & Hansson, 2001; Di Bitetti, 2019). Although bark often represents a minor component of annual intake, it can induce significant ecological effect over particular species targeted for their bark, during harsh seasons, or in specific environmental contexts favourable to bark feeding. In some mammals, such as elephants and porcupines, bark can be consumed year-round in minor proportion of their diet but can become a major food resource during specific periods (Pradhan et al., 2008; Akram, Ilyas & Haleem, 2017), whereas in other species, bark feeding appears to be more occasional or strictly seasonal, as observed in deer and primates (Verheyden et al., 2006; Di Bitetti, 2019). Nevertheless, bark-feeding intensity has been shown to increase in response to seasonal or episodic food shortages (Marshall et al., 2009), particularly in ecosystems with pronounced seasonality or high herbivore densities, where access to preferred resources becomes temporarily restricted (Khan et al., 1994; Akashi & Terazawa, 2005; Jiang et al., 2005; Harrison & Marshall, 2011). Therefore, while bark is often regarded as nutritionally poor or unpalatable and is relatively rare in the diets of many mammals, it remains available year-round and may play, at least episodically, a disproportionate role in mammalian ecology and evolution by helping maintain performance during periods of food stress.

Beyond its role in herbivore survival, bark feeding can have substantial ecological impacts. Unlike foliage that can become inaccessible for ground mammals, bark is reachable to both small and large mammals, and even modest bark removal—especially in the form of ring debarking, which severs the continuous cambial connection between roots and crown—can lead to tree mortality. Debarking directly impairs plant physiological function, growth, reproduction, and survival (Noel, 1970; Scogings & Macanda, 2005), contributing to broader shifts in forest structure and composition, and altering successional trajectories (Miquelle & Van Ballenberghe, 1989; Gill, 1992c; Mountford, 1997; Akashi & Nakashizuka, 1999; Yokoyama et al., 2001; Ihwagi et al., 2009). Additionally, bark damage can increase susceptibility to fire (Helm et al., 2011), wind (Shibata & Torazawa, 2008), pathogens (Kranjec Orlović et al., 2024), and insect outbreaks (Wigley et al., 2019), potentially promoting vegetation openness and influencing broader ecosystem assembly.

Despite this ecological relevance, bark feeding remains poorly studied. It is typically treated in ecological syntheses as a residual or marginal dietary behaviour (Kissling et al., 2014; Gainsbury, Tallowin & Meiri, 2018), and has been largely excluded from models of mammal community composition and vegetation dynamics—even though it likely played a more prominent role in past ecosystems, when large herbivores and megafauna were more diverse and globally widely distributed. To address this gap, we reviewed existing literature to explore key questions:

For mammalian herbivores:

- Is bark feeding widespread across Mammalian herbivore groups, or restricted to a few specialized species?
- What ecological, physiological, or dietary traits make certain mammal species more likely to adopt bark feeding?
- Can bark feeding function as a fallback resource for mammalian herbivores? If so, how does it contribute to maintaining or improving mammal fitness?
- If bark feeding function as a fallback resource, is it associated with biomes characterized by seasonal resource scarcity?

For woody plants:

- How does bark feeding translate into tree mortality? Is it sufficient to drive vegetation replacement and community restructuring?
- Under what environmental conditions does bark feeding lead to tree mortality, and can these observations inform broader ecological trends?
- Are there plant adaptations preventing bark feeding suggesting that it could have acted as a selective pressure?
- Is there evidence that bark feeding could have been historically an important evolutionary driver?

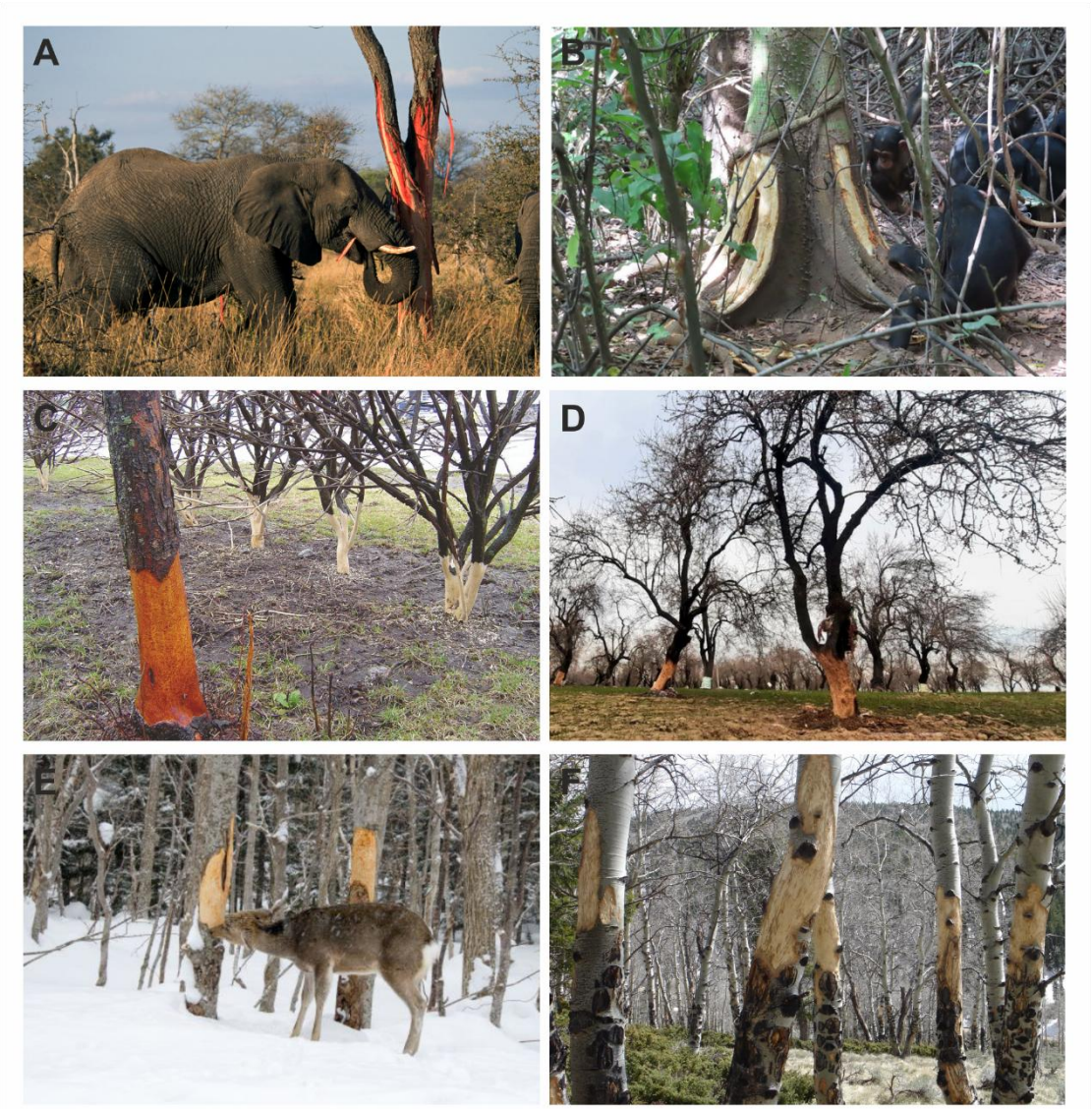


Figure 1: Pictures of trees debarked by mammals. A) Tree debarked by African bush elephant (*Loxodonta africana*) in a savanna of Kruger National Park (photo by Andrew Shiva). B) *Ceiba pentandra* tree debarked by Chimpanzees (*Pan troglodytes verus*) in Senegal (photo by Jill Pruetz, Fongoli Savanna Chimpanzee Project). (C) Shrub debarked by rabbit (*Sylvilagus floridanus*; photo by Mircea Costina, stock.abode.com). (D) trees debarked by porcupine (*Hystrix indica*) in an orchard from Kashmir (photo by Qayoom Khan). (E) Trees debarked by deer (*Cervus nippon*) in Japan (photo by Tatsuo Nakamura). (F) Trembling aspen (*Populus tremuloides*) with feeding damage by elk (*Cervus canadensis*) in Southern Rocky Mountains, Colorado, USA—the black parts below the fresh wounds are callused wounds from winter feeding in previous years (photo by Jim Worrall, forestpathology.org).

II. Diversity, ecology, and biogeography of mammalian bark feeders

Despite being generally overlooked, bark feeding is taxonomically widespread across mammal groups and its high representativeness in clades that suffered severe extinctions suggest that it could also have played an important ecological role in the past. Based on a compilation of scientific literature and the IUCN database (IUCN, 2022;

see Supplementary material for the method), we identified 215 wild extant terrestrial mammalian species—spanning 45 families and 10 orders—that feed on bark at least occasionally (Tab. S1). In absolute numbers, many bark-feeding species belong to highly speciose orders (Fig. 2; Tab. S2), particularly Rodentia (85/2236; 3.8%), Primates (61/439; 13.9%), Artiodactyla (25/233; 10.7%), followed by Diprotodontia (15/139; 10.8%) and Lagomorpha (11/91; 12.1%). However, when considering the relative representation within each order, bark feeding is most frequent in clades with few extant species, such as Perissodactyla (7 out of 16 species; 43.8%) and Proboscidea (3 out of 3 species; 100%), groups that were dominant in the past and present globally (Bai, Wang & Meng, 2018; Cantalapiedra et al., 2021), suggesting that bark feeding could have been common among the past megafaunas. Other groups such as Carnivora (6/287; 2.1%), Didelphimorphia (1/96; 1%), and Hyracoidea (1/5; 20.0%) contribute only marginally to the overall total. The number of species doing debarking is probably underestimated as debarking is not considered an important diet (absent from many databases), is less likely to be observed if this occurs during a particular season, and since there are few studies globally describing food uptake during harsh season.

While bark feeding occurs across a broad taxonomic range, it is particularly prevalent in medium- to large-bodied mammals (Fig. 2; Tab. S3, S4, and S5). Of the 215 bark-feeding species identified, 99 exceed 5 kg in body mass when adult. When excluding Carnivora, bark feeders make up 20% of all extant medium- to large-bodied herbivorous mammals in the corresponding clades (94 out of 470 species). This includes most species in Perissodactyla and Proboscidea, where all known bark feeders are large-bodied. In comparison, only 4.1% of small-bodied herbivores (115 out of 2788 species) are documented as bark feeding. This size-related pattern likely reflects physiological and ecological constraints: large species generally exhibit longer gut retention times, greater digestive efficiency, and higher tolerance for fibrous, low-quality forage (Owen-Smith, 1988), making them likely better suited to exploit bark as a food resource.

Diversity of bark-feeding mammals across body sizes

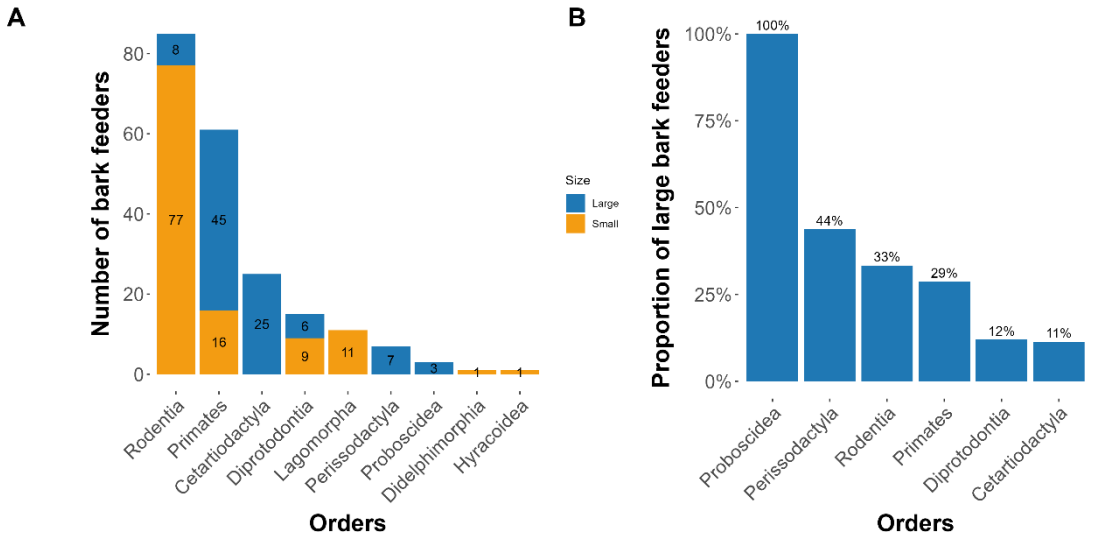


Figure 2: A) Number of small and medium/large-bodied extant herbivorous mammals feeding on bark. B) Proportion of medium/large-bodied extant herbivorous mammals feeding on bark. Mammals are classified as small versus medium- to large-bodied using a 5-kg threshold, based on body-mass information reported in the PHYLACINE 1.2 database (Faurby et al., 2018, 2020).

Mammals with a generalist diet (including fruits or seeds), browser diet (leaf specialist) or mixed-feeder diet (consuming both leaf and grass) are more likely to perform bark feeding (Fig. 3; Tab. S6 and S7). Across all medium- to large-bodied bark feeders from those clades, bark feeding is found in 32% of browsers, 21% of generalists, and 17% of mixed-feeders, representing up to 21% of woody plant feeders (browser, generalist, mixed-feeder). In contrast, obligate grazers, which specialize on grasses and herbaceous plants, show lower bark-feeding incidence—9%. However, bark feeding is not entirely absent in grazers, suggesting that some species within this guild may opportunistically consume bark. These patterns suggest that bark feeding is most likely to occur in species with either regular woody vegetation consumption or a flexible diet.

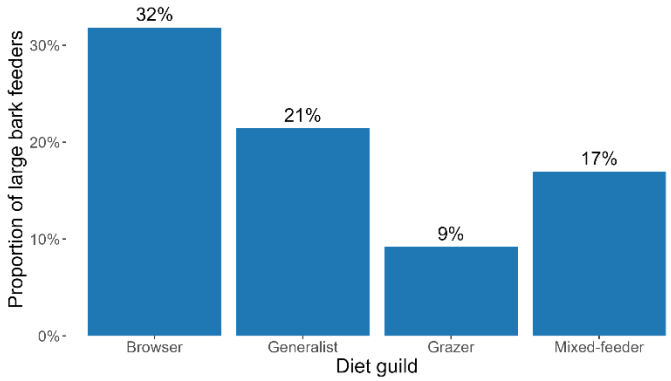


Figure 3. Proportion of medium- to large-bodied extant herbivorous mammals that feed on bark according to their main food source. Diet classifications follow Kissling et al., (2014), who define food items as primary (dominant), secondary (intermediate), rare, or not consumed. Here, only primary and secondary food sources were considered, and weighted equally, to allow some flexibility in the feeding mode (see Supplementary materials for method). Mammals were categorised as browsers (leaf specialists), grazers (grass specialists), mixed-feeders (consume both grasses and leaves), or generalists (include fruits or seeds).

Bark feeders are distributed across all continents and climatic zones, with a predominance in seasonal environments (Fig. 4 and 5), particularly in vegetation with high seasonal variation in food availability. Both the current species richness and the present-natural pre-human impact relative prevalence of bark feeders suggest a greater relevance of bark feeding in tropical seasonal forest/savanna, subtropical desert, and woodland/shrubland. These environments are characterized by pronounced seasonality, with distinct dry periods during which preferred food sources—such as leaves, fruits, and grasses—are often scarce, suggesting that bark feeding may give an ad-

vantage in these environments. This is consistent with broader theory linking dietary flexibility to environmental variability (Illius & O'Connor, 1999; Staver & Hempson, 2020) and with observations that bark intake increases during seasonal or episodic shortages (Jiang et al., 2005; Ihwagi et al., 2009; Harrison & Marshall, 2011). The prominence of bark feeding in such environments underscores its potential role in supporting persistence and stability in herbivore communities facing fluctuating resource availability.

Despite its broad ecological and taxonomic distribution, the current understanding of bark feeding is likely shaped by uneven research effort across regions. Although the absolute number of bark-feeding species is highest in tropical ecosystems, relative prevalence appears disproportionately higher in temperate regions, suggesting that bark feeding may also play a role in temperate ecosystems. This discrepancy may also reflect the greater concentration of ecological studies in temperate areas, where bark feeding may have been more likely systematically recorded across medium- to large-bodied mammals. In contrast, the behaviour is likely underreported in tropical regions, where species richness is high, but dedicated studies remain limited. As a result, the role of bark feeding in the foraging ecology of many tropical species may be underestimated. Improving the recognition and reporting of this feeding mode, especially in trait databases and conservation assessments, could provide valuable insights into mammalian responses to food scarcity, habitat disturbance, and long-term environmental change.

Together, these patterns indicate that bark feeding is a widespread but underdocumented foraging strategy that is likely shaped by body size, diet, and environmental context. Its association with large-bodied, generalist, and woody-vegetation-feeding species suggests that it may play a key role in supporting mammalian herbivores under resource-limited conditions, whereas its prevalence among large-bodied animals and clades with extinct megafauna may highlight its possible implication in driving vegetation structure. Given its likely ecological importance and current underrepresentation in trait datasets, bark feeding should be more systematically recorded and integrated into studies of herbivore ecology, especially in tropical systems where it may be most relevant but least documented.

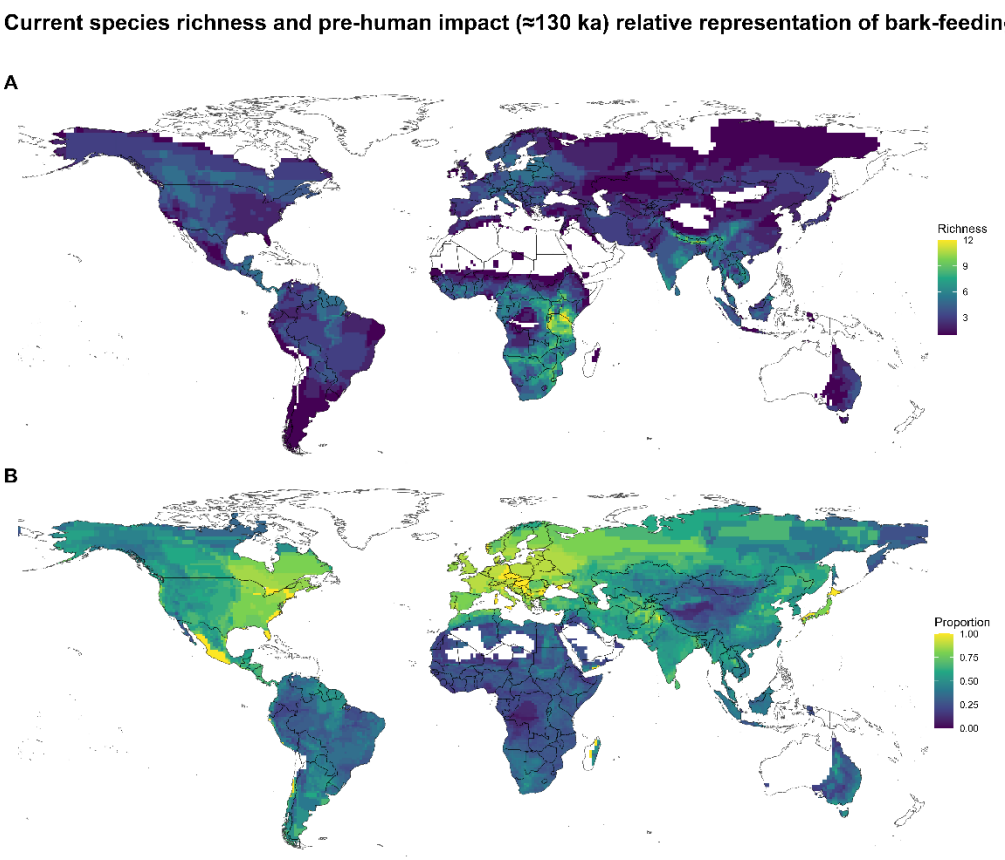


Figure 4: A) Current global species richness distribution of medium- and large-bodied herbivorous mammal bark feeders. The species richness was estimated by stacking binary presence rasters (0/1) of current range distribution of mammals that were identified feeding on bark, and by summing values per grid cell (0.25° × 0.25°). **B) Present-natural pre-human impact relative richness distribution of medium- and large-bodied herbivorous mammal bark feeders.** The relative richness was computed per raster cell as the proportion of present-natural species richness distribution of herbivorous mammal bark feeders and the present-natural species richness distribution of herbivorous mammals for the same orders (Fig. S1 and S2). Mammal distributions were extracted from the PHYLACINE 1.2 database (Faurby et al., 2018, 2020).

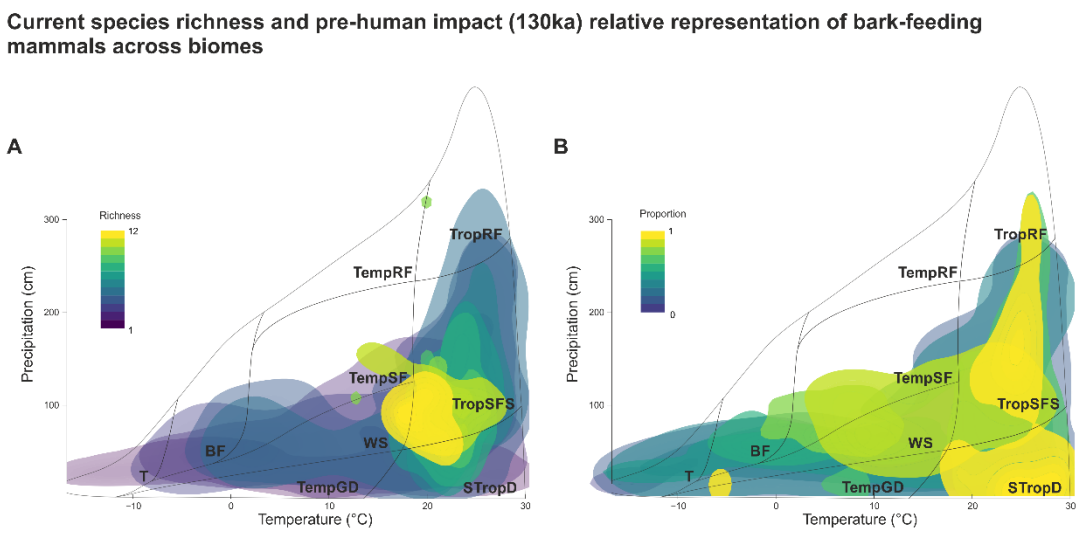


Figure 5: A) Current species richness of medium- to large-bodied herbivorous mammal bark feeders across biomes. B) Present-natural pre-human impact relative species richness of medium- to large-bodied herbivorous mammal bark feeders across biomes. Richness classes and relative richness proportion are shown as coloured kernel density estimation surfaces in Whittaker temperature–precipitation space (Stefan & Levin, 2022). For each richness class and each 10% of relative richness proportion, a normalized two-dimensional kernel density was computed and split into six bands; the lowest band was omitted to avoid noisy areas with low occurrences and improve readability across richness layers. T = Tundra; BF = Boreal Forest; WS = Woodland/Shrubland; TempGD = Temperate Grassland/Desert; TempSF = Temperate Seasonal Forest; TempRF = Temperate Rain Forest; STropD = SubTropical Desert; TropSFS = Tropical Seasonal Forest/Savanna; TropRF = Tropical Rain Forest.

III. Ecological significance of bark feeding for mammals

(1) Bark as a fallback and functional food in mammalian ecology

Although often perceived as nutritionally poor and of low quality, the inner bark may nonetheless play a critical ecological role for mammals. Particularly during periods of resource scarcity, it may serve as an alternative or supplementary food source that supports performance and survival (Ueda, Takatsuki & Takahashi, 2002; Jiang et al., 2005; Min et al., 2012). The outer bark—composed of dead cells rich in lignin, suberin, and other structural compounds (Leite & Pereira, 2017)—is generally indigestible and nutritionally limited, making it unappealing to most mammalian herbivores. In contrast, the inner bark (i.e., the phloem) can have substantial nutritional value, as it contains non-structural carbohydrates (e.g., starch and sugars), proteins, essential minerals, and moisture (Seki et al., 2019). These nutrients are often available year-round, positioning the inner bark as a potentially important fallback resource—such as during seasonal shortages, climatic extremes, or restricted habitat access—for mammalian species. Accessibility further requires that species are capable of overcoming the mechanical and physiological challenges of accessing and digesting inner bark.

There is considerable evidence that bark functions as a fallback resource—consumed when preferred food sources become scarce. Numerous species across var-

ious mammalian orders—including Proboscidea (Pradhan et al., 2008; Ihwagi et al., 2009), Perissodactyla (Pradhan et al., 2008; Klich, 2015), Artiodactyla (Verheyden et al., 2006; Klich, 2015), Primates (Di Bitetti, 2019), and Rodentia (Baxter & Hansson, 2001)—increase their bark consumption when access to leaves, grasses, fruits, or seeds become limited (Baxter & Hansson, 2001; Verheyden et al., 2006; Campbell-Smith et al., 2011; Di Bitetti, 2019).

For example, in Japan, sika deer (*Cervus nippon*) intensify bark feeding during snowy winters—periods marked by both increased energetic demands and reduced forage availability (Ueda et al., 2002; Jiang et al., 2005). Likewise, sambar deer (*Cervus unicolor*) in India's tropical deciduous forests relies heavily on bark during drought conditions (Khan et al., 1994). In Nepal, bark comprises up to 51% of the Asian elephant (*Elephas maximus*) diet annually, peaking at 73% during the cool-dry season (Pradhan et al., 2008). Even smaller mammals, such as the Indian crested porcupine (*Hystrix indica*), demonstrate increased bark consumption when primary resources decline (Akram et al., 2017).

Bark may thus form part of the broader suite of fallback resources that become particularly important when preferred foods are scarce, buffering animals against seasonal or unpredictable periods of resource limitation (Constantino & Wright, 2009; Marshall et al., 2009). In primates, repeated reliance on fallback foods has been hypothesized to shape food-processing adaptations, including jaw robustness, enamel thickness, specialized molar morphology, and digestive capacity, while also influencing foraging and ranging patterns, grouping behaviour, and broader socioecological organization (Marshall & Wrangham, 2007; Marshall et al., 2009; Harrison & Marshall, 2011). By affecting access to food during periods of scarcity, fallback resources may also modify competitive interactions and potentially influence reproductive and other life-history outcomes (Marshall & Wrangham, 2007; Marshall et al., 2009; Harrison & Marshall, 2011). Fallback resources, including bark, may therefore mediate short-term ecological responses to food scarcity while also acting as longer-term selective pressures on mammalian morphology, physiology, and behaviour.

However, bark-feeding behaviour is not limited to fallback resource and can varies substantially among species and environments leading to different degrees of importance in the mammal diet. This variability is influenced by multiple factors, including primary productivity, climate (e.g., snow or drought), herbivore population density, and habitat type and use (Anderson, Hawke & Moore, 1985; Khan et al., 1994; Yokoyama et al., 2001; Verheyden et al., 2006; Ligot et al., 2013; Candaele et al., 2021). While bark consumption generally increases during periods of scarcity, mammals can also consume bark even when more nutritious resources are available (e.g., deer or elephant), indicating that other drivers—such as the need for dietary fibre (Gill, 1992a), mineral supplementation (Ando, Yokota & Shibata, 2004, Ando et al., 2005), pharmacological effects (Freymann et al., 2024), or hydration (Ciani et al., 2001)—might also contribute to this behaviour. Assessing the frequency and intensity of bark feeding within and across mammalian clades, using clear and reproducible methods across environments, would greatly improve our understanding of how bark

feeding intensity relates to mammalian taxonomy, body size, diet, morphology, digestive physiology and ecological context.

(2) Physiological effects of bark consumption in mammals

Only a few studies have investigated the physiological benefits of bark consumption on animal performance and survival, limiting the ability to generalize findings across species. Nonetheless, available experimental evidence suggests that bark can positively affect mammalian condition, particularly during periods of food scarcity.

Bergeron (1996) investigated whether the protein content of the regular diet affected bark use by meadow voles (*Microtus pennsylvanicus*). Three groups were maintained on 15%, 8%, and 4% protein diets supplemented with red oak seedlings for two weeks. Voles maintained on the lowest-protein diet gained body mass during the experiment, whereas those receiving the other diets lost mass, and apparent protein digestibility did not differ significantly among treatments. These results suggest that bark may contribute to nutritional balance when dietary protein availability is limited. This benefit may have resulted from a combination of bark protein intake and vole adaptations allowing them to tolerate or process bark secondary compounds, such as tannin-binding salivary proteins or microbial degradation in the gut (Shimada, 2006; Dai et al., 2014). Voles also showed changes in faecal recovery of non-structural carbohydrates, with a higher concentration of phenolics and non-structural carbohydrates than those from the 15% treatment. Overall, these results suggest that bark may serve as a nutritionally viable supplementary or fallback resource under protein-limited conditions.

A comprehensive study by Min et al., (2012) further demonstrated the physiological value of bark under controlled conditions. Domestic goats fed with up to 30% pine bark (*Pinus taeda*) supplementation exhibited a range of benefits, including improved growth rates, greater energy efficiency, and reduced parasite loads. These effects were linked to favourable changes in rumen fermentation, particularly due to the condensed tannins in bark, which reduced ruminal protein degradation. This increased the flow of undegraded dietary protein—or "bypass protein"—to the small intestine, improving nitrogen retention and overall protein efficiency. Importantly, blood chemistry and organ function parameters remained within normal ranges across all treatment groups, supporting the safety and nutritional potential of bark for herbivores.

Together, these studies highlight the role of bark not only as an emergency food during periods of scarcity but also as a strategic dietary component that can enhance physiological resilience. This may be especially relevant for species with digestive adaptations—such as tannin-binding salivary proteins, specialized gut microbiota, or fermentation chambers—that allow them to tolerate or detoxify bark's secondary compounds. However, the physiological mechanisms underlying effective bark use remain poorly understood and likely vary by context. Key factors may include the concentration and chemical nature of condensed tannins, the nutritional quality of bark tissue, and species-specific traits such as gut morphology, enzymatic systems, and detoxification capacities. In particular, the roles of salivary proteins, rumen or hindgut microbiota, and microbial enzymatic potential deserve further investigation.

Physiological studies evaluating the effects of bark on mammalian performance remain scarce and are needed across different body sizes, feeding guilds, and phylogenetic lineages.

(3) Determinants of tree selection for bark feeding

Tree selection for bark feeding by mammals is influenced by a complex interplay of animal physiology, nutritional requirements, tree structural and chemical characteristics, and broader ecosystem factors influencing local food availability and quality (Tab. 1). Although empirical evidence varies significantly across taxa and habitats, two primary determinants appear central: (1) the physical ability of animals to access inner bark tissues for a given plant species and (2) the nutritional payoff derived from bark consumption.

Table 1: Plant and mammal factors affecting the mammal tree feeding choice to feed on bark.

Characteristics	Factors	References
Tree characteristics		
Physical		
Attractive	Inner bark thickness	Kenward & Parish, 1986; van Rooyen & du Toit, 1993; Whitten & Whitten, 1987; Wigley et al., 2019; Gill, 1992b
Deterrent	Outer bark thickness	Jiang et al., 2005; Månsson & Jarnemo, 2013; Whitten & Whitten, 1987; Gill, 1992a, b
	Outer bark hardness	Jiang et al., 2005; Ando et al., 2003
	Outer bark roughness	Kuiters et al., 2006; Jiang et al., 2005; Whitten & Whitten, 1987; Gill, 1992a
	Outer bark detachability	Klich, 2017; Ando et al., 2003; Whitten & Whitten, 1987; Gill, 1992a, b
	Number of main stems	O'Connor et al., 2007
	Number of branches	Månsson & Jarnemo, 2013; Anderson et al., 1985; Gill, 1992a
	Trunk spines	Lefebvre et al., 2022
Nutritional		
Attractive	Crude protein	Shimada & Moriya, 2018; Hansson, 1994; Heroldová et al., 2009
	Na	Au et al., 2017; Snyder, 1992; Stephens et al., 2006
	Ca	Stephens et al., 2006; Randveer & Heikkilä, 1996
	P	Randveer & Heikkilä, 1996
	K	Randveer & Heikkilä, 1996; Stephens et al., 2006
	Total non-structural carbohydrate	Snyder, 1992; Tamura & Ohara, 2005
	Soluble sugar	Kurek et al., 2019; Page et al., 2013
	Water	Ciani et al., 2001; Wigley et al., 2019
	Sap flow	Kenward & Parish, 1986; Beeson, 1987; Gill, 1992b
Deterrent	Terpene	Bucyanayandi et al., 1990; Snyder, 1992
	Total phenol	Shimada & Moriya, 2018
	Hydrolysable tannins	Whitten & Whitten, 1987

	Crude fibre	Hansson, 1994; Heroldová et al., 2009
	Fe, Hg	Snyder, 1992
Mammal characteristics		
Dexterity	Ability to separate outer from inner bark	Ando et al., 2004; van Rooyen & du Toit, 1993; Jiang et al., 2005; Rogers et al., 1994

(a) Physical determinants influencing bark feeder preferences

The ability of animals to access inner bark hinges on both animal and tree morphologies. Outer bark characteristics—including thickness, hardness, roughness, and ease of detachment—may affect tree selection by influencing the animal ability to break the outer bark barrier and reach the inner bark (Ando, Yokota & Shibata, 2003; Jiang et al., 2005; Kuiters, van der Sluijs & Wytema, 2006; Månsson & Jarnemo, 2013; Klich, 2017). Trees possessing thick, hard, rough, or tightly adherent bark might be debarked less frequently, whereas those with thinner, softer, or easily detached bark might be more vulnerable, depending on the animal's dexterity (Gill, 1992a, b; Whitten & Whitten, 1987). For instance, porcupines prefer large trees with thick outer bark because they can efficiently separate and discard the outer bark to consume the more digestible thick inner layers (van Rooyen & du Toit, 1993). Together, these observations suggest that animals may select particular tree species and size or age classes partly according to how easily the inner bark can be accessed and how much can be obtained for a given handling effort.

Tree architectural traits may also influence accessibility to bark. Fluted stems, as seen in species such as *Balanites maughamii*, protect up to 70% of bark surfaces from large herbivores (Williams, Balkwill & Witkowski, 2007). The difficulty to access trunk areas from trees due to their shape may partly explain the survival of heavily debarked large *Ceiba pentandra* trees reported utilized by chimpanzees in Ivory Coast (Lapuente et al., 2020). Additional structural attributes, such as branching architecture, stem multiplicity, and trunk spines may also further deter accessibility (Anderson et al., 1985; Gill, 1992a; Månsson & Jarnemo, 2013; O'Connor, Goodman & Clegg, 2007; Lefebvre, Charles-Dominique & Tomlinson, 2022). These structural attributes can be interpreted as physical barriers that alter the costs and feasibility of bark feeding by either decreasing access to inner bark or increasing the time and difficulty required to extract the resource. For example, dense branching or long spines may reduce an animal's ability to position its head, mouth, tusks, or forelimbs close to the trunk. Small conical trunk spines or thick outer bark may reduce the ability of mammals to insert their teeth and reach the inner bark. The effect of trunk spines on bark feeders still requires experimental testing (Lefebvre et al., 2022), but observational evidence suggests that hard conical trunk spines, such as those produced at the base of the trunk by *Bombax ceiba*, may deter well-known specialized bark feeders such as *Hystrix indica* (Greaves & Khan, 1978). Similarly, low bark detachability, or strong adhesion to the trunk, may reduce the amount of edible tissue that can be removed during a single feeding event. For example, Klich (2017) showed that selective bark stripping by Polish primitive horses was related to bark detachability, with the

relative force required to detach bark influencing the selection of different tree species. However, the defensive value of these traits should depend on the morphology and behaviour of the bark feeder. Traits that deter gnawing mammals, for instance, may not deter large herbivores capable of breaking or peeling bark with tusks, incisors, trunks, or strong forelimbs. Although many structural traits may also have other functions, such as protection against fire or insect damage, they may nevertheless reduce losses to mammalian bark feeders and could therefore contribute to the evolutionary interplay between mammalian feeding strategies and plant structural defences.

(b) Nutritional needs influencing bark feeder preferences

In addition to physical accessibility, the nutritional payoff of bark consumption likely plays a key role in tree selection. Animals may target specific trees based on a complex interplay between attractive nutrients—such as non-structural carbohydrates (sugars and starches), proteins, minerals, and moisture—and deterrent secondary metabolites, including phenolics, terpenoids, and alkaloids, as well as their own physiological capacity to cope with these compounds (Tab. 1). The quantity of edible bark available may also partly influence these choices (Kenward & Parish, 1986; Whitten & Whitten, 1987; Wigley et al., 2019; Gill, 1992b), especially when alternative forages become scarce.

While folivory is strongly shaped by plant secondary compounds—affecting taste, nutrient availability, and animal health (Robbins et al., 1987; Bryant et al., 1991; Dearing, Foley & McLean, 2005; Iason, 2005)—their role in bark feeding remains less clear. Bark is often rich in tannins, phenolics, and terpenoids, which typically deter herbivores. Indeed, some studies have reported negative correlations between bark feeding and levels of phenols, hydrolysable tannins, or monoterpenes (Whitten & Whitten, 1987; Bucyanayandi, Bergeron & Menard, 1990; Shimada & Moriya, 2018). Nevertheless, their effect should be considered together with the detoxification strategies that mammals possess. Some species secrete tannin-binding salivary proteins that precipitate tannins in the mouth, preventing them from interfering with digestion or binding dietary proteins (Hagerman & Robbins, 1993). Others host gut microbes capable of degrading phenolics and tannins (McSweeney et al., 2001), or employ behavioural tactics such as discarding tannin-rich outer bark (van Rooyen & du Toit, 1993). These biochemical, microbial, and behavioural defences allow mammals to tolerate chemically defended tissues while minimizing anti-nutritional costs.

While outer bark has high concentrations of secondary compounds that reduce digestibility, inner bark offers various nutritional benefits. Non-structural carbohydrates (NSCs)—vital for plant growth, defence, and energy storage (Hartmann & Trumbore, 2016)—are abundant in inner bark. For instance, trees in seasonally deciduous tropical forest showed the highest total NSC concentrations in the inner bark, as high as 417.2 mg/g dry mass, while mean NSC concentration was highest in savanna compared to seasonally deciduous tropical forest and tropical rainforest (Rosell et al., 2021). Several studies suggest that mammals favour bark rich in sugars (Snyder, 1992; Faber, 1996), though it has been argued that sap volume may be more relevant than sugar concentration (Kenward & Parish, 1986; Page et al., 2013). Moreover, bark

sugar levels often increase after mechanical damage (Saint-Andrieux et al., 2009), potentially partly explaining why previously debarked trees are preferentially targeted (Vospernik, 2006). Advances in analytical techniques, such as near-infrared reflectance (NIR) spectroscopy, may also improve future NSC quantification and improve comparability across studies (Li et al., 2022).

Bark may also provide protein, though typically at lower levels than foliage and possibly less accessible due to the associated higher condensed tannins content that limit absorption. Proteins can accumulate in the phloem and parenchyma during late summer and autumn, and are later remobilized for spring growth (Wetzel, Demmers & Greenwood, 1989). Despite the high tannin content found in bark, these reserves may provide an advantage during food shortages. For example, meadow voles were able to maintain their body mass while feeding on red oak (*Quercus rubra*) bark, rich in both tannins and protein (Bergeron, 1996), likely due to salivary proteins or gut microbes (Shimada, 2006; Dai et al., 2014). Likewise, goats fed pine bark diets exhibited reduced ruminal protein degradation, increased amino acid flow to the small intestine, and improved growth and feed efficiency (Min et al., 2012). Some field studies also report correlations between bark protein content and tree selection (Hansson, 1994; Heroldová et al., 2009; Shimada & Moriya, 2018), though findings are inconsistent.

Minerals and moisture may further influence bark selection. Koalas and ringtail possums appear to target trees rich in calcium, sodium, or potassium (Stephens, Salas & Dierenfeld, 2006; Au et al., 2017). However, mineral-driven bark selection is not always supported by physiological evidence. For example, deer showed no apparent mineral benefits from bark consumption when preferred foods were available (Ando et al., 2005). Similarly, the hypothesis that bark is consumed for calcium was not supported by a study showing that squirrels appear unable to assimilate the calcium stored in bark, because it occurs mainly in the form of calcium oxalate (Nichols et al., 2018). Water content may also drive bark feeding, especially in arid environments: elephants prefer bark with high moisture levels (Wigley et al., 2019), and Moroccan macaques have been reported debarking trees to access water (Ciani et al., 2001).

While several studies have examined tree selection during debarking, evidence that this is linked to nutritional availability differences among tree species remains unresolved. This may partly reflect the need to consider methodological approaches in a more integrative and comparative way. Tree selection and bark function may vary across animal species and ecological contexts, highlighting the need for standardized approaches that allow comparisons across studies. On the plant side, this requires standardized assays that quantify nutrients, secondary metabolites, plant physical traits, and environmental context, thereby helping to link selection with function. On the animal side, it requires identifying the mammal's manipulative strategy, since some animals can discard the highly unpalatable outer bark, as well as its physiological strategy, including gut type and dietary guild. Deterrents should therefore be interpreted relative to each species' detoxification capacity, including tannin-binding sali-

519 vary proteins, gut microbial communities, and gut passage time, rather than in isola-
520 tion.
521 These two-sided characterizations are important because they determine an an-
522 imal's ability to extract energy from plant tissues. This ability is not determined only
523 by the absolute amount of any single compound, but also by interactions among com-
524 pounds and by the animal's capacity to deal with deterrent plant parts. For instance,
525 non-structural carbohydrates can reduce tannin-induced precipitation of salivary pro-
526 teins and thereby diminish the anti-nutritional effects of tannins (Soares, Mateus & De
527 Freitas, 2012). Similarly, tannin-binding proteins, such as proline-rich proteins, can
528 shield dietary protein from complexation (Hagerman & Robbins, 1993), and in some
529 ruminants, condensed tannins may even improve protein digestibility by reshaping
530 rumen microbial communities (Min et al., 2012). High-throughput profiling, such as
531 near-infrared spectroscopy and metabolomics, together with a multidimensional
532 framework that evaluates nutritional and deterrent compounds simultaneously, would
533 make such comparisons more tractable and transferable across systems. This integra-
534 tive approach should help clarify why mammals feed on bark, predict which trees and
535 tissues are selected, and connect feeding behaviour to its ecological and evolutionary
536 consequences for woody plants and vegetation structure.

537 **IV. Influence of bark feeding on trees and vegetation**

538 **(1) Effects of bark feeding on individual plants**

539 Bark feeding by mammals directly compromises the vascular integrity of woody
540 plants and can be fatal to trees. Unlike foliar herbivory—which typically reduces pho-
541 tosynthesis or growth without causing immediate mortality (Grubb, 1992)—debarking
542 affects the main stem or trunk, disrupting the phloem that transports carbohydrates
543 from the canopy to the roots. This interruption impairs root metabolism and resource
544 allocation, suppresses growth, reduces reproductive output, alters foliar chemistry and
545 defence production, and may ultimately result in tree death (Noel, 1970; Scogings &
546 Macanda, 2005). Ring debarking, involving the complete removal of bark and cambi-
547 um around the trunk, usually leads to mortality by fully severing vascular connections
548 (Noel, 1970). However, even partial bark loss can be lethal (Akashi & Nakashizuka,
549 1999), particularly in young trees. Effect of debarking is therefore different from foli-
550 ar browsing, which rarely kills mature trees unless canopy leaves are reachable, and
551 damages are both severe and repeated.
552 Tree vulnerability to debarking is shaped by a complex set of interacting fac-
553 tors that influence both exposure to damage and recovery capacity. Some individuals
554 may survive for years following complete ring debarking (Noel, 1970), suggesting
555 variation in resilience strategies across species and life stages. Some trees can regen-
556 erate bark tissue, compartmentalize wounds, or resprout from the base, reducing phys-
557 iological stress and improving survival chances. However, these responses are highly
558 context dependent. Environmental stressors such as drought, insect outbreaks, nutrient
559 limitations, and fire can severely limit regenerative capacity. Fire is particularly dam-
560 aging to debarked trees, as exposed tissues increase flammability and reduce thermal
561 protection (Yeaton, 1988; Vanak et al., 2012).

Two primary axes—likelihood of damage (covered in the previous section) and resilience following injury—may be governed by species-specific traits, tree size and age, herbivore behaviour and body size, and prevailing environmental conditions. Small-diameter trees are generally more vulnerable, due to their thinner bark and reduced structural defences, which make them easier to ringbark and more prone to rapid mortality (Yokoyama et al., 2001). In contrast, larger trees are less likely to be fully debarked in a single event and can harbour more structural defences, but they may accumulate damage over time, especially where herbivore pressure is sustained. Moreover, trees already debarked are more likely to be revisited after initial damage (Akashi & Nakashizuka, 1999; Vospernik, 2006; Månsson & Jarnemo, 2013; Nagaike, 2020), possibly due to increased NSC concentrations in the phloem following injury (Vospernik, 2006; Saint-Andrieux et al., 2009).

In summary, tree responses to debarking depend not only on species traits and ontogenetic stage but also on damage extent and frequency, physiological resilience, and broader environmental conditions. Understanding this interplay is critical for predicting tree mortality risk and evaluating how bark feeding shapes vegetation structure and ecosystem dynamics over time.

(2) Broader impacts on vegetation dynamics and ecosystems

Bark feeding affects not only individual tree physiology but also broader vegetation dynamics by influencing tree survival, recruitment, and interspecific competition. Mortality induced by debarking can change plant communities by altering species composition and creating canopy gaps.

The influence of bark feeding on vegetation dynamics depends strongly on both temporal and spatial scales. At short temporal scales, severe debarking can kill individual trees rapidly, especially when stems are small and completely ring-barked (Akashi & Nakashizuka, 1999; Yokoyama et al., 2001). At longer temporal scales, repeated seasonal bark feeding may gradually suppress recruitment, accumulate damage on surviving trees, and shift age structure or canopy composition (Miquelle & Van Ballenberghe, 1989; Mountford, 1997; Akashi & Nakashizuka, 1999; Yokoyama et al., 2001). Bark feeding can also occur as episodic pulses (Khan et al., 1994; Jiang et al., 2005; Verheyden et al., 2006; Candaele et al., 2021), such as during droughts or snowy winters, producing sudden mortality events rather than continuous annual pressure.

Spatially, these effects may differ according to mammalian social structure and movement behaviour. Solitary or less social herbivores may affect vegetation more locally and relatively homogeneously, whereas social herbivores may generate more patchy impacts through aggregation and repeated use of particular areas of the landscape. For example, baobab damage by elephants was found to increase closer to perennial water sources, and lower baobab density and basal area near water were interpreted as consistent with elephant-induced disturbance (Ndoro et al., 2016). These spatial and temporal patterns are likely further shaped by the bark-feeding regime, such as whether feeding is regular, seasonal, or episodic, as well as by herbivore movement behaviour, aggregation around limiting resources, population density, and

the seasonality of bark feeding. However, direct comparisons among bark-feeding mammals with different social and spatial behaviours remain scarce.

The direction and magnitude of such changes depend on herbivore selectivity and the traits and composition of local plant communities (Akashi & Terazawa, 2005; Verheyden et al., 2006; Kiffner et al., 2008; Ligot et al., 2013; Iijima & Nagaike, 2015; Candaele et al., 2021). In temperate forests, selective bark feeding by large herbivores such as moose and deer can reduce tree diversity by repeatedly targeting preferred species (Miquelle & Van Ballenberghe, 1989). Conversely, in Canadian hemlock forests, porcupine activity has increased woody species richness by creating regeneration opportunities for subordinate species following the death of dominants leading to a mixed forest (Woods & Zeglen, 2003). The preference of small bark feeders like squirrels can even result in species composition shifts over decades (Mountford, 1997).

Tree size preferences further shape these ecological effects. Bark feeders often disproportionately impact saplings, which are more likely to be fully girdled in a single event due to their thin bark and limited reserves. High sapling mortality can suppress regeneration, skew age structures, and eventually lead to canopy loss, increased light availability, and community turnover (Yokoyama et al., 2001). Larger trees, while less vulnerable to single debarking events, can still succumb to cumulative damage over time, contributing to changes in canopy structure (Akashi & Nakashizuka, 1999). This capacity to cause mortality in mature canopy trees sets bark feeding apart from most other plant-animal interactions.

For example, in a cool-temperate mixed forest in Japan, Akashi & Nakashizuka (1999) showed that intensive bark stripping by sika deer affected forest dynamics through both recruitment failure and mortality of established trees. Small *Abies homolepis* stems were often completely girdled in a single event and died soon after, whereas larger stems accumulated bark damage gradually and died only when girdling became complete; trees larger than 20 cm DBH were also girdled and killed. Over 15 years, the density of small trees declined, and recruitment eventually ceased, while mortality of bark-stripped species increased, especially during the final five years of monitoring. Thus, bark feeding can contribute to canopy opening not only by preventing sapling replacement, but also by causing cumulative mortality of larger trees, thereby accelerating gap formation and potentially shifting mixed forest towards more open vegetation.

These effects are often compounded when bark feeding interacts with other stressors, amplifying its ecological impact. Open wounds provide entry points for fungal pathogens (Vasiliauskas, 1998; Čermák et al., 2004; Arhipova et al., 2015; Burneviča et al., 2016; Cukor et al., 2019a, b; Kranjec Orlović et al., 2024) and insects (Tanaka & Nakamura, 2015; Wigley et al., 2019), and increase susceptibility to windthrow (Shibata & Torazawa, 2008). Damage to the cambial and vascular tissues can exacerbate drought sensitivity, while bark removal also raises tree vulnerability to fire (Yeaton, 1988; Helm et al., 2011; Vanak et al., 2012; Wigley et al., 2019). In fire-prone systems such as savannas and woodlands, repeated burning after debarking may

prevent tree maturation and favour a persistent mosaic of grasslands and scattered woody patches (Yeaton, 1988; Vanak et al., 2012).

Together, these dynamics highlight the dual role of bark feeding—as both a selective filter shaping species composition and a disturbance agent restructuring vegetation. Depending on context, bark feeding can promote either homogenization or diversification of plant communities, while influencing vegetation structure. However, its effects in high-diversity, closed-canopy systems—such as tropical forests or ecotonal mosaics—remain largely unexplored. This represents a critical gap in ecological understanding. Clarifying the broader consequences of bark feeding might be essential for understanding long-term vegetation establishment, especially in ecosystems with high mammal diversity and under climatic stress.

(3) Mammal bark feeding in past ecosystems

Although contemporary bark-feeding mammals can still have marked local effects on vegetation succession, tree diversity, abundance and canopy structure (Miquelle & Van Ballenberghe, 1989; Mountford, 1997; Akashi & Nakashizuka, 1999; Yokoyama et al., 2001), modern herbivore assemblages represent a strongly defaunated subset of the large-mammal communities that characterized many terrestrial ecosystems before the late-Quaternary extinctions and subsequent historical declines (Malhi et al., 2016; Galetti et al., 2018; Svenning et al., 2024). Before these losses, richer and functionally broader assemblages of large-bodied browsers and mixed feeders—including non-ruminant megaherbivores—occurred across most continents (Svenning et al., 2024; Pringle, 2020). These animals influenced woody-plant recruitment, nutrient cycling, seed dispersal, fire regimes and the maintenance of open or heterogeneous vegetation (Owen-Smith, 1987; Bakker et al., 2016; Malhi et al., 2016; Trepel et al., 2024). Yet their effects on vegetation are usually interpreted primarily through grazing, folivory, and the browsing of shoots and saplings, whereas bark feeding has received comparatively little attention. The greater taxonomic and functional diversity of large herbivores in past faunas, together with the diversity patterns collected in this review as well as the modern evidence that debarking can cause tree mortality and alter vegetation composition and structure, therefore provides a strong basis for the hypothesis that bark feeding was formerly a more widespread and influential component of woody-plant herbivory, with consequences for plant evolution, community composition, vegetation dynamics and structural heterogeneity.

Before global defaunation, many ecosystems supported a broader array of large herbivores, including numerous browsers, non-ruminants and megaherbivores. Many of these animals possessed the body size, digestive physiology and dietary flexibility required to process fibrous and comparatively low-quality forage, making the occasional exploitation of bark physiologically plausible. Dental mesowear and microwear analyses, for instance, support the long-held view that chalicotheres—which were widely distributed during the late Miocene—as well as gomphotheres such as *Platybelodon grangeri* were primarily browsers and may have included bark in their diets (Semprebon, Sise & Coombs, 2011, Semprebon et al., 2016; Wood & Ridgwell, 2015). Chalicotheres included large European species such as *Anisodon grande*,

691 which reached several hundred kilograms and may have exploited bark (Coombs &
692 Göhlich, 2020).
693 The composition of Pliocene African mammal communities further illustrates
694 how strongly past herbivore assemblages differed from those observed today. Around
695 four million years ago in Kenya, for example, the diversity of mammal species ex-
696 ceeding 1,000 kg was approximately three times greater than at present, and megaher-
697 bivores were predominantly non-ruminants—the inverse of the modern pattern (Prin-
698 gle, 2020). Given that the diversity patterns identified in this review show a higher
699 prevalence of bark feeding among large-bodied mammals and woody-plant feeders,
700 such communities probably contained a larger and more functionally diverse pool of
701 potential bark feeders. This does not demonstrate that all extinct browsers regularly
702 consumed bark, but it suggests that the behaviour may have been more widespread
703 and ecologically important in past ecosystems.
704 High megafaunal diversity persisted across continents into the late Quaternary,
705 including elephantids, gomphotheres, mastodons, stegodonts, rhinocerotids and other
706 large browsing or mixed-feeding taxa. Bark feeding may therefore have remained an
707 ecologically relevant process across broad geographical areas until relatively recently.
708 Among extant species, elephants provide the clearest evidence of the vegetation con-
709 sequences that this behaviour can generate when applied by particularly large mam-
710 mals: selective debarking can increase tree mortality, alter woody-plant abundance
711 and modify vegetation structure (Ihwagi et al., 2009). When proboscideans were
712 widespread across Afro-Eurasia and the Americas, comparable effects may have oc-
713 curred over much larger geographical areas. Other recently extinct megaherbivores,
714 including browsing ground sloths such as *Megatherium* in South America (Boscaini et
715 al., 2025), may also have incorporated bark into their diets. Collectively, these species
716 probably exerted stronger and more varied pressures on woody vegetation than those
717 observed today, marking a recent and profound shift in mammal–vegetation interac-
718 tions and a likely reduction in bark feeding as an ecological function.
719 Although bark-feeding megaherbivores were likely to have exerted substantial
720 effects on vegetation, smaller mammals may also have contributed to vegetation dy-
721 namics and plant evolution through bark feeding. Unlike foliar herbivory, whose ef-
722 fects generally increase with the quantity of photosynthetic tissue removed, bark feed-
723 ing can severely damage or kill a tree through the removal of relatively little biomass.
724 Circumferential bark removal can girdle a stem, meaning that even small-bodied
725 mammals, particularly rodents, can cause substantial mortality among saplings and
726 small trees, as is still observed in contemporary ecosystems. Rodents were already
727 taxonomically and ecologically diverse in past ecosystems, having undergone repeat-
728 ed evolutionary radiations and occupied a wide range of dietary and ecological niches
729 (Fabre et al., 2012). Some past faunas also contained extinct rodent lineages and
730 body-size classes with no direct contemporary equivalents, particularly among South
731 American caviomorphs (Vucetich et al., 2015). Bark feeding may consequently have
732 represented a low-biomass but high-impact form of herbivory operating across a

broad range of mammalian body sizes, allowing even occasional or seasonal consumption to influence tree survival and vegetation dynamics.

These effects were probably especially pronounced in seasonal environments because bark frequently functions as a fallback resource during periods of food scarcity. Past bark-feeding pressure may therefore have combined a persistent background effect produced by regular bark feeders with intense, intermittent pulses during seasonal or episodic resource bottlenecks. In the richer herbivore assemblages of the past, synchronised dietary shifts towards bark could have produced concentrated episodes of stem damage involving mammals of different body sizes and affecting both young and mature trees. Such damage may also have been spatially concentrated around specific areas, such as remaining water sources, seasonal refuges and other areas where mammals aggregated during periods of scarcity.

The resulting effects could have been amplified by secondary stressors such as fire, insects and pathogens. By increasing tree mortality, creating canopy gaps and delaying woody recovery, bark feeding may have contributed to the maintenance of open or semi-open habitats, including savannas, woodlands and forest–grassland mosaics. Its historical influence was therefore probably strongest where several conditions coincided: pronounced climatic seasonality, prolonged or intense periods of food scarcity, high mammal abundance or diversity, spatial aggregation around limiting resources and recurrent disturbances such as fire. These environments may consequently retain particularly strong ecological and evolutionary signatures of past interactions with bark-feeding mammals.

Over evolutionary timescales, the persistent interaction between woody plants and megafauna likely imposed selective pressures favouring structural defences (e.g., thick bark or fluted trunks, trunk spines) and regeneration strategies such as bark healing or basal resprouting. Recognizing the historical role of bark feeding provides a valuable perspective for understanding long-term vegetation patterns, community assembly processes, and the evolution of plant defences. It also offers insight into future ecosystem trajectories under conservation and rewilding strategies. Reintroducing large herbivores may help restore lost ecological processes—including bark feeding—that once maintained landscape heterogeneity. Anticipating how these pressures will interact with modern vegetation and climate conditions is essential for guiding biodiversity and ecosystem management into the future.

V Conclusions and perspectives

This review highlights bark feeding as a widespread but underappreciated mammalian behaviour with significant ecological and evolutionary implications. Despite its rarity in global trait databases and its marginal treatment in conservation and animal/vegetation studies, the evidence synthesized here suggests that bark feeding should be more fully integrated into ecological theory and management frameworks.

We identify five central insights from the available literature:

1. Bark feeding is widespread among medium- to large-bodied mammalian herbivores across multiple taxonomic groups and biogeographic regions.

2. It serves as a critical fallback resource, supporting herbivore survival during resource-scarce seasons, likely affecting individual fitness and potentially population dynamics.
3. The behaviour can cause lethal damage to both small and large trees, influencing regeneration patterns, altering canopy structure, and contributing to shifts in vegetation composition and landscape openness.
4. Bark feeding is associated with distinctive plant traits, including bark characteristics and trunk morphology, suggesting a role as a selective pressure in plant evolution.
5. Historically, bark feeding was likely a more prominent ecological force, especially during the pre-Anthropocene era of megafaunal abundance, when non-ruminant species with broad dietary niches likely exerted stronger bark-feeding pressure.

These findings point to bark feeding as an under-recognized driver of both animal and plant strategies. Expanding our understanding of this interaction could reshape our interpretations of vegetation dynamics, particularly in systems where herbivory, fire, and climate intersect, as well as how survival strategies could affect mammal adaptation/resilience, speciation, and community composition.

We propose several priorities for future research. First, bark feeding should be systematically recorded in mammal dietary databases, including its seasonality, frequency, and the tree species targeted. Second, trait-based approaches linking mammalian morphology, digestive physiology, and foraging strategy with bark-feeding behaviour could reveal broader ecological rules. Similarly, comparative analyses of bark chemistry and structure across ecosystems would help explain tree-level vulnerability and patterns of selection. Third, bark feeding should be explicitly modelled in reconstructions of historical vegetation dynamics and scenarios of ecosystem rewilding. As conservation efforts increasingly focus on restoring trophic interactions, bark feeding may represent a missing component of herbivory regimes that once shaped the openness and turnover of woodlands and savannas. Integrating this behaviour into assessments of ecosystem resilience could improve predictions of vegetation response to megafaunal reintroduction or defaunation reversal.

Moreover, the fallback resource framework provides an important lens for understanding how mammals buffer themselves against seasonal or stochastic resource shortages (Illius & O'Connor, 1999; Marshall et al., 2009). Although bark typically contributes little to annual dietary biomass for most mammals, its availability during critical bottlenecks may disproportionately influence fitness. As climate change and ecosystem fragmentation may intensify the frequency and severity of food stress events, understanding the role of fallback behaviours—such as bark feeding—will be essential for anticipating herbivore vulnerability and adaptive capacity.

Finally, debarking intensity may serve as an ecological indicator of both herbivore stress and habitat condition. High rates of bark feeding may signal insufficient availability of primary resources, while shifts in bark-feeding patterns could flag changes in herbivore density, health, or vegetation composition. Monitoring this behaviour could

thus offer a practical tool for evaluating thresholds of herbivore pressure, forest regeneration potential, and ecosystem stability under novel environmental regimes.

In sum, bark feeding represents a complex but ecologically meaningful interaction that bridges herbivore foraging ecology, plant defence evolution, and long-term vegetation dynamics. Its integration into ecological monitoring, historical interpretation, and conservation planning holds significant potential for advancing our understanding of herbivory in a changing world.

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