forests

Review

Bite by Bite: How Ungulate Browsing Shapes North America's Forest Future

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Abstract

Ungulate browsing represents a contemporary issue for forest development, influencing forest regeneration, composition, and management practices across the world, especially in North America. This review synthesizes findings from 101 studies conducted between 1980 and 2025 to examine patterns of herbivory damage through browsing by moose, elk, white-tailed deer, black-tailed deer, and bison. Despite regional variation, high ungulate density consistently emerges as the primary factor driving browsing intensity and ecological and economic impact, leading to decreased social acceptance of coexistence with ungulates. This review highlights the selective suppression of palatable species such as balsam fir, red oak, and white cedar, leading to shifts toward less-preferred conifers. Preventive and control measures, ranging from fencing and repellents to regulated hunting, are widely implemented but vary in effectiveness and social acceptability. Although predator presence is an evident controlling factor, it was not statistically associated in this review with reduced browsing, nor with behavioral or trophic cascade effects. Ultimately, this study underscores the importance of integrated management strategies that combine silvicultural adaptation, population control, and, where feasible, predator reintroduction to ensure forest resilience and sustainability in the face of increasing pressure from climate change.

Keywords: ungulate; browsing; deer; moose; elk; whitetail; blacktail; bison; regeneration; forest management

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1. Introduction

While previous authors have suggested a prominent human role in affecting populations of large ungulates during the Mid–Late Holocene [1,2], this study begins with an analysis following European settlement, when a broad transformation of North American forests began in the eastern region. Here, settlers initiated large-scale clearing and timber extraction as early as the 17th century, targeting coastal and riverine hardwood forests for shipbuilding, agricultural clearings, and various fiber and fuel needs. This exploitation marked the first wave of forest frontier expansion. Then, in the early 19th century, the Lewis and Clark expedition (1804–1806) symbolically opened the Western frontier, initiating a century of mapping and scientifically assessing vast, undeveloped territories. This effort accelerated the spread of resource extraction and land conversion across the continent [3]. Even in this early period, the expedition noted both the large abundance of game in the broad open landscapes from St Louis to the foothills of the Continental Divide and the apparent scarcity of wild game from the Continental Divide to the Pacific Ocean [3]. Their journals portray reduced wildlife populations around native settlement areas while noting abundant wildlife in the "no man's land" between tribal areas of influence [2].

Around the same period, even-aged forest management emerged in the 18th and early 19th centuries in Germany as part of the rise of the Industrial Revolution, and scientific forestry focused on sustained timber yields [4,5]. This forest management approach, emphasizing uniform stand structures and predictable harvests, was later adopted in North America during the late 19th and early 20th centuries, aligning with the rise of industrial forestry and post-clearcut regeneration strategies [6,7]. Attempts to quantify the effects of large herbivores on ecosystem processes are markedly scarce in past and contemporary studies [8].

Native ungulate species inhabit a diverse range of habitats across North America, from the high Arctic of Canada and the USA to the deserts of Mexico [9,10]. Since the expansion of early pioneers in the 18th and 19th centuries, many wildlife species have undergone significant declines compared with legendary accounts of early explorers [3]. Estimates suggest that ~95%–99% of terrestrial mammal predators have been extirpated from North America, mainly due to persistent persecution by humans [11]. Predators were commonly exterminated through bounty systems, poisoning, and trapping under the belief that their removal would support ungulate recovery and increase hunting opportunities [12]. These policies were based on the simplistic predator–prey dynamic assumptions prevalent in North American wildlife management at the time. Nonetheless, the rise of conservation awareness, the development of protected area systems, improvement in wildlife management plans, and the reintroduction and natural recolonization of predator populations have led to recoveries in many areas of North America (e.g., the Rocky Mountains, Great Lakes, and southwestern regions) [3,5,13].

Wildlife conservation had its beginnings in Canada and the USA in the late 1800s [14]. Wildlife management in North America progressed through six stages that elevated cervids from being unmanaged and overexploited to successfully managed and conserved: the creation of laws and regulations, appropriate predator control, establishment of reservation land refuges, reintroductions, environmental controls, and habitat management [15]. The North American Model has been credited with expanding wildlife species populations across the continent [16].

Predation by wolves (*Canis lupus* L.), along with sympatric bears (*Ursus* spp.), generally limits cervid densities [17]. In North America, both black bears (*Ursus americanus* Pallas) and brown bears (*Ursus arctos* L.) commonly prey on neonatal cervids, taking a large percentage of the annual offspring that are less than one month old [18]. Across the continent, cervid densities in areas without wolves have been, on average, nearly six times higher than in areas with wolves [19]. As early as the 1940s, dramatic deer population increases—and corresponding range expansions—were documented throughout western and eastern Canadian forests following the decline in wolves and other predators [9,10]. Over the past century, white-tailed deer have likewise surged in abundance and expanded their geographic range [20], reaching densities higher than any recorded in the past several hundred years [21,22].

High densities of ungulate: moose (*Alces alces* L.), white-tailed deer (*Odocoileus virginianus* Zimmermann), bison (*Bison bison* L.), elk (*Cervus canadensis* Erxleben), and black-tailed deer (*Odocoileus hemionus* Rafinesque) in North America have been associated with significant ecological and economic impacts, particularly in the agriculture and forestry sectors [23]. Intensive herbivory alters plant community composition, reduces biodiversity, and impedes forest regeneration [22,24]. These effects compromise ecosystem functioning and incur significant financial losses, especially through crop damage, failed recruitment of saplings, and diminished timber yields [25–27]. Indeed, many temperate and boreal forest ecosystems have historically exhibited semi-open, heterogeneous canopy structures maintained by large herbivores, which can enhance biodiversity and structural complexity [28]. Ecosystem functioning, in its broad sense, can be understood as the capacity of biotic and abiotic components to sustain key processes such as primary production, nutrient cycling, energy transfer across trophic levels, and the maintenance of species diversity [29]. Timber production and stand density are only one expression of those processes. Forest managers aim to control stand density and the quality of future crop trees, from the establishment stage until harvest, thereby mirroring natural successional phases [30,31]. The current concern is not a low tree density per se, but rather the point at which chronic, selective browsing pushes vegetation beyond its historical range of variability, suppressing the regeneration of palatable species and simplifying community structure in ways that degrade multiple ecosystem services and exceed economic thresholds [32]. In response to these damages and losses, compensation programs in the United States are estimated to pay approximately USD 6 to USD 13 billion annually for losses attributable to direct herbivory on crops and indirect impacts on overall agricultural productivity and economic viability [33]. Given the scale of these impacts and associated economic burdens, there is a critical need to better understand ungulate browsing dynamics and effective mitigation strategies.

Similar to the study conducted in Europe regarding ungulate browsing [34], this review investigates the effects of ungulate browsing on forest regeneration across North America, synthesizing browsing intensities, species preferences, and management responses. At the same time, this study aims not only to understand the magnitude of ungulate browsing but also to explore in depth the preventive and control measures for cervids and to identify appropriate management solutions for both wildlife and forestry managers.

2. Materials and Methods

2.1. Literature Review Approach

This literature review was performed using a semi-systematic approach in four steps, following a methodology similar to that described in [35]. Relevant keywords were established based on the two research questions:

- What are the known effects and magnitude of ungulate browsing on forest regeneration across North America?
- Which preventive and control measures for ungulates have the greatest potential as management solutions for both wildlife and forestry managers?

2.2. Search Strategy, Inclusion Criteria, and Screening Process

Firstly, relevant literature was identified through searches in Web of Science and Google Scholar using combinations of keywords such as ungulate, deer, moose, elk, white-tail, blacktailed, bison, wood bison, browsing, and tree damage. Boolean operators were used to refine the search. To ensure geographical relevance, the terms North America, Canada, and the United States were added. The investigation concluded in May 2025 and included studies published between 1980 and 2025.

Secondly, the screening process involved reviewing titles, abstracts, and keywords to exclude clearly irrelevant studies. In addition, this step included reviewing the reference lists of the selected papers to identify additional sources.

Thirdly, full texts of the remaining articles were evaluated for eligibility based on defined inclusion and exclusion criteria. These criteria ensured that the studies focused on the effects of ungulate browsing in North American forests and employed relevant ecological or economic analyses.

Finally, in step 4, we applied the inclusion and exclusion criteria to further refine the selected studies. The inclusion criteria were as follows: (a) studies that focused explicitly on ungulate browsing on tree species; (b) studies conducted in North America; (c) studies that measured browsing intensity using specific indicators; (d) studies presenting significant results and providing substantial support for future research, even if no quantitative analysis was conducted; (e) studies that measured the browsing intensity of ungulates, even if their primary objectives were broader; (f) studies that analyzed the ecological or economic impact of browsing; and (g) studies employing natural or field-based experimental approaches.

On the other hand, the exclusion criteria were as follows: (A) studies focused solely on the browsing of non-tree plant species; (B) studies where the browsers were species other than ungulates (e.g., marsupials, rodents, or hares); (C) studies conducted in fields unrelated to wildlife research or forestry; (D) studies utilizing repetitive datasets with no significant improvements; (E) studies lacking descriptions of the ungulate or tree species studied; and (F) studies based on laboratory experimental approaches. By applying these inclusion and exclusion criteria, the selected studies were carefully filtered to ensure their relevance and suitability for research on ungulate browsing. The steps followed to identify the papers included in the review are illustrated in Figure 1.

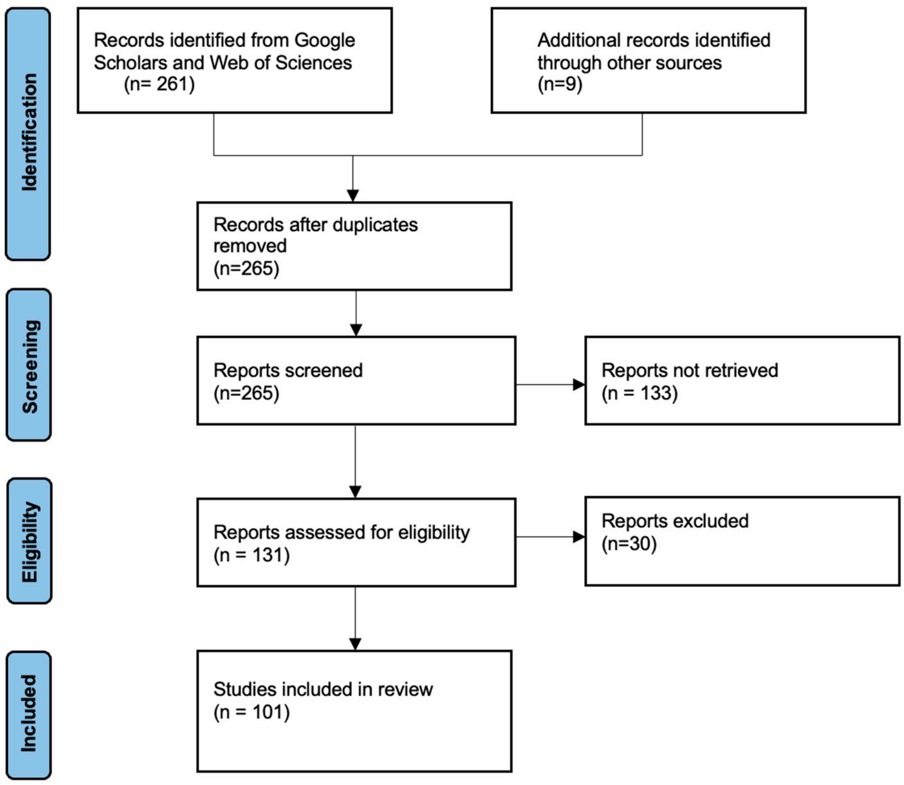

Figure 1. Flow diagram of literature review and study selection process. The number of works (n) identified, screened, included, and excluded was identified at each step of the literature review process.

2.3. Analytical Framework

As a first approach to understanding the phenomenon under study, a thorough analysis of patterns, trends, and specific cases regarding the impact of different ungulate species on forest development is essential. To explore potential ecological relationships between predator presence and ungulate density, we performed a contingency analysis. Ungulate density was categorized into three ecologically meaningful classes based on animal density (ungulates per 1 km^2) in relation to the animal's body mass, as both moose and bison are considerably larger than deer species (Table 1). Similarly, the browsing rate was recoded in 3 classes: Low, Medium and High (Table 2)

Table 1. Ungulate density classification by ungulate species.

Class	Ungulate Size	Density Range (Animals/km^2)
Low	Deer species	0–15
	Moose or bison	0–0.7
Medium	Deer species	>15–30
	Moose or bison	0.7–1.25
High	Deer species	>30–50
	Moose or bison	>1.25

Table 2. Classification of browsing intensity based on browsing rates.

Class	Browsing Rate (%)
Low	0–30
Medium	31–70
High	71–100

Similarly, browsing levels were categorized and recoded as follows:

We constructed a comparison between predator presence (Yes or No) with the categorized ungulate density classes and applied a chi-square test of independence to assess statistical association [36]. Given the absence of variance estimates or repeated observations per site, each record was treated as a single observation with equal weight. We applied linear models to assess the effect of each moderator on browsing intensity. Specifically, subgroup meta-regression-style analyses were performed using statsmodels [37] in Python 3.9.6 to replicate the structure of traditional meta-analyses (e.g., subgroup comparisons and pooled estimates). The independent variables used as moderators were

- Predator presence (yes or no);
- Dominant browsed species (broadleaves, coniferous, or mixed);
- Ungulate density per 1 km^2 (low, medium, or high);
- Ungulate species (e.g., blacktail, elk, moose, or a combination of these species based on their presence).

A meta-analytical framework was conducted in order to explore the variation in browsing intensity among ungulates in relation to environmental and ecological characteristics. The response variable was the browsing level, an ordinal variable categorized as low, medium, or high, and recoded numerically (1, 2, or 3, respectively) to allow continuous modeling. Since the data lacked individual study weights or variance estimates, each observation was treated equally. Linear models were fitted using ordinary least squares (OLS) regression [38] to assess whether browsing levels significantly differed across subgroup categories. All statistical analyses were performed using Python's statsmodels [37] and seaborn [39,40] libraries.

To assess whether predator presence was associated with ungulate density, we constructed a chi-square test of independence was performed. Both variables were treated as categorical, with ungulate density categorized as low, medium, or high. The test was applied using Python's SciPy 1.15 library [41].

3. Results

3.1. Overview of Ungulate Browsing Studies in North America

Across North America, in Canada and the United States of America, 101 studies focused on ungulate browsing were identified through our filtering criteria. The main ungulate species in the selected studies were moose (n = 59), white-tailed deer (n = 35), bison (n = 14), elk (n = 11), and black-tailed deer (n = 6).

3.1.1. Canada

In Canada, the main study area of white-tailed deer browsing is represented by Anticosti Island, Quebec. The existing population of introduced whitetail deer on Anticosti Island is jeopardizing the growth and recruitment of balsam fir (*Abies balsamea* L.) to the canopy in favor of white spruce (*Picea glauca* Moench) [42–46]. White spruce is also slightly damaged by the ungulates, as to achieve a balance in their diet, they have to consume both high-nutrient species like balsam fir and low-quality food such as white spruce (but in lesser quantities) [47]. Besides the preference for balsam fir, white-tailed deer also highly prefer paper birch (*Betula papyrifera* Marshall) [21]. The only solution that increased seedling growth and decreased balsam fir mortality was a substantial reduction in ungulate density via culling [48].

Similarly, in Newfoundland, moose browsing is altering the share of balsam fir (*Abies balsamea* L.) in black spruce (*Picea mariana* Mill.)-dominated sites [49]. For a successful reintroduction of red spruce (*Picea rubens* Sarg.) in the Quebec area, managing the browsing pressure created by moose is required [50], as again, the high density or overabundance of moose is considered to be the main cause.

Since their introduction to the Haida Gwaii archipelago, black-tailed deer (*Odocoileus hemionus* Rafinesque) have heavily browsed Western redcedar (*Thuja plicata* Donn) [51], Sitka spruce (*Picea sitchensis* Bong.) [52,53], and Western hemlock (*Tsuga heterophylla* Raf.) [54] resulting in a drastic reduction in regeneration and a low growth rate in the surviving saplings [51]. The top-down and bottom-up consequences of unchecked black-tailed deer browsing on plant and animal diversity in temperate forests of Haida Gwaii include the simplification of vegetation within a habitat, reduction in differences between habitats, and potential changes in biodiversity due to the elimination of certain canopy elements [55]. The absence of natural predators in the archipelago makes hunting an effective solution for controlling the ungulate population, and the future occurrence of redcedar stands in second-growth forests may be influenced by the amount and distribution of deer hunting [56], as the ecosystem can be considered altered through the introduction of an alien ungulate species.

Canadian research shows that bison shape woody vegetation in two very different landscapes. In the prairie–parkland, plains bison browsing in Riding Mountain NP keeps trembling aspen (*Populus tremuloides* Michx.) and green ash (*Fraxinus pennsylvanica* Marshall) stems below escape height (the height above which tree species escape browsing) and favors rough-fescue grassland, while aspen–parkland enclosure trials confirm that bison (and other native ungulates) reduce aspen recruitment more strongly than cattle [57,58]. Further north, wood bison affects post-disturbance succession in hemi-boreal mixed woods. Herd composition and nutritional studies reveal that animals aggregate where high-quality food (young willow and aspen) is abundant, creating local hotspots of pressure [59]. Clear-cut experiments in North–Central Alberta show that these concentrations delay deciduous canopy closure and limit conifer establishment, making early seral cut-blocks prime bison foraging habitat [60]. Winter diet analyses across Yukon and the Northwest Territories confirm a heavy reliance on willow and aspen, with little use of conifers [61]. GPS-collar data further indicate that bison and moose overlap minimally in winter range, bison prefer open, recently disturbed patches, leaving browse refugia where conifers can escape [62]. Collectively, evidence suggests that keeping bison densities below ≈15 animals/1 km^2 or using rotational grazing and patch-burn regimes can balance their role as disturbance engineers without suppressing mixed-wood recruitment.

3.1.2. United States of America

White-tailed deer browsing preferences in Southern New England are red oak (*Quercus rubra* L.), black birch (*Betula nigra* L.), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and sugar maple (*Acer saccharum* Marshall), in descending order [63]. Red oak is also the most preferred species in South Carolina [53], Massachusetts [64–66], and Minnesota [66]. Eastern hemlock (*Tsuga canadensis* L.) is another species highly affected by whitetail browsing, with the species missing from the seedling and sapling strata [67–69]. In North-eastern Minnesota, white-tailed browsing inhibited the establishment and recruitment of white pine in pine-dominated forests [70,71]. The presence of black locust (*Robinia pseudoacacia* L.) in pine stands makes Jack pine (*Pinus banksiana* Lamb.), pitch pine (*Pinus rigida* Mill.), and Austrian pine (*Pinus nigra* J.F.Arnold) more susceptible to white-tailed browsing, as the nitrogen produced by the black locust may have caused more succulent tissue in the pines [72]. In the Upper Great Lakes region, a substantial reduction in ungulate density is necessary for white cedar (*Thuja occidentalis* L.) regeneration efforts to succeed [73]. Whitetail deer can cause damage to tree nurseries during winters [74], with a preference for yew species (*Taxus* sp.) [75]. The trend of balsam fir browsing observed in Canada is also present in West Virginia, despite differences in area and management practices [76]. In the United States, various alternative methods have been studied to prevent white-tailed deer damage, including postseason hunting [77], the use of slash [78], treefall mounds [69], and tree shelters [79]. However, none of these methods are feasible on a large scale or can be applied nationwide.

One of the most affected areas of moose browsing in the U.S.A. is Isle Royale, where the browsing pressure from moose has been so intense that it has hindered the growth of white spruce and balsam fir saplings, preventing them from reaching the tree canopy stage [80]. Also, in the same area, the abundances of red-osier dogwood (*Cornus sericea* L.) [74] and Canadian yew (*Taxus canadensis* Marshall.) [81] have greatly decreased due to browsing. In Northeastern Vermont, the consequences of moose browsing were observed 20–30 years after the damage occurred, with the plots containing fewer commercially valuable hardwood stems [82]. The high levels of browsing by moose can indirectly affect the recruitment of trees into the canopy, negatively impacting nitrogen mineralization and net primary production [83].

The most preferred browsing tree species in Alaska are willow species (*Salix* sp.) [84]. Moose browsing has been recognized as a significant cause of the shift from willow (*Salix* sp.) and balsam poplar (*Populus balsamifera* L.) to less palatable species such as alder (*Alnus* sp.) and spruce (*Abies* sp.) [85]. In the taiga, browsing indirectly affects the soil and vegetation dynamics, influencing the establishment and development of the forest [86]. This is linked to a paludification issue in the taiga, where excessive browsing can cause a retrogressive succession from healthy forests to flooded fens and wet meadows due to the thawing of permafrost [87]. In Grand Teton National Park, the lack of predators and high moose density have affected vegetation, and the only viable solution to control browsing is the replacement of natural predators with hunting by humans [11].

In America, a subspecies of the common red deer, commonly referred to as elk (*Cervus canadensis* Erxleben), is found in many of the ungulate studies as a browser. The high densities of elk in Yellowstone National Park have limited quaking aspen (*Populus tremuloides* Michx.) regeneration and tree recruitment due to intense browsing [88]. However, with the reintroduction of the gray wolf in the altered ecosystem, the resulting trophic cascade, elk movements, density, and foraging behavior were modified, restoring balance to the ecosystem and promoting the recovery of quaking aspen [13,19,88,89]. Intensive hunting in areas adjacent to Yellowstone National Park during the elk winter migration period from the park area, because of the lack of food, reduced the number of ungulates to a level that wolves could control, concurrent with their predation within the protected park area [90–92]. The presence of wolves also significantly impacted browsing levels in the Rocky Mountains, the density of predators being proportional to the damage intensity [79]. Elk browsing slows forest recovery following bark beetle outbreaks, as high rates of juvenile browsing may indicate a shortage of the desired density of Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* Hooker), with 95% of juvenile plots affected by browsing [93].

The bison (*Bison bison* L.) in the studies selected from the United States are clustered in two regions: Yellowstone's northern range and the Great Plains tallgrass prairie. On the Yellowstone floodplain, a bison herd that now exceeds 4000 animals repeatedly snaps young aspen, cottonwood, and willow stems, preventing them from growing above 2 m and resetting stands to shrub height [94–96]. Browsing and stem breakage have reduced cottonwood recruitment by >70% relative to pre-1980 cohorts, and shoot architecture records show that damage rates intensified after herd size more than doubled in the early 2000s [97,98]. Even where spring floods create fresh germination sites, subsequent herbivory eliminates most seedlings before they reach 1 m, decoupling fluvial disturbance from forest recovery [99]. Narrowleaf cottonwood on high terraces fares slightly better, but combined elk and bison use still cuts sapling survival in half at densities above ≈20 animals/1 km^2 [100]. In riparian meadows, the selective removal of palatable willows shifts communities toward sedge-dominated graminoid flats and lowers shrub diversity [101].

Further south and east on the Great Plains tallgrass prairie, plains bison have shaped woody dynamics through physical disturbance as much as browsing. Horning, rubbing, and repeated wallowing uproot saplings and create bare-soil patches that favor grasses over woody plants, slowing woody encroachment into tallgrass prairie and maintaining a heterogeneous grass–forb mosaic [102,103]. Collectively, U.S. evidence shows that when bison densities exceed ~15 animals/1 km^2 in the absence of sustained predator control, woody recruitment is curtailed, and the riparian structure is simplified.

3.2. Browsing Intensity Drivers

Due to the lack of continuous data and the presence of incomplete datasets in the analyzed papers, the outcomes regarding the relationship between browsing levels and various parameters were statistically insignificant, even when clear patterns seemed apparent. Predator presence, browsed species, and ungulate density did not significantly affect browsing levels ($p > 0.05$). This may indicate false negative results and underscores the inadequacy of data collection and reporting in the reviewed studies.

Browsing intensity varied considerably across ungulate species. A subgroup analysis by species revealed marked differences (Figure 2). For example, species such as elk exhibited higher average browsing levels than blacktail deer. Sample sizes varied markedly among species, and the 95% confidence intervals for most estimates overlapped; consequently, any apparent interspecific differences should be interpreted with caution. Moreover, the evidence base is strongly weighted toward forestry-oriented studies, which focus on browsing effects in production stands. As a result, Figure 2 largely reflects browsing intensity under timber management contexts and may under-represent browsing dynamics in less managed or strictly protected forests.

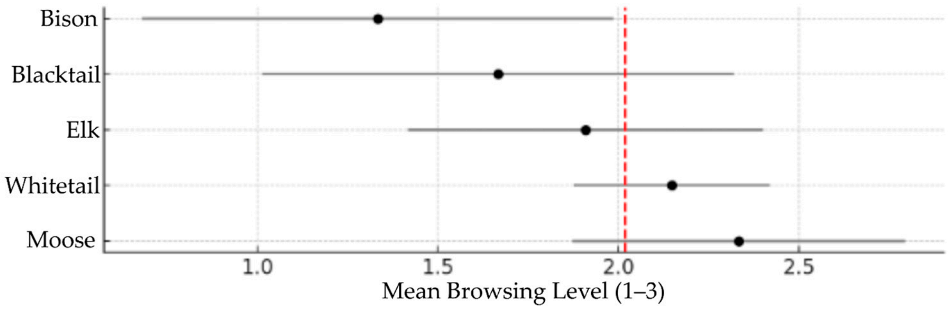

Figure 2. Browsing level by ungulate species and overall median value of browsing level (red line).

Our analysis reveals a pronounced difference in browsing pressure between bison and moose. This difference is primarily driven by their contrasting foraging behaviors: bison are mainly grazers, feeding on herbaceous vegetation with minimal interaction with woody plants, while moose are browsers that feed heavily on shrubs and tree species, particularly during winter when other food sources are scarce.

3.3. Relationship Between Predator Presence and Ungulate Density

The contingency table revealed that predator-absent areas exhibited a more even distribution across all ungulate density classes, with a relatively higher proportion of observations in the medium and high categories. In contrast, predator-present areas were predominantly classified as having low ungulate density:

The chi-square test indicated no statistically significant association between predator presence and ungulate density (χ^2 = 2.14, df = 2, p = 0.344). Although the data suggest that predators may be more frequently associated with areas of lower ungulate density, the observed differences were insufficient to reject the null hypothesis. This lack of significance may be attributed to a limited sample size or an uneven distribution of observations. Moreover, the absence of standardized data analysis across the selected studies further hindered the ability to validate patterns that appear ecologically evident.

4. Discussion

Based on the analysis of the papers included in this review, it is evident that the primary factor driving ungulate browsing is the high density or overabundance of ungulates—an issue consistently highlighted throughout the history of research on ungulate impacts [24,32,34,104–107], particularly as ungulate populations have increased significantly in recent decades [108–110]. Ungulate density emerges as the central driver within the conceptual system of continuous interaction between ungulates and the forest ecosystem, influencing a wide range of ecological processes and management reactions, highlighted by the fuzzy conceptual map (Figure 3).

The regulation of ungulate densities is primarily shaped by natural predator presence (which is missing from most modern landscapes) and hunting pressure, both of which exert a limiting effect on ungulate populations [111,112]. When ungulate density increases, browsing intensity rises accordingly, placing significant pressure on young and multi-aged forest development by reducing sapling survival and tree recruitment, thus altering successional pathways that require additional efforts by forest managers and owners. This direct and indirect impact of high ungulate numbers results in shifts in trophic interactions and forest composition shifts [113], reduced structural and functional diversity [114], and compromised regeneration [48]. In response, managers implement various preventive measures, such as fencing, repellents, or targeted culling, to mitigate ungulate damage. Simultaneously, high ungulate density influences silvicultural strategies, necessitating adjustments in planting schemes (e.g., adopting higher planting densities per hectare) and in forest treatments, opting for closer-to-nature silvicultural systems. These silvicultural adaptations, while essential for maintaining forest productivity, lead to increased operational complexity and costs while simultaneously increasing biodiversity and replicating a successional climax in a much shorter period. Controlling ungulate density is not only key to protecting young forest stands but also fundamental to balancing ecological resilience, economic feasibility, and social acceptability within forest and wildlife management frameworks. It is crucial to understand that most habitats and ecosystems are altered because intensive forest management promotes high-density closed-canopy forests, and large carnivores are missing from the broader landscape, enabling ungulates to expand both numerically and geographically. Moreover, it has been shown that temperate forest vegetation in Europe is associated with heterogeneous semi-open canopy conditions that have been shaped by large herbivores over millennia [28]. Under projected warmer and drier summers, semi-open, savanna-like structures can reduce stand-level evapotranspiration and fire intensity. Moderate browsing that maintains such heterogeneity may thus increase resilience to aridification [115,116]. The concern arises only when browsing intensity suppresses the recruitment of palatable species below replacement levels, leading to structurally simple, low-diversity mosaics with a reduced adaptive capacity.

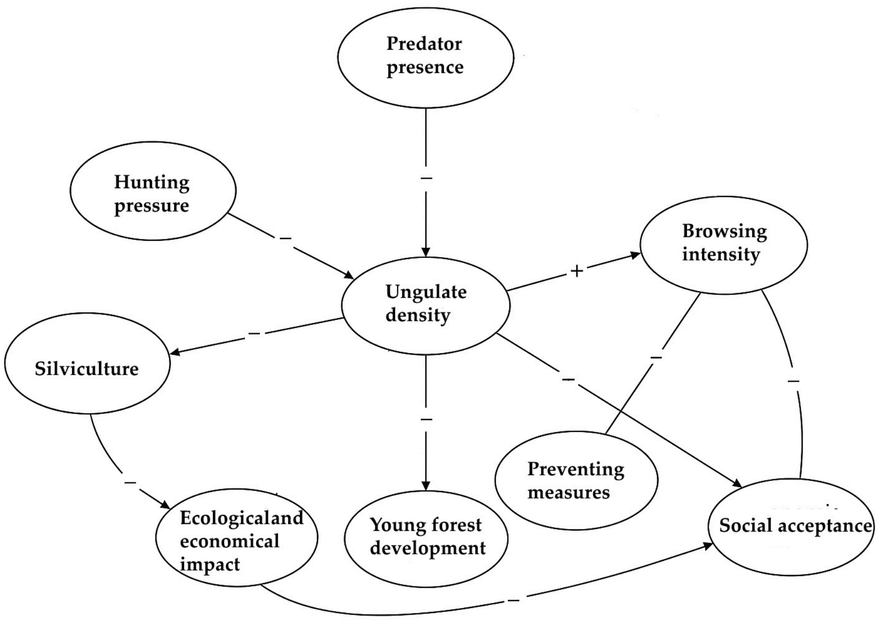

Figure 3. Fuzzy conceptual map of the ungulate density impact of forest ecosystem and wildlife and silvicultural management implications.

Although no statistically significant link was found between predator presence and either ungulate density or browsing intensity, this may be due to inconsistencies and gaps in the underlying dataset rather than a true absence of effect in this paper [117,118]. Several studies suggest that ungulates tend to avoid areas with high predator activity or active hunting, instead preferring safer, low-risk habitats [119–122]. In regions with elevated predator populations, ungulates alter their behavior, becoming more cautious in their movements and avoiding high-risk areas such as forest gaps and large, open clear-cuts with little or no cover [123–125]. These behavioral shifts may contribute to a reduction in browsing intensity, as prey animals limit their exposure in vulnerable areas [126,127]. In regions where predators are absent, the reintroduction of large carnivores should be considered as a potential strategy to help regulate ungulate populations and mitigate their ecological impact [128–130]. The reintroduction of carnivores in areas with ungulate overabundance should not be carried out in isolation; active hunting should also be implemented to reduce ungulate numbers to a level that predators can effectively control [131–133].

Ungulate browsing has emerged as a significant ecological force shaping forest regeneration and stand composition across North America. Intensive herbivory alters successional pathways by selectively suppressing palatable species such as balsam fir, red oak, and white cedar, thereby facilitating dominance by less-preferred or browse-resistant species, usually coniferous species [17,18]. Browsing preferences vary widely among ungulate species. For instance, moose, elk, and white-tailed deer differ in both dietary selectivity and the magnitude of their ecological impact [24], with moose often associated with the most severe browsing effects due to their substantially higher daily intake, which correlates with their larger body mass [83]. Regional variation is substantial: for instance, deer on Anticosti Island preferentially target balsam fir, while bison in the Great Plains shape woody recruitment through both browsing and physical disturbance [55,134]. These patterns underscore the need to disaggregate browsing impacts by species and ecological context and to adapt silvicultural management based on wildlife presence and their abundance in the area. In areas with higher ungulate densities, preventive and control measures are needed: while preventive methods such as fencing and the use of repellents are only short-term solutions and place financial pressure on forest owners and managers, control measures such as numerical reduction are long-term solutions that also address issues in other sectors (e.g., agriculture, human safety) [34].

The ecological consequences of chronic browsing extend beyond tree regeneration to broader ecosystem functioning. Sustained pressure on preferred plant species leads to a simplified understory structure, a loss of native plant diversity, and homogenization of habitats [22,26]. Altered successional trajectories limit the establishment of long-lived tree species and contribute to ecosystem instability [31]. Browsing also disrupts nutrient cycling by modifying litter input and soil composition, particularly in boreal and temperate forests, where shifts from mixed to coniferous dominance have been documented [25]. Over time, these changes reduce forest resilience and adaptive capacity, increasing vulnerability to perturbations such as fire, pests, and climate change. Modern forest ecosystems lie at the confluence of three overarching forces: intense ungulate grazing and browsing ("brown"), recurrent forest fires ("black"), and climatic constraints that intrinsically limit woody biomass ("green") [135]. In the face of the main issue that humanity is facing these days, climate change, ungulate browsing represents another impediment to forest development, which needs to be solved urgently in order to ensure sustainability and resilience. Hunting is one of the most reliable solutions [136].

This review revealed that browsing intensity is shaped by multiple interacting factors, though predator presence alone was not a statistically significant predictor of browsing pressure. Areas lacking predators showed a tendency toward higher browsing levels, consistent with expectations from trophic cascade theory [9], yet variability across regions, forest types, and species composition complicates this pattern. These habitats, from a conceptual point of view, can be considered altered, as the natural numerical control through predator–prey interactions is missing, allowing ungulate populations to grow uncontrollably and deviate from natural population dynamics.

Broadleaved and mixed-species stands generally exhibited higher browsing rates than conifer-dominated areas, possibly due not only to their traits or nutritional content, but also to their palatability and chemical composition, which make them easier for ungulates to digest [137]. On the other hand, less palatable conifers are mainly consumed due to food shortages during winter and early spring, or occasionally to meet the need for certain microelements required during the antler growth period [47,138]. In the North American continent, similarly to Europe, the trend of the reduction in the recruitment and growth of balsam fir in favor of white spruce is valid [42,46,47,49,76,93,139]. Forest treatment—particularly the planting scheme and density—plays a vital indirect role in browsing preference. In areas where food is insufficient to support high ungulate densities, animals tend to browse either on available saplings or selectively on species with higher palatability [140,141].

Mitigating ungulate impacts requires a multifaceted approach that combines lethal control (e.g., regulated hunting), mechanical barriers (e.g., fencing), and silvicultural adaptations such as dense planting or the use of less-preferred species [25]. These strategies must be tailored to species-specific behaviors and landscape context; for example, methods effective for moose may be ineffective for bison. Scaling interventions across large forested landscapes remains a challenge due to cost, logistics, and social acceptability. Moreover, non-lethal approaches do not decrease damage but only relocate it to other unprotected stands within the landscape. Long-term success depends on integrating ecological, economic, and cultural considerations into adaptive management plans. Reintroducing or maintaining predator populations can offer natural regulation but requires careful planning within socio-political constraints [142]. Ultimately, effective ungulate management must embrace complexity and foster collaboration among forestry and conservation stakeholders as well as local landowners.

This study highlights an issue of broad relevance, not only for the field of ungulate browsing but also for ecological science more generally. Several of the analyzed studies failed to report critical information or presented key findings using poorly defined parameters. For future research on ungulate browsing, certain aspects should be considered essential and consistently reported: ungulate density in the study area, forest management practices, the presence and density of predators, and browsing intensity measured through standardized, quantifiable parameters. These elements are necessary for facilitating meaningful comparisons across studies worldwide. Future research should prioritize addressing these data gaps to inform and support effective management strategies for both wildlife and forest managers, as well as other stakeholders. A transdisciplinary approach, integrating silviculture, wildlife ecology, and socio-political perspectives, is crucial for developing sustainable and resilient management practices and for gaining a deeper understanding of behavioral adaptations in ungulate ecology.

5. Conclusions

Ungulate browsing is listed among the most important factors affecting the composition of tree species and natural forest dynamics in North America. Increased ungulate densities negatively affect tree species regeneration, juvenile growth, and the resilience of entire forest ecosystems. The analyzed ungulate species exhibit distinct preferences that depend on tree species availability and vary among the studied regions.

The statistical analysis did not show significant correlations between predator presence, ungulate density, or browsing intensity. However, the data suggest a strong indirect effect through altered ungulate behavior, browsing characteristics, and habitat selection. The reintroduction or restoration of large predators such as wolves is unlikely to have a regulatory effect unless accompanied by the targeted culling of excessively abundant ungulate populations.

In the face of climate change, forests should be adapted to maintain their resilience. The overabundance of ungulate populations represents an additional, challenging, and destabilizing factor. Climate change adaptation programs should consider browsing when planning silvicultural measures, tree species, and stand structures. Higher browsing risk often occurs in mixed and deciduous forests.

The consequences of ungulate browsing are long-term and affect both stand- and landscape-level dynamics. The key to the successful mitigation of ungulate damage lies in a combination of silvicultural adaptations, mechanical barriers, and lethal control. Effective control requires social acceptance and long-term forestry planning.

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