Current Forestry Reports (2021) 7:305–320
https://doi.org/10.1007/s40725-021-00148-5

ECOLOGICAL FUNCTION (J BAUHUS, SECTION EDITOR)

A Review of Ungulate Impacts on the Success of Climate-Adapted Forest Management Strategies

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Accepted: 23 September 2021 / Published online: 1 November 2021

Abstract

Purpose of Review Climate change is modifying the dynamics of forests and threatens the supply of ecosystem services from managed forests. In response, managers are developing climate-adapted strategies, mostly focusing on changes in abiotic conditions. Ungulate populations, however, also impact forest integrity and productivity, and the effects of ungulate browsing likely interact with the effects of climate change. This raises the issue of whether climate-adapted strategies will be compatible with abundant ungulate populations. Here, we endeavour to (1) review if/how climate-adapted strategies currently consider ungulates and (2) to highlight how browsing could affect the success of these strategies, using a systematic mapping protocol and available knowledge of ungulate browsing.

Recent Findings We identified 57 references discussing climate-adapted forest management that mentioned ungulates, almost exclusively in boreal and temperate forests. The majority (35/57) of these considered browsing to be a threat to climate adaptation. Ungulates could especially prevent the achievement of changes in tree species composition or forest state desired to increase forest resilience. Browsing could also interact with the success of proposed climate-adapted approaches (e.g., nature-based silvicultural approaches and assisted migration), based on known effects of browsing.

Summary Potential interactions between large ungulate populations and climate-adapted forest management are sometimes considered but are not a large part of adaptation strategies. More empirical and modeling data would be beneficial, especially on the interactive effect of climate variables and browsing on tree regeneration. Without this, the climate-adapted strategies implemented today could result in future regeneration failures and exacerbate the pressure on forests.

Keywords Plant–herbivore interactions · Adaptive forestry · Silviculture · Cervids · Climate change

Introduction

Climate change is modifying the dynamics of forests at a speed and intensity that threatens their integrity and, especially for managed forests, the supply of ecosystem services [1]. For example, changes in drought and disturbance regimes could reduce wood production, despite the positive effects of a warmer climate and greater CO_2 availability on tree growth [2–4]. In response, forest managers develop strategies to accommodate increased climate-related risks and to preserve ecosystem services [5]. The forest sector already has access to a large toolbox of stand-level actions and planning options that could be adapted to take into account predicted future climate conditions [6]. The diverse effects of climate change on the environment, however, will require a careful consideration and integration of multiple threats to forest dynamics.

This article is part of the Topical Collection on *Ecological Function*

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Current Forestry Reports (2021) 7:305–320

Most climate-adapted strategies focus on changes in abiotic conditions, such as temperature, CO_2 concentration, or occurrence of extreme weather events. Changes in biotic conditions such as insect epidemics or large mammal populations, however, could also impact forest integrity and productivity [2, 6]. Abundant ungulate populations are increasingly recognized as an issue for the regeneration of North American and European forests [7–9]. Climate change could further augment ungulate populations by increasing individual survival and reproductive rates through milder environmental conditions and promoting range expansion [10, 11]. Ungulate browsing can regulate forest regeneration by reducing seedling and sapling growth and survival sufficiently to prevent both natural and artificial regeneration [7, 12]. Browsing and related activities such as bark stripping can reduce stand productivity and timber quality [13]. Moreover, ungulates are often selective in the food items they consume and, consequently, may transform mature forest composition, structure, and functions [7, 14]. Under heavy browsing pressure, large herbivores can change the pace and direction of successional pathways [15, 16]. The magnitude of ungulate impact on forest dynamics can even override the effects of climate change in some systems [9, 17, 18•, 19•].

The effects of ungulates on forest regeneration dynamics pose several questions, especially whether climate-adapted management approaches will be compatible with abundant ungulate populations. Although the effects of ungulates on current forest management have been investigated, little is known about how they could affect new strategies and approaches aimed at adaptation to climate change. Our objectives herein are to (1) review to what degree climate-adapted strategies currently consider ungulate browsing and then (2) to highlight how ungulate herbivory could impact the success of these strategies. We provide a review of the current literature based on a systematic mapping protocol and explore how ungulates could influence climate-adapted forest management, by synthesizing available knowledge.

A Systematic Map of Ungulates in Adaptation Strategies

Review Methods

We used a systematic search approach to sample how ungulate browsing is currently included in climate-adapted forest management strategies. We searched Web of Science Core Collections (Indexes: SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI) on 22 May 2020 using the following search (with * to obtain all word declinations):

TOPIC: (forest OR tree* OR seedling* OR regeneration) AND TOPIC: ((“climate change” OR “warming” OR “global change”) AND (adaptati* OR adapti* OR “assisted migration” OR “managed relocation” OR “management”)) AND TOPIC: (herbivor* OR ungulate* OR brows* OR deer OR cervid* OR *deer OR alces OR cervus OR odocoileus).*

We constrained the search to references with at least one mention of an ungulate species to fit our objective, i.e., describe current consideration of ungulates in climate-adapted strategies. Because of the exclusion of references without ungulates, this review is not necessarily representative of all references discussing climate-adapted strategies. This search uncovered 424 references, all of which were evaluated for relevance by title and abstract (i.e., screening phase) against the criteria detailed in Fig. 1. Of the initial 424 references, 216 were retained for a full-text evaluation

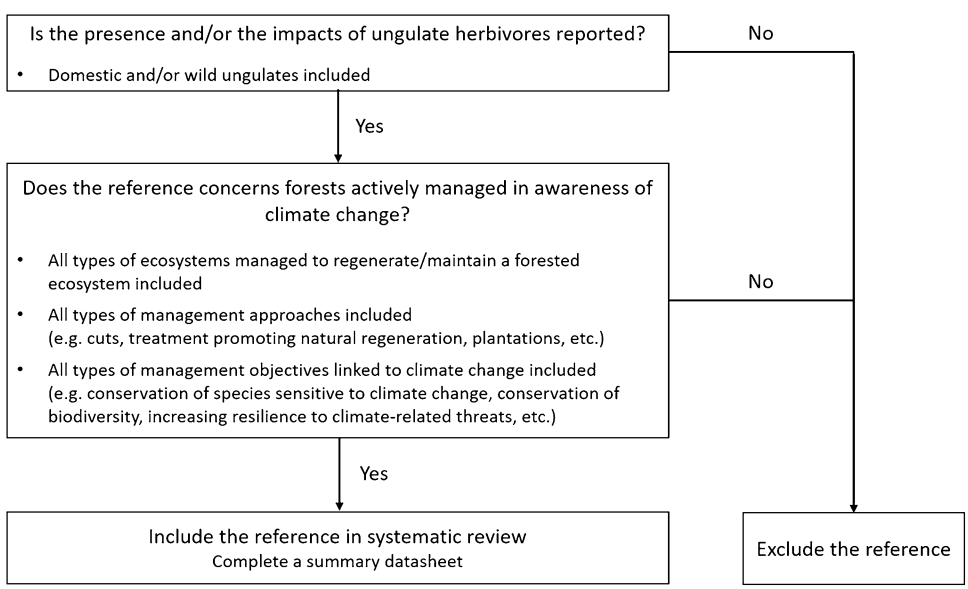

Fig. 1 Article selection process. Each reference was assessed with this chart to decide to include it or not in the systematic map, firstly in a screening phase using the title and abstract, and secondly using the full-text

using the same criteria. From those references, 57 were retained for a qualitative review, and we noted the rejection cause for the 159 excluded references (see Online Resource 1 for the list of 216 references). We excluded references for which we could not acquire the full text ($n=2$) and those in languages other than English, French, and Spanish ($n=3$). One observer screened all the references (EC), and we ensured the repeatability of the screening phase by comparing the main observer selection to that of four other observers (PR, JPT, AAR, and JDMS), with four random subsets of 51 references. We evaluated if the main observer could have missed potential references at the screening phase (reference excluded by EC, but kept by alternative observer). Of the 204 references of the validation (48% of all references), only four potentially missed references were identified. The full-text evaluation of these four references led to their exclusion from the review. Thus, the probability of having missed a relevant reference from our initial search is very low.

We summarized the content of the 57 selected references by extracting descriptive information (type of reference, location, name, and type of ungulates present; Table 1) and information regarding study objectives, management objectives, silvicultural and management approaches used, and consideration (or not) of ungulate impacts (see Table 1 for metadata; Online Resource 1 for the extraction table). We used the descriptive information to assess the geographic,

Table 1 Information compiled in the extraction datasheet for the 57 references included in the systematic mapping. Each reference was also identified by a unique identification number, and we noted the geographical area (continent, country, and province/state/region) to evaluate the worldwide coverage of the review.

Field	Description of content
Type of reference	Among these categories: empirical studies (i.e., experiments and/or observational studies), model and/or simulation studies, review and opinion references, social and economic studies, combination of above categories
Ungulate present	Latin name when available
Type of ungulate	Among these categories: domesticated/semi-domesticated, wild, both types present
Study objectives	Brief summary of the objectives of the study or the review reported in the reference
Management objectives	Management objectives described in the reference linked to climate change
Silvicultural and other management approaches	Silvicultural and other management approaches used or proposed to attain management objectives. We define approaches as the actions a forest manager can perform to achieve management objectives. For example, regeneration cuts, thinning, plantation, insecticides are commonly used silvicultural approaches
Management strategy linked to climate change	Based on the information provided within the reference, the type of management strategy among these options: resistance/resilience (sensu Millar et al. 2007), transition (sensu Millar et al. 2007), mitigation (e.g., carbon stockage), combination of above categories
Are the effect of ungulates on management and approaches considered?	Yes/No
How are or are not the effect of herbivores on management approaches considered?	Description of how, considering only management and approaches linked to climate-adapted management strategy (e.g., consideration of the negative effect of browsing on the promotion of diverse forest stands)
Are ungulates considered to be a threat to management?	Yes/No. Based on the information provided in the reference and the evaluation by the observer
Why/How herbivores considered to be a threat to management?	Description of why/how, considering only management and approaches linked to climate-adapted management strategy
Threat on which ecological component	Which ecological component could ungulate affect among composition of species, diversity (species or stands) and forest state. Classification based on threats identified by the authors but also on our assessment of the management objectives and information provided in the reference regarding ungulates impact
Are the effect of management on ungulates considered?	Yes/No with description of how, considering only management and approaches linked to climate-adapted management strategy (e.g., impact of silvicultural approaches on forage availability)

taxonomic, and methodological coverage of the review. Using information from the reference and our knowledge, we classified the management objectives into Millar et al.'s [5] framework of adaptation options (see also [20], p. 1): Resistance, i.e., managing forests so that they can remain in their current condition; (2) resilience, i.e., promoting the ability of forests to return to their initial or desired state following climate-change-related disturbance; (3) transition, i.e., facilitating/enabling forests transition to new conditions. Ultimately, we had to merge the resistance and resilience objectives, because these objectives were often hard to distinguish with the information provided in the references. We also noted the presence of mitigation objectives, for example, management to increase carbon sequestration, even if these actions are not an adaptation strategy.

Systematic Mapping Results

The 57 references were published between 1995 and 2020, with 91% ($n=52$) from the last 10 years, and mostly concerned European ($n=31$) and/or North American forests ($n=17$; Figs. 2 and 3). Consequently, this review is more representative of boreal and temperate forests, although it includes references about sub-Saharan forests and semi-arid floodplain red gum forests [21–23]. Wild ungulates were present in the majority of the studies ($n=50/57$), although 14 of those references also included domestic or semi-domestic ungulates such as reindeer (*Rangifer tarandus*); the remaining 7 references concerned only domestic/semi-domestic ungulates (see Fig. 3d for repartition among continents). We found as many empirical studies (experiments = 9, observation = 15) as opinion/review references ($n=24$), and a few model and simulation studies ($n=7$), as well as social or economic studies ($n=5$).

We summarized the management objectives and related silvicultural approaches linked to a climate-adapted strategy in Table 2. Most of the references presented management objectives corresponding to a resistance/resilience adaptation strategy ($n=50$), often combined with mitigation objectives (i.e., increase carbon sequestration; $n=35$). An additional four studies focused solely on mitigation objectives. Transition strategies were combined with resistance and resilience in 17 of the studies, and three studies considered only a transition strategy. Objectives including a transition aspect were slightly more abundant in North American references, but well distributed among the types of references (e.g., empirical studies, review, etc.; Fig. 3b, c). Studies generally recommended (or utilized) conventional silvicultural approaches to achieve climate-adapted objectives (e.g., uneven-aged systems). However, 11 references recommended the more "novel" assisted migration approach, to deal with current and impending changes. The management objectives and silvicultural approaches described in this review are not necessarily representative of forest management for the geographical area covered by the systematic map. Indeed, we restricted our search to references with a mention of ungulates, which could bias our results towards areas with high ungulate populations. Still, 12 references

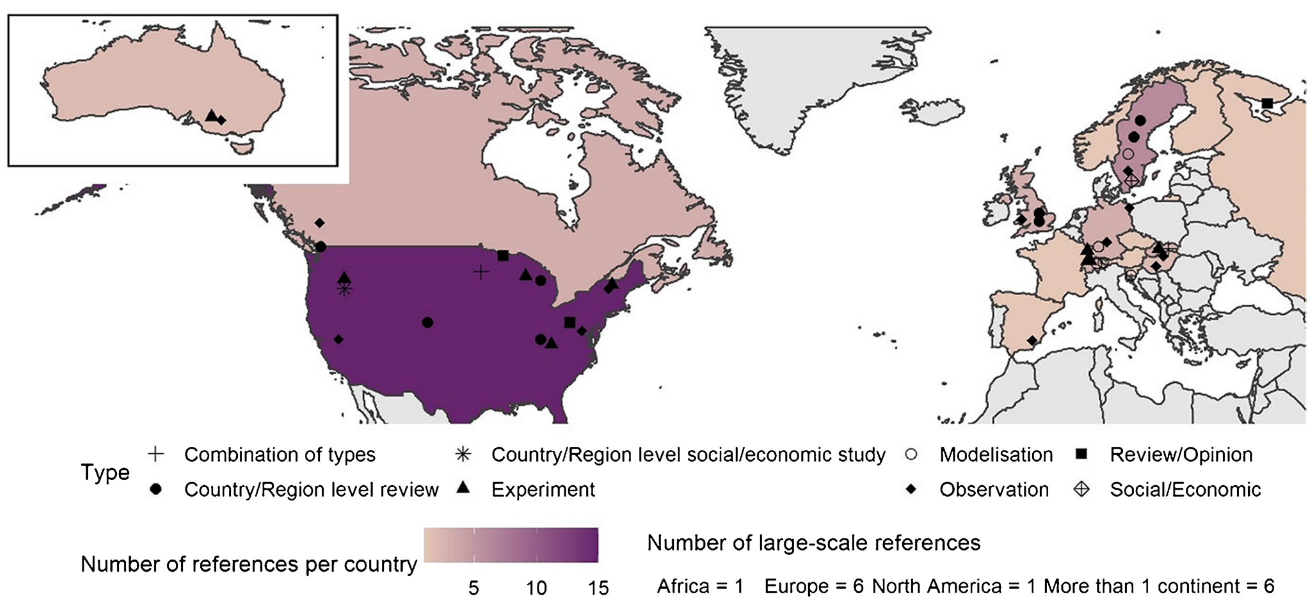

Fig. 2 Geographical distribution of selected references. Color gradient indicates the number of studies per country, not including large-scale studies (one continent or more). We classified each selected reference in one or more types of study category and used coordinates available in the reference. When multiple coordinates were provided, we plotted the centroid. For some studies, mostly of the review/opinion review categories, we used approximate coordinates corresponding to the centroid of the region/country concerned

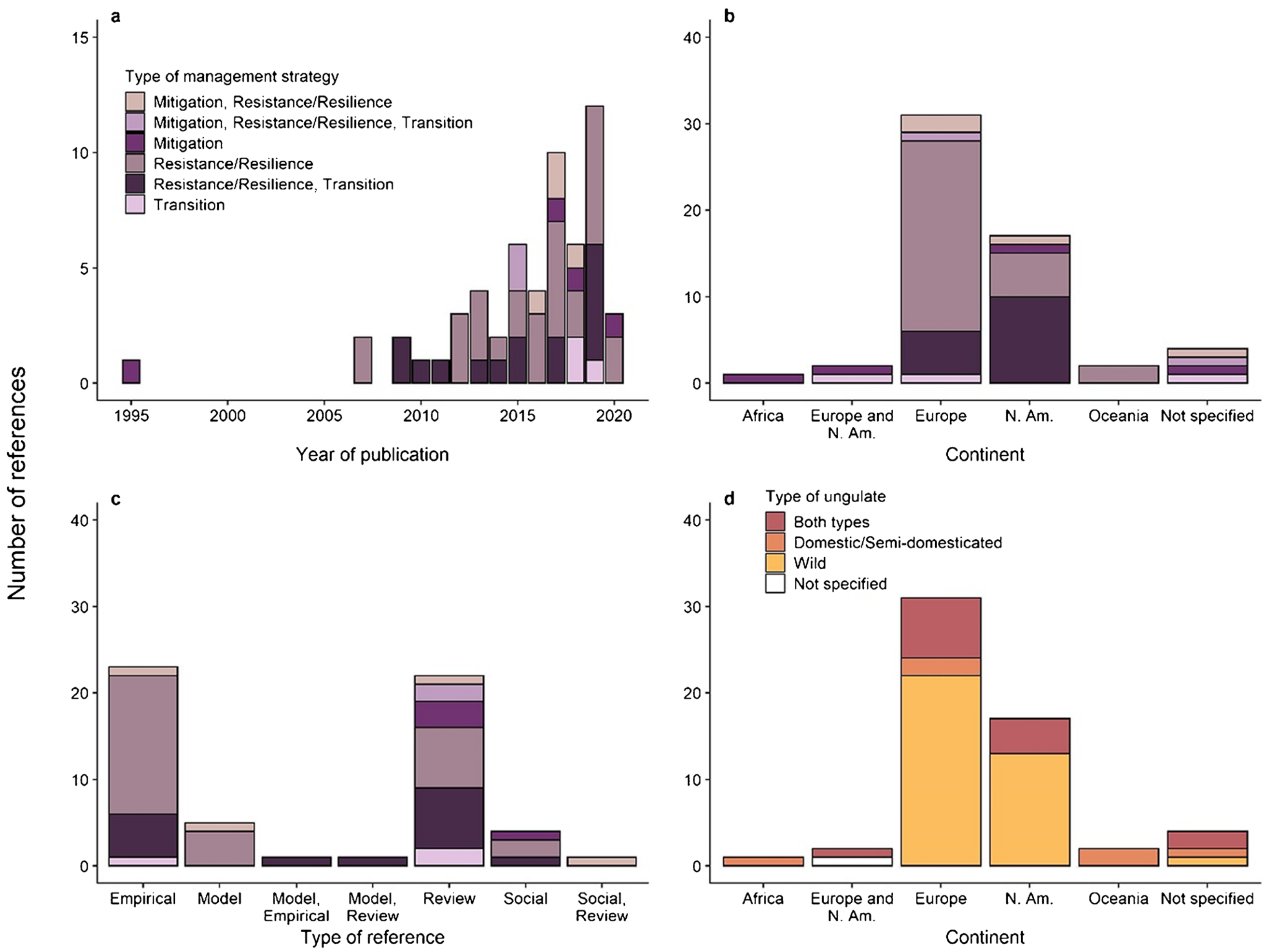

Fig. 3 Distribution of selected references among descriptive fields included in the extraction datasheet and broken down across types of management strategies: a year of publication; b continent; c type of reference (categories: empirical studies, model and/or simulation studies, review and opinion references, social and economic studies, combination of categories). Categories for type of management include mitigation, resistance/resilience, transition, and combination of above categories. d The distribution of references across continents broken down by type of ungulates

did not consider the effects of herbivores on objectives and approaches for climate adaptation, which suggests that we also covered areas with low herbivory pressure. The majority of these references, however, considered domestic or semi-domestic ungulates, whose density can more easily be controlled. Of the 45 references that did consider the effects of ungulates, the majority (35/45) considered them a threat to the climate-adapted management strategies.

In the following review section, we discuss how ungulates could prevent the achievement of climate-adapted management objectives ("*The Impacts of Ungulates on Achieving the Objectives of Climate-Adapted Strategies*") or interact with the most prominent or novel silvicultural approaches identified in the systematic review ("*The Impact of Ungulates on the Silvicultural Approaches Used to Achieve Climate-Adapted Management Objectives*"), and how these impacts could be mitigated ("*Management Actions to Reduce Ungulates Impacts*").

The Effects of Ungulates on Climate-Adapted Forest Management

The Impacts of Ungulates on Achieving the Objectives of Climate-Adapted Strategies

The management objectives listed in Table 2 are designed for adaptation to climate change but do not necessarily consider the presence of ungulates. Ungulates could impact these objectives through their effects on (i) tree species composition, (ii) diversity in tree species assemblage and/or in ecological communities, and (iii) forest ecosystem state.

Table 2 Climate-adapted management objectives and related silvicultural approaches identified in the systematic mapping, categorized under mitigation, and adaptation to climate change strategies, with relevant examples from the systematic map. Adaptation to climate change is divided in three subcategories (resistance, resilience, transition), based on Millar et al. [5]. We identified the potential interactions with ungulates browsing using both the information from the systematic mapping references, outside references and our expertise of browsing. This list of management objectives and silvicultural approaches is not necessarily representative of all existing possibilities, because we selected references containing at least one mention of ungulates.

Strategy	Climate adaptation management objectives	Related silvicultural approaches	Ungulates potential interactions
Mitigation	Increase carbon storage using forests, e.g., [21, 127]	Forest rehabilitation/reforestation, e.g., [21]	Browsing can prevent seedling establishment, reduce growth, and lead to regeneration failures
		Select silvicultural treatments maximizing wood production and storage, e.g., [127]	
Resistance	Conservation of current species mix and/or species vulnerable to climate change, e.g., [23, 31, 128]	Monitoring of forest regeneration status, e.g. [47],	Selective browsing can promote browse-resistant species and thus change forest composition
	Combat species invasion and undesirable species increase linked to climate change, e.g., [27, 129]	Plantation of mixed species tolerant to stressors (e.g., drought, wind, or fire) and enrichment planting of current species with climate-adapted genotypes (i.e., conservation assisted migration), e.g., [17]	Browsing can reduce the growth and survival of planted seedlings Selective browsing can promote browse-resistant species and thus change forest composition
		Retention of unmanaged areas for conservation, using seed source and refuge habitat, e.g., [47]	Selective browsing can promote browse-resistant species and thus change forest composition Browsing can promote browse-resistant invasive species
		Active protection of stands and refuge habitats (e.g., insecticides, herbicides), e.g., [27, 56]	Browsing can promote browse-resistant undesired species
		Use of silvicultural treatments that increase tree vigor and resistance to stressors in stands with current desired composition (e.g., selection cutting to increase tree vigor, thinning to increase drought tolerance, prescribed fire, vegetation control treatments). E.g., [17, 23, 130]	Browsing can counteract or amplify the desired effects of the silvicultural treatments via its selective effect on regeneration
Resilience	Maintain/increase forest cover to decrease vulnerability to climate-related threats, e.g., [45, 126]	Forest rehabilitation/reforestation, e.g., [131, but to maintain a specific species]	Browsing can prevent seedling establishment and lead to regeneration failures
	Integration of climate-related risk to planning of stand and land management, e.g., [33]	Use of risk assessment analyses, e.g., [132]	
	Promotion of specific stand types, species mix and/or species for their suitability for future climate conditions and disturbance regimes, e.g., [26, 133, 134]	Use of silvicultural treatments ensuring stand continuity with regeneration and biological legacies, while promoting structural complexity and species diversity (e.g., uneven-aged, irregular, and other even-aged systems creating high heterogeneity, variable density, or mixed-species thinning), e.g., [133, 135]	Selective browsing can go against desired species mix
		Plantation of species with diverse functional traits, suitable for future climate conditions, e.g., [131]	Browsing can reduce the growth and survival of planted seedlings Selective browsing can go against desired species mix
	Diversification of stand types, age and structure, and species composition to decrease vulnerability to threats related to climate change, and to reduce economic risk (diversify production), e.g., [57, 136]	Use of silvicultural systems promoting diversity and complexity at all scales, e.g., [136, 137]	Browsing can increase or reduce diversity in regeneration Selective browsing can lead to regeneration failure

Table 2 (continued)

Strategy	Climate adaptation management objectives	Related silvicultural approaches	Ungulates potential interactions
		Diversification of silvicultural systems and treatments at the landscape scale, e.g., [138]	The diversification of approaches could change resource availability to ungulates with potential impact on their landscape use and population dynamics Ungulates can alter/nullify desired effect of approach on regeneration
	Manage to preserve and/or maximize ecosystem functions or services, e.g., [139]	Adopt a nature-based silvicultural approach, e.g., [133, 139]	Nature-based silviculture could change resource availability to ungulates with potential impact on their landscape use and population dynamics Heavy selective browsing can push ecosystems outside of their natural range of variability
Transition	Facilitate the transition of forest ecosystems to future climate conditions (i.e., new stand types, species mix, species, non-forested ecosystems), e.g., [55, 124]		Ungulates can transform ecosystem types and generate new ecosystems
		Forestry assisted migration and transformational restoration, e.g., [55, 138, 140]	Browsing can reduce the growth and survival of planted seedlings
		Insuring sexual reproduction to increase the potential for adaptation of species, e.g., [124]	
		Use climate-adapted seedlings (either species or provenances) as enrichment planting in managed forests to facilitate transition, e.g., [17]	Selective browsing can go against desired species mix
		Allowing the loss of species maladapted to future climate conditions, e.g., [124]	Ungulates can promote this transition

Species Composition

Management activities that promote species that are more tolerant to climate-induced perturbation are commonly implemented in order to enhance forest resilience (Table 2). Tree species, however, also vary in their ability to resist and tolerate ungulate browsing. For example, fostering *Quercus.* spp. regeneration is sometimes recommended given their drought resistance; however, ungulate browsing often limits regeneration of this species [24, 25]. Similarly, *Abies alba* could be selected for its adaptation to future climate conditions, but it is also more browsed than the alternative species, *Picea abies* [26]. Among all references included in our review, 63% proposed adaptation through changes in species composition, and thus potential interaction with ungulate herbivory could factor into the adaptation equation. This interaction can occur through ungulate selective preferences [27], tree species-specific responses to browsing, or tree species-specific responses to changed biotic (e.g., competition) or abiotic (e.g., nutrient cycling) conditions. Thus, the success of desired tree species compositional shifts will hinge on whether ungulates disproportionately affect (directly or indirectly) the desired species compared to its competitor(s) [19•] or whether ungulate impacts on a species are greater than the impacts of climate [17].

Deciduous tree species were often identified in reviewed references as potential candidates to promote climate change adaptation (for example, [25, 28, 29]). These species, however, are usually more palatable than co-occurring coniferous species, due both to higher nutritional quality of broadleaves and higher defence compound concentrations of conifers [30•]. Nevertheless, conifers can also be highly impacted by ungulate populations [7]. For example, Sedmakova et al. [31] and Vencurik et al. [32] documented how natural regeneration of yew (*Taxus baccata*) is limited by herbivory. These detrimental browsing effects, combined with the deleterious impacts of a changing climate, necessitated tree protection for successful yew regeneration [31, 32]. The interaction between species composition objectives and ungulates impact could thus be best predicted by taking into consideration tree-specific susceptibility to herbivores.

Diversity in Tree Species Assemblage and in Ecological Communities

Several of the reviewed references discussed the promotion of polycultures and forests with mixed and diverse tree species composition (e.g., [33]), often with the objective of improving resilience to disturbance (Table 2). This measure would increase the diversity of forage types available to herbivores. Although the effects of diversity on invertebrate herbivores have been well researched, less is known about their effects on ungulates [34–36]. Tree species diversity can both increase or decrease damage by ungulates [37–40]. These contradictory results could be explained by the foraging behavior of ungulates, a process aimed at optimizing resource intake based on forage availability and quality [41, 42]. The type and abundance of different forage types, rather than their diversity per se, influences the selectivity of ungulates and the resulting browsing pressure [39]. Consequently, the effect of diversifying forests on browsing intensity will depend on the identity of the added species. If diverse stands contain more preferred species, overall browsing pressure could be higher in those stands than in monocultures [37, 38]. On the other hand, if diverse stands have a lower concentration of high-quality resources, browsing pressure could be lower than in monospecific forests [39]. Diverse stands could also allow ungulates to satisfy their nutritional needs more quickly, generating overall a lower browsing pressure [43]. It is worth noting that because of the higher prevalence of plantations in Europe [44], North American and European forests might present divergent responses to increases in diversity.

Higher browsing pressure in more diverse stands is not necessarily a threat to climate-adapted strategies, as long as it does not prevent regeneration [45]. The key element to consider is the motivation behind the promotion of diverse stands. If the goal is to increase the relative abundance of certain species or groups of species, the issues discussed above regarding the promotion of browse-sensitive species remain, although diverse stands could generate protection (i.e., associational resistance). For example, browsing on *Pinus strobus*, a species moderately selected by white-tailed deer, decreased in diverse plots [39]. On the other hand, when the objective of diversifying forest composition is to avoid risk-prone monocultures, moderate browsing could be harmless. Diverse communities, although more frequently used by deer, could even be more resistant to browsing because damage is spread across several seedlings and saplings [40, 46].

Forest Ecosystem State

The objective of some of the proposed climate-adapted forest management is to modify forest composition and structure from the current condition to a future desired state that is better suited for projected future climatic conditions. Because there is strong evidence that ungulates can alter successional trajectories [15, 16, 18•], there is potential for ungulates to influence management objectives [47]. Primarily, because browsing can prevent regeneration [48], ungulates could prevent the increase and maintenance of forest cover, a management objective identified in mitigation, resistance, and resilience strategies (Table 2). For example, ungulates can cause forest regeneration failure [45] or stand conversion [49••]. Taking this to the extreme, high-intensity ungulate browsing could accelerate the climate-related transition from forest to non-forested ecosystems [50, 51]. Heavy browsing may also hinder any scheme aimed at retaining forest integrity [52•]. On the other hand, ungulates could benefit some climate-adapted management objectives, such as reducing the fuel load in fire-prone ecosystems [53•], or promoting the transition to non-forested ecosystems [54, 55]. The latter is one of the boldest propositions for a transition-type adaptation strategy, and the desirability of it remains to be evaluated.

The Impact of Ungulates on the Silvicultural Approaches Used to Achieve Climate-Adapted Management Objectives

To attain climate-adapted management objectives, managers can select among a variety of silvicultural approaches such as thinning, plantations, or pest control methods (Table 2). Several of the silvicultural approaches described in the review are already widely applied around the world and there is a large amount of literature regarding their interaction with ungulates. However, we have less information on how ungulates could affect the more "novel" propositions found in the systematic map: nature-based silvicultural approaches and forestry assisted migration.

Nature-Based Silvicultural Approaches

Nature-based silvicultural approaches (e.g., close-to-nature forestry, ecological forestry, etc.) are not new, but 33% of the reviewed references suggested implementing them to achieve adaptation to climate change based on resistance and resilience strategies (e.g., [17, 31, 56, 57]). Nature-based silviculture is founded on the premise that forest management approaches that emulate natural disturbance dynamics can achieve economic goals while exerting fewer disruptions to forest ecosystem biodiversity and functions than timber-oriented silvicultural approaches [58, 59]. In general, these approaches aim at maintaining high taxonomic, functional, and structural diversity and, by doing so, to foster greater resilience in natural ecosystems [60–62]. Given that forest structure (e.g., variation in tree sizes, stand density, and complexity) has strong direct impacts on functional diversity, the choice of the silvicultural systems helps dictate a forest's response to environmental changes [63].

Variants of multi-aged silvicultural systems, such as selection cutting and irregular shelterwood, are often associated with nature-based silvicultural approaches because of their greater ability to promote structural complexity and species diversity, while ensuring forest continuity with regeneration and biological legacies [63, 64, 65•]. Depending on the outcome of these multi-aged systems (e.g., spatial arrangement of regenerating cohorts and their composition), ungulates can compromise regeneration success, and thus the adaptation effort [17, 64, 66]. For example, silvicultural systems that create large gaps, including group-selection and group irregular shelterwood, can increase tree species diversity (see section "Diversity in Tree Species Assemblage and in Ecological Communities"), but they also tend to create nutrient-rich forage reservoirs for herbivores [67, 68]. Additionally, gap-based silviculture increases edge-to-area ratio relative to the fewer, larger openings utilized in even-aged applications. Because ungulates are often positively associated with edge habitat [69], these approaches may intensify browsing pressure and heighten the risk of recruitment failures. Under high ungulate density, browsing can alter or even nullify any benefits of gap-based silviculture on regeneration ([70–72], reviewed by [68]). Therefore, optimizing the sequence and spatial application of silvicultural interventions to achieve regeneration goals can succeed at low to moderate browsing pressure, but generally not under high browsing pressure [31, 64, 73]. At larger spatial scales, the utilization of uneven-aged silviculture may diminish landscape-level forage availability by creating smaller forage-rich patches and shifting composition to slower-growing and often less-nutritious species and thus, potentially intensifying browsing pressure on the understory layer [74]. Therefore, diversification of silvicultural systems and their spatio-temporal arrangement at the landscape scale should be considered to distribute browsing-related risks and maintain long-term forest resilience at large spatial scales [65•, 75, 76].

Forestry Assisted Migration

As changing environmental conditions grow increasingly divergent from the range of tolerances governed by local adaptations in tree populations, any efforts to delay or forestall climate-related changes using resistance or resilience approaches ultimately risk failure [5], thus jeopardizing forest management objectives and the provision of ecosystem services. Confronted with this challenge, scientists and managers are researching, planning, and implementing the concept of intentionally moving species or genotypes along expected climate gradients under a framework broadly known as assisted migration (AM) [77, 78]. Assisted migration encompasses three variants that differ chiefly in the degree to which genetic material is translocated; namely, within current range (assisted population migration), slightly beyond current range (assisted range expansion), and far beyond current range (assisted species migration). These approaches represent a gradient in both boldness and risk as the farther one purposefully moves genetic material, the greater the chance translocated species may be maladapted to the novel environmental conditions or, in contrast, become invasive [79].

These AM approaches are largely predicated on the principle that abiotic conditions shape species' distributions (i.e., fundamental niche) [80, 81] and, thus, employ modelling approaches that leverage correlations among climate, geographic locations, and species distributions to identify potential future climate-adapted genetic material [82–84]. These models, however, largely ignore the role of biotic interactions, including herbivory, on tree species establishment, growth, and distribution ([6, 85, 86], but see [87]). Underestimating the effect of browsing in assisted migration plantings may be imprudent as successful implementation may hinge on managing ungulate effects [8, 88•].

Planting seedlings in an AM context, either through enrichment plantings or the creation of mixed species plantations, reshuffles the community composition at the recipient sites, including the formation of non-analog communities [89, 90]. In these novel communities, scale-dependent factors ranging from the individual plant level to the community and, ultimately, to the landscape will affect how browsing affects the success of these artificial regeneration efforts [91]. At the individual scale, transplanted seedlings may suffer an intensified browsing pressure if, for example, fertilization applied in the nursery or at the time of planting increases plant nutritional value (e.g., greater nitrogen [92–94]). Additionally, ungulate herbivores may cautiously approach novel food resources, but ultimately incorporate them into their diet if they are physiologically desirable [95]. Thus, transplanted seedlings may possess a cryptic maladaptation (sensu [96]) to browsing that may manifest itself only when herbivores integrate transplanted individuals into their diet. Cryptic maladaptation might be more probable in long-distance seedling translocations, rather than in short-distance translocations within the distribution range of a widespread ungulate. At the patch or community level, variation among transplanted and local species in traits that determine plant palatability and tolerance will further modulate plant–herbivore interactions. For example, expected gains in hardwood recruitment and growth of hardwood species may be counteracted by browsing because hardwoods are, in general, more susceptible to browse damage than conifers ([18•, 97, 98]; see also "***Species Composition***"). The spatial arrangement of the seedling neighborhoods may also alter ungulate foraging decisions and impacts via associational effects [99, 100] in ways that may either intensify or mitigate browsing risk on introduced species [101]. Thus, AM-planting success may be contingent on, not only identity and palatability differences in chosen species, but also the spatial configuration of the planting layout.

Existing intra-specific variation in key functional traits arising from local, population-level adaptation to abiotic and biotic contexts [102] further complicates our ability to predict browsing impacts in AM plantings. Across populations, localized herbivory regimes may shape variation in palatability and tolerance among individual trees [103–105], while climatic gradients strongly influence variation in phenology [106]. Information on how variation in plant phenology and herbivore susceptibility may result in maladaptation following translocation is currently scant, and the current literature is heavily skewed towards plant-arthropod interactions [107•], but see [108]. Evidence suggests, however, that herbivory and climate maladaptation (e.g., frost damage due to mismatched phenology) may interact and negatively impact fitness. For example, climate-mediated stress events in late winter and early spring can reduce seedling growth and diminish browse tolerance later in the growing season [109, 110•]. In sum, although it is clear that browsing can strongly mediate tree species establishment success, we currently lack the evidence necessary to predict the direction and magnitude of these effects in either a changing climate and, particularly, under the novel biotic and abiotic interactions created by forest assisted migration [96, 111•].

Management Actions to Reduce Ungulates Impacts

Confronted with the task of planning and undertaking management actions for an uncertain future in the absence of complete scientific information, managers may seek advice on what to do. If the past is prologue, we suggest managers rely on existing guidelines on how to manage ungulate impacts in extant regenerating plant communities [8, 88•]. Firstly, local knowledge or observations may offer clues as to whether current ungulate density and browsing pressure may impede tree seedling regeneration. If so, managers may opt to employ any of a range of approaches that have a long history of use in directly reducing browse damage, including fencing, bud capping, tree shelters, repellents (reviewed by [88•]), as well as newer approaches that are being tested such as slash retention as browsing refugia [112], or the use of low value and non-merchantable woody material to build barriers to herbivores (e.g., slash walls; see [113]). Fencing is recommended in fifteen of the references from the systematic map, and is a successful method to protect seedlings [88•]. These approaches are more realistically used at fine spatial scales, for the protection of stands. Population control of wild and domestic ungulates is the other popular method proposed in the systematic map to mitigate browsing impacts on regeneration ($n = 16$). The objective of population control is to maintain ungulate populations at densities compatible with silvicultural goals [114–116]. Population control, through sport hunting or culling, is not a realistic option in some jurisdictions and, even where it can be applied, benefits can take a long time to be apparent on regeneration [7, 88•, 117]. Both physical barriers and culling require significant financial investments and some, like creating large fenced areas or intensified culls, may not always be socially acceptable (e.g., [118]). Sport hunting can be inexpensive, acceptable and provide economical benefits, but the desired ungulate densities will result from a compromise between hunting and silvicultural objectives [8]. Another solution could be to increase alternative forage resource availability by appropriate silvicultural approaches [24, 32, 88•], a method called diversionary feeding [119]. Diversionary feeding, however, has not proved especially effective at reducing damage by ungulates and can have unintented effects, such as ungulates' population growth [119] or increased interspecific competition. We also lack the primary sources to provide recommendations on how to implement this approach, and on how to limit the risk of this approach backfiring. The potential feedback of climate-adapted actions on ungulate population dynamics was considered in only 15 references of the systematic map and will require more investigation.

In forestry assisted migration, the use of artificial regeneration means that managers can potentially mitigate browse impact through their choice of species and genotypes, planting design, and scale of implementation. Managers could select genetic material from areas where chronically high browsing pressure may have caused local adaptation towards greater herbivore defense [104] or identify more-resistant genotypes by their chemical content [30•]. Understanding the relative browse palatability and differences in tolerance of candidate species may afford opportunities to plan the planting design in ways that may alter the browse risk neighborhoods through associational effects [120, 121]. Trait-driven considerations already inform mixed-species plantation planning to design planting schemes that improve productivity by considering species' resource complementarity and the potential for facilitative effects [122]. Finally, consideration of the landscape context is critical as research has found tree regeneration is often excessively browsed in high ungulate use areas (e.g., wintering grounds) or when nested in landscapes lacking abundant alternative forage resources [74, 123].

Conclusions

While our systematic map illustrates that potential interactions with large ungulate populations are sometimes considered in adaptation strategies, this is often a simple mention of the need to manage large herbivores' damage. Ungulates could prevent the achievement of management goals, especially those defined in terms of tree species and forest states. Assessing the dynamics of ungulate populations and their potential impact on management objectives can be a minimal action to the development of climate-adapted strategies. Ideally, ungulate management would be integrated to climate-adapted forest management, in a multi-resource adaptation management framework [8, 124]. Moreover, because the distribution of several ungulates could expand with climate change [10, 11], this integration should also be considered for forest ecosystems not covered by this review, such as temperate and boreal forests where ungulates are currently absent or at low density.

To provide recommendations for managers, more empirical data need to be obtained, especially on the interactive effect of climate variables and browsing on tree regeneration. Such data could be obtained in experimental settings with simulation treatments of climate change and browsing, and in natural environments. Experiments in natural environments could be particularly useful to determine the parameters favoring the success of assisted migration plantations, for example, the species and provenance to use or the spatial configuration of the plantation. Such experiments have already begun and are at early stages [30•, 125]. Large spatio-temporal experiments would also be beneficial to evaluate the sustainability of nature-based silvicultural approaches under varying ungulate density, as well as their effects on forage availability and ungulate population dynamics. These experiments could help identify situations in which herbivores contribute to the achievement of adaptation schemes, for example by increasing regeneration diversity or reducing fuel loads; ecosystem services that are tightly linked to the density of ungulates [126]. Additionally, we need models of forest dynamics and productivity to better integrate ungulate presence, abundance and impacts, in interaction with climatic factors. This consideration is especially critical in systems where ungulates could have a stronger impact than climate change on forest dynamics. Models could be especially valuable as the empirical data regarding outcomes of silvicultural approaches on forest regeneration and productivity can take many years to obtain, a luxury that cannot be afforded, considering the rate of climate change. Without empirical data and model-based predictions regarding the interactions between ungulates and forest management, the strategies implemented today could result in future regeneration failures and exacerbate the pressure on forests.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s40725-021-00148-5.

Funding No funding was received for this project. EC was supported by an NSERC postdoctoral fellowship.

Declarations

Conflict of Interest The authors no conflict of interest. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Humain and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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• Of importance
•• Of major importance

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