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RESEARCH

Identifying strategies to manage boreal forests: simulating moose and timber management scenarios at a landscape scale in the face of changing environmental conditions

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Abstract

There are ongoing debates among different stakeholders about which forest and ungulate management strategies will sustain high levels of timber and animal harvest and maintain important ecosystem functions under climate change. Ungulate-forest interactions are complex, including periods where forest regeneration is sensitive to browsing pressure, making it difficult to predict the consequences of a given strategy over time. To aid decision-making, we simulated the impacts of moose browsing on forest succession under 18 different combinations of moose (*Alces alces*) harvest rate levels and forest management scenarios in a boreal forest landscape in southern Sweden given projected changes in forest growth due to climate change. We found that the current management practices are important for sustaining a moose-forest system. Increasing moose harvest rates led to slightly smaller moose populations, larger estimates of landscape carrying capacity, and less biomass removal of Scots pine (*Pinus sylvestris*), a commercially valuable species. However, minor changes in the moose harvest were hardly affecting timber production. Increasing the timber harvest rotation time led to the highest estimates of Scots pine biomass, while thinning younger cohorts lead to the highest estimates of Norway spruce (*Picea abies*) biomass. These changes came without much effect to moose population dynamics. However, the increased broadleaf production scenario had a very large positive effect on total aboveground live biomass of deciduous species and on landscape carrying capacity and moose density. This scenario subsequently resulted in the greatest estimates of biomass removal of Scots pine, highlighting the tradeoffs associated with increased moose production.

Keywords Ungulates · Ecological modeling · Disturbance ecology · Forest simulation model · Herbivory · Browsing

Introduction

The harvesting of timber and the hunting of ungulates are among many factors impacting forest production and biodiversity in numerous managed northern forest ecosystems (Mysterud et al. 2006; Apollonio et al. 2010; FAO 2020). Forest practices shape both the production of aboveground forest biomass and tree species composition (Lavsund et al. 2003). Timber harvest has fundamentally transformed many forested boreal landscapes in Europe during the last century by reducing and fragmenting old growth habitats (Linder and Östlund 1998; Axelsson and Östlund 2001; Achim et al. 2022), and increasing the abundance of young forage-rich stands. As the capacity of forest landscapes to support dense ungulate populations increases post-harvest, foraging impacts can, in return, have substantial negative effects on timber production (Cairns and Moen 2004), leading to economic losses (Clasen et al. 2011) and reducing biodiversity

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(Suominen 1999; Persson et al. 2000; Mathisen and Skarpe 2011). Yet, ungulates are an important ecological component of the boreal forest (Persson et al. 2005; Girona et al. 2023a). They create substrate vital to an array of organisms (e.g., dead and dying wood) (Edenius et al. 2002; Angelstam et al. 2000). Hunting also provides a valued recreational activity (Heberlein and Ericsson 2005; Widemo et al. 2019; Linnell et al. 2020). Because both timber harvest and hunting are valued economic activities that take place within multifunctional landscapes (Raudsepp-Hearne et al. 2010; Turner et al. 2014; Neumann et al. 2022), identifying appropriate levels of each requires balancing ecological and economic goals. Moving forward, it is unclear what timber harvest strategies will best balance management goals related to sustainable ungulate harvest, timber production, biodiversity, and maintenance of resilient forest landscapes given anticipated effects of climate change (Neumann et al. 2024).

Northern Europe has the highest population densities and harvest rates of moose (*Alces alces*) globally (Cederlund and Markgren 1987; Østgård 1987; Jensen et al. 2020), as large predators have been functionally extinct during the past century and human harvest is the major tool for population control, even in areas where large predators like wolves (*Canis lupus*) and bears (*Ursus arctos*) have returned (Sand et al. 2006; Swenson et al. 2007; Wikenros et al. 2015). Hunting is an important and valued recreational activity throughout Sweden (Heberlein and Ericsson 2005; Neumann et al. 2022) and the intensively managed Scots pine (*Pinus sylvestris*) forests can lead to high amounts of forage (Persson et al. 2000) and large local moose populations. These moose populations can lead to substantial negative impacts to timber production due to browsing damage that impacts the growth and survival of individual trees through tissue removal from saplings and seedlings and through debarking (e.g. Putman 1996; Ramirez et al. 2018; Neumann et al. 2024). Developing models and tools to better understand and forecast what moose population densities can help to sustain a healthy moose population for hunters, and minimize the adverse impacts to forest productivity can aid decision making. Results of such models may be useful for management agencies to evaluate and select from available management options given anticipated effects of climate change.

Landscape modelling represents a powerful tool to support forest management decisions, by quantifying the outcome of different goals for forest ecosystems in different management scenarios (Hof et al. 2021). Several studies have utilized the LANDIS-II modelling platform to examine the effects of different management practices on temperate and boreal forests across the world (Lucash et al. 2017; Hof and Hjältén 2018; Swanteson-Franz et al. 2018; Wu et al. 2019; Krofcheck et al. 2019; Molina et al. 2022; Ameray et al. 2024). Further, recent development of an ungulate browsing extension for LANDIS-II has allowed for examination of the herbivore population and its impact on the ecosystems as per different management actions (De Jager et al. 2017a). While several attempts have been made to represent browsing impacts in forest ecosystems using different models (Bennett et al. 2006; Weisberg et al. 2006; Rammig 2007; Vospernik and Reimoser 2008; Gillet 2008; Didion et al. 2009; Nilsson et al. 2015; Honkaniemi et al. 2021), the novel aspect of the LANDIS-II framework is the ability to track biomass production available to foraging animals across large landscapes as it responds to factors such as past ungulate browsing (i.e., damage) (De Jager et al. 2017b), climate change (De Jager et al. 2020), insect pest outbreaks, fire, and timber management. Available forage biomass also determines the capacity of landscapes to support ungulate populations, thus providing a quantitative measure of landscape carrying capacity. Such a quantitative measure of landscape carrying capacity allows for the simulation of density-dependent ungulate population dynamics and thus reciprocal plant-animal interactions (De Jager et al. 2017a). However, we are unaware of a study that has utilized this or another modelling platform to evaluate the interactive effects of different forest and herbivore population management actions on large-scale, long-term forest ecosystem and population dynamics in the face of changing environmental conditions.

The objective of this study was to compare the effects of alternative timber harvest and moose harvest scenarios on forest productivity, composition, and the carrying capacity of moose given changes to forest growth due to climate change. We specifically evaluated how alternative timber and moose management strategies affect: (1) moose population density and dynamics through time, (2) the carrying capacity of moose, (3) total forest biomass, (4) biomass of selected species (as an index for landscape composition), and (5) biomass removal by moose on Scots pine, a commercially valuable species (SLU 2021) as well as an important forage for moose in winter (Shipley et al. 1998; Hörnberg 2001; Spitzer et al. 2020; Felton et al. 2020). Our primary question is how different moose harvest and/or timber harvest strategies could change forest composition, production of total tree biomass, and the capacity of the landscape to support various moose population densities when compared to current management strategies. We examined a Business as Usual (BAU) and three alternative timber harvest strategies. First, we explored strategies expected to decrease overall forage availability for moose in the landscape, based on Beguin et al. (2016) and Neumann et al. (2024), which could lead to smaller moose populations and weaker effects of browsing on the plant community. These alternative strategies included lengthening of rotation period and removing more young tree cohorts. Then we contrasted these strategies with one aimed at increasing broadleaf production in the landscape, which would be expected to increase overall forage biomass for moose and lead to larger moose population densities as broadleaf species tend to be a preferred forage for moose and benefit moose recruitment (Hörnberg 2001; Felton et al. 2020), it may also help reduce the browsing damage on pine (Felton et al. 2022). In combination with the above forest management strategies, we simulated increases and decreases in moose harvest rates, which could directly alter the degree to which moose affect the landscape.

Here we simulated the effects of moose browsing on a boreal forest landscape in Sweden. Like in most of Europe, Sweden has multi-functional landscapes where different interests in land use co-occur and changes in land use affect forests (Kuemmerle et al. 2016; Neumann et al. 2022; Svensson et al. 2020). Within the European Union, Sweden is the country with the biggest forest surface (28 million ha) and accounts for 6% of global pulp exports, 8% of global paper exports, and 11% of sawn timber exports (KSLA 2015). For this reason, Swedish forests are also intensively managed and the vast majority of Swedish forestland 84% (SLU 2017) is used for timber production. Intensive management has transformed the landscape from uneven aged old growth stands regenerated after natural disturbances (e.g., fire, storms) to early successional forests regenerated after clear felling. These shifts in forest age structure have resulted into forage-rich landscapes that greatly benefit browsing ungulates such as moose and other deer species (Lavsund et al. 2003). To reduce the effects of browsing on timber production, the forest management community within Sweden aims at having less than 5% (2% for low productivity stands) of main stems damaged by browsing in young pine production stands (Swedish Forest Agency 2022; Pfeffer 2020).

Materials and methods

Study area

Our study area is located in a boreal forest landscape (12,500 ha) on the border of the Swedish counties Västra Götaland and Värmland at the border between the boreal and hemi-boreal zone (Fig. 1). At present, the landscape is dominated by stands of Norway spruce (*Picea abies*, henceforth referred to as spruce), Scots pine (henceforth referred to as pine), and silver birch (*Betula pendula* henceforth referred to as birch). Low numbers of pedunculate oak (*Quercus robur,* denoted as oak) are also present in the area. Each of these species was simulated according to their specific life history characteristics (Table 1; Korzukhin et al. 1989; Perala and Alm 1990; Prentice and Helmisaari 1991; Hofgaard 1993; Reyes et al. 1997; Welander and Ottosson 1998; Tinner et al. 2000; Pennanen and Kuuluvainen 2002; Deiller et al. 2003; Chalupka 2007; Modrzynski 2007; Proença 2009; Conedera et al. 2010) as per Hof and Hjältén (2018). Other deciduous trees, including Norway maple (*Acer platanoides*), common alder (*Alnus glutinosa*), and white birch (*Betula pubescens*) were simulated as a single "other deciduous" species because they only occur in low densities. The initial distribution of species and ages across the landscape

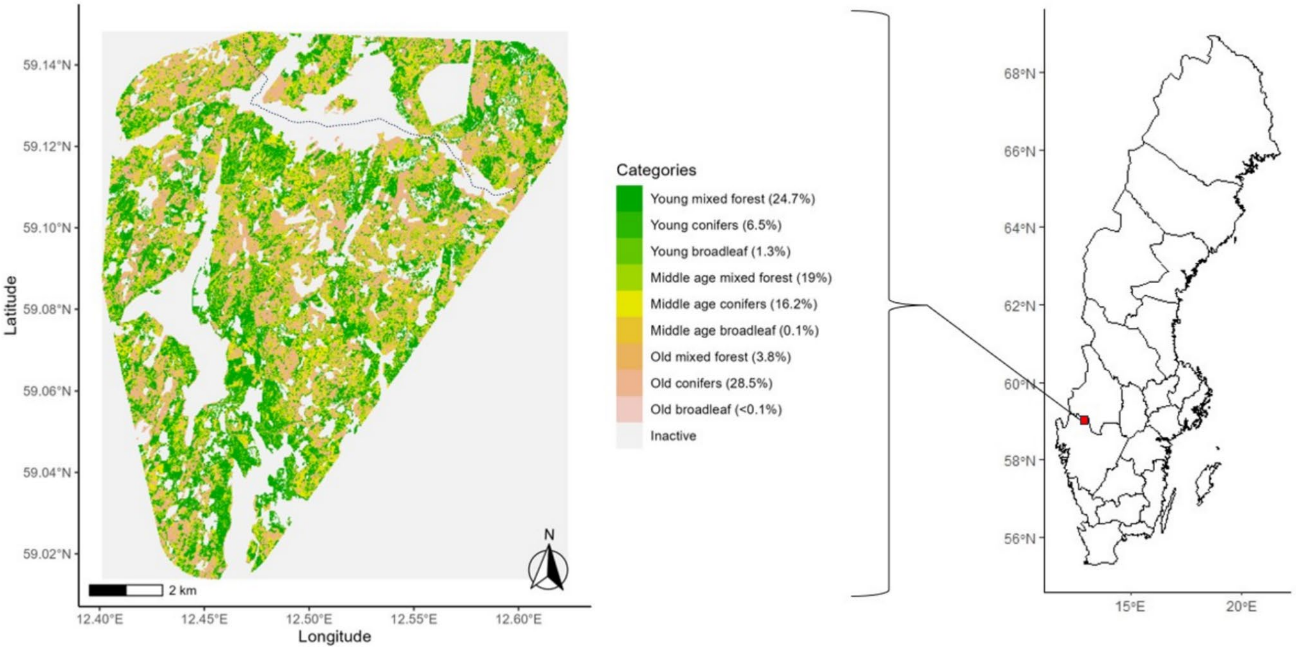

Fig. 1 The initial forest communities used in simulation modelling for a 12,500-ha landscape situated on the border of the Swedish countries Västra Götaland and Värmland (county border shown with the dashed line). Adapted from Hof and Hjältén (2018)

Table 1 Species life history characteristics used in forest simulation modelling, along with forage preference values (Persson et al. 2005; Månsson et al. 2007)

Species		Spruce	Pine	Birch	Oak	Broadleaf
Longevity (years)		500	500	250	1000	250
Age at Maturity (Years)		50	10	10	40	10
Shade tolerance		3	1	2	3	3
Browsing preference		0	0.25	0.15	0.3	0.15
Growth Reduction	Threshold	N/A	0.25	0.5	0.25	0.5
	Maximum	N/A	0.6	0.4	0.6	0.4
Mortality	Threshold	N/A	0.8	0.9	0.9	0.9
	Maximum	N/A	0.1	0.1	0.1	0.1

Longevity and age at sexual maturity are in years, all other values are unitless. Longevity is the maximum lifespan for each species while age at maturity is when each species begins to reproduce via seed. Shade tolerance parameters range from 1 (least shade tolerant) to 5 (most shade tolerant). The growth reduction threshold is the proportion of available forage biomass removed by moose that begins to impact annual net primary productivity in the next year. The growth reduction maximum is the maximum proportional reduction in annual net primary productivity in the next year when all available forage biomass is removed from a cohort. The mortality threshold is the proportion of available forage biomass removed by moose that begins to impact cohort survival. The mortality maximum parameter is the maximum proportional impact on cohort survival when all available forage biomass is removed from cohorts. Species preference values are the target proportions of available biomass removed from species at sites by moose. These parameter estimates were generated based on previous model calibration and validation studies (De Jager et al. 2017a, b) of similar species and based on measured plant responses to simulated moose browsing (Persson et al. 2005; De Jager and Pastor 2008, 2010)

was generated using forest data from the Swedish National Forest Inventory (NFI) from 2010 (SLU 2015) combined with satellite images from SPOT 4 and SPOT 5 (Reese et al. 2003). To differentiate among successional states and thus biomass and forage availability for moose, individual trees were grouped into three forest age classes (young < 41 years, middle-aged 41–59 years, old > 60 years) and four species relative abundance classes, based on the biomass share of the average age-groups on the grid cell (25 × 25 m) scale in the study region (10–25, 25–50, 50–75, and 75–100%). Once an initial map of species and age classes was generated, we classified each pixel (i.e., 25 × 25 m grid cell) based on the proportion and age of each tree species (pine, spruce, birch, oak, other deciduous). We created four classes based on the biomass share (10–25, 25–50, 50–75, and 75–100%); we ignored species that were present with less than 10% in a grid-cell. These methods resulted in each grid-cell being assigned to one of 44 forest communities based on the presence and abundance of species and age classes in our forest inventory dataset. An example community might be a young community dominated by one or up to five age classes of birch, pine, and spruce or an old community dominated by one or up to five age classes of other deciduous and birch. In general, 28% of the landscape was classified as old conifers, 25% as young mixed forest (broadleaves and conifers), 18% as middle-aged mixed forest, and 17% as middle-aged conifers (Fig. 1). Although our young age class spans from 0 to 40 years and thus does not specify e.g. seedlings and saplings specifically, this age class does indirectly consider forage availability within the forest as *Vaccinium* ssp in the field layer are a key staple forage for moose (Spitzer 2019; Spitzer et al. 2021), which need up to 40–50 year of recovery after clear-cutting (Hedwall et al. 2013; Eldegard et al. 2019). Moose population densities within the area range from 8 to 11 moose per 1000 ha after harvest, with an average of 3.8 moose per 1000 ha harvested annually (CAB 2021). As most of the study region is within Västra Götaland, we used the statistics for numbers of moose from the management plans of the moose management unit nr 1, Norra Dal as approved by the County Administrative Board of Västra Götaland.

Landscape simulation modelling

We used the LANDIS-II forest simulation model (Scheller et al. 2007) to simulate reciprocal interactions between forest succession and moose population dynamics under different scenarios of moose and timber harvest. LANDIS-II is a process-based, spatially dynamic forest simulation model that groups individual trees of similar ages into ‘cohorts’. It represents forest generative processes, such as seed dispersal, growth, and competition as well as forest degenerative processes such as senescence and disturbance at large spatial scales (> 1000 ha) and over long-time scales (centuries) (Mladenoff et al. 1993). The model has a flexible framework that utilizes different extensions to represent different management actions or ecological processes across a series of grid cells (i.e., the landscape). We used the Biomass Succession Extension (version 3.2; Scheller and Mladenoff 2004) to simulate species establishment, growth, and competition across the landscape. The area of the landscape we simulated was the subject of previous modelling studies in 2018 (Hof and Hjältén 2018; Hof et al. 2018). Thus, we used many of the same model input files and parameters developed for those studies. PnET-II developed by Xu et al. (2009) was used to generate parameter estimates for current and future potential species establishment probabilities (P_{est}), maximum potential growth rate (ANPP_{max}), and maximum aboveground biomass (AGB_{max}) as part of the study by Hof and Hjältén (2018). They obtained current and future climate data through the Earth System Grid Federation (https://esgf.llnl.gov/). They extracted monthly current and future predictions of the mean precipitation and minimum and maximum temperature from The HadGEM2-ES model from the Met Office Hadley Centre (representative concentration pathway [RCP] 4.5, ensemble r2i1p1). They extracted current and future concentrations of O_3 and CO_2 in the atmosphere from the CanESM2 model from the Canadian Centre for Climate Modeling and Analysis (RCP 4.5, ensemble r2i1p1). Current and future concentrations of O_3 and CO_2 in the atmosphere were not extracted from the HadGEM2-ES model. This discrepancy may affect the results to some extent. As both models stem from Phase 5 of the Coupled Model Intercomparison Project (CMIP5) and newer models from CMIP6 are currently already available, and seeing the large amount of time (up to a year, see Furniss et al. 2022; Hof et al. 2024) it generally takes to parametrise Forest landscape models, we opted to use the same model. They further extracted data on current photosynthetically active radiation levels from the STRÅNG model from the Swedish Meteorological and Hydrological Institute (http://strang.smhi.se/) and on future levels from the GEOSCCM–GEOS5 2.5 b20 model from the NASA Goddard Space Flight Center. Finally, they obtained species-specific physiological parameters from the Plant Trait Database (http://www.try-db.org/TryWeb/Home.php). Rather than updating the climate change scenarios to the most current scenarios available, we used values from Hof and Hjältén (2018) in the present study. RCP 4.5, is considered to be an intermediate emission scenario (IPCC 2013) and may be most comparable to the Shared Socio-economic Pathway (SSP) 2–4.5. The SSP2-4.5 scenario is a scenario with intermediate greenhouse gas and CO2 emissions and the assumption is that they remain around current levels until the middle of the century (IPCC 2021). Within the modelling framework, climate change impacts the maximum potential establishment and growth parameters by species over time. But actual species establishment rates differ from potential rates based on local seed supply and light conditions. Actual growth of a cohort depends on competition and age. Competition is represented by available growing space, and age-related mortality is represented by a decline in growth as cohorts near longevity. Biomass production is also affected by other disturbances included in the model, such as moose browsing and timber harvest.

Forest management simulation

We simulated forest management using the Biomass Harvest extension v2.1. (Scheller and Domingo 2013). Information regarding current management strategies like the average amount of forest that is clear-cut or thinned per year, the average size of clear-cuts, and economic values of tree species were taken from the Swedish forestry statistics from 2013 (Nilsson and Cory 2013). Based on these values, a business as usual (BAU) forest harvest strategy was created for the managed forest. This strategy reflects current clear-cut and thinning strategies (Table 2, e.g., the clear-cut prescription was applied to 0.9% of the area each year, which means that, each year, in 0.9% of the area, all cohorts older than 80 years were removed and pine and spruce were planted. NB. It is not possible to specify the fraction that is planted, just the species. They will be then planted in equal proportion (Scheller et al. 2019). Furthermore, we designed three alternative forest management scenarios based on insights from Beguin et al. (2016) and our own expert knowledge: a scenario with the aim to (1) maintain a similar rotation period and harvest characteristics as currently implemented (business as usual (BAU)), (2) increase the area thinned from young cohorts, as young cohorts are generally targeted by moose (YC), (3) increase the harvest rotation times from harvesting over 80-year old stands to harvesting > 100-year-old stands (IRT), and (4) increase the production of broadleaf species by planting birch after harvest, in addition to spruce and pine (IB) (Table 2).

Moose harvest and browsing simulation

We simulated reciprocal interactions between a moose population and forest biomass and succession using the Dynamic Ungulate Browse Extension (Version 0.8) (De Jager et al. 2017a, b). The browse extension uses a series of parameters to define the fraction of total aboveground biomass of cohorts available to foraging moose. Available forage biomass, in turn, affects the size and dynamics of the moose population, and the moose population affects both total aboveground biomass and available forage biomass via their foraging effects on plant growth and survival. Each of these processes is described briefly below and more completely in De Jager et al. (2017a).

Within the model framework, the ungulate population is temporally dynamic, responding to annual fluctuations in available forage biomass across the landscape. Such fluctuations can be driven by any factor that affects the forest community and hence biomass production. In our model system, these factors include forest successional changes, timber harvest, and damage to plant cohorts due to moose browsing. Within the model, available forage

Table 2 Timber Harvest Scenarios

Scenario	Prescription
Business as usual (BAU)	Clear-cut: Remove all cohorts in stands older than 80 years, plant pine and spruce, applied to 0.9%* of the area each year Thinning 1: Remove 25% of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.5%* of the area each year Thinning 2: Remove the youngest cohorts of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.2%* of the area each year
Youngest cohorts (YC)	Clear-cut: Remove all cohorts in stands older than 80 years, plant pine and spruce, applied to 0.9%* of the area each year Thinning 1: NA Thinning 2: Remove the youngest cohorts of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 2.7%* of the area each year
Increased rotation time (IRT)	Clear-cut: Remove all cohorts in stands older than 100 years, plant pine and spruce, applied to 0.9%* of the area each year Thinning 1: Remove 25% of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.5%* of the area each year Thinning 2: Remove the youngest cohorts of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.2%* of the area each year
Increased broadleaf (IB)	Clear-cut: Remove all cohorts in stands older than 80 years, plant pine, spruce, and birch, applied to 0.9%* of the area each year Thinning 1: Remove 25% of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.5%* of the area each year Thinning 2: Remove the youngest cohorts of pine, spruce, and birch in stands aged between 15 and 30 years, applied to 1.2%* of the area each year

*Values were based on the Swedish forestry statistics from 2013 (Nilsson and Cory 2013). Adapted from Hof and Hjältén (2018)

biomass is a fraction of total aboveground live biomass considered to be in the height reach of the ungulates for woody plant species with non-zero preference values (see De Jager et al. 2017a for calculations). A series of parameter estimates described in De Jager et al. 2017a, b determine per cohort available forage. Most notably, there is a minimum amount of available forage biomass considered to be within the height reach of moose (MinBrowsePropinReach = 0.3) for a cohort to be considered 'available' and an option to use the entire biomass for year 1 cohorts as forage (UseInitBiomassAsForage). We chose not to use the entire cohort biomass but rather a proportion of cohort ANPP as was the case for all other cohort ages. Available forage biomass is summed across the landscape and then divided by the annual forage requirements of a single (average) animal to determine the annual carrying capacity (K_t in Eq. 1) of the landscape (i.e., the number of animals that can be supported by the woody forage biomass available). For moose, we used an annual intake rate of 2327 kg dry mass per year, which was derived from an average daily intake rate of 5 kg per day in winter and 10 kg per day in summer, assuming half of each year is winter, and assuming that 85% of the annual food requirements for moose are from woody plants (Persson et al. 2000). This temporally dynamic estimate of carrying capacity affects the growth rate of the moose population from year to year through a discrete-time quadratic model (Eq. 1):

$$\Delta N_t = R_t N_t \left(1 - \frac{N_t}{K_t}\right) - N_t(H_t - P_t - M_t) \tag{1}$$

where ΔN_t is the change in population size (N) at time t. R_t is the intrinsic rate of population growth (birth rate—death rate) at time t, and K_t is the carrying capacity at time t. Equation 1 thus simulates density dependent population growth. Additional, non-density dependent sources of mortality include H_t harvesting (population management), P_t predation, and other miscellaneous factors such as M_t, traffic deaths, disease outbreaks, and were based on information in the local management plan within the moose management area (CAB 2021).

An initial population size is provided by the user at time 0, with subsequent population sizes determined by Eq. 1. The reproductive rate, harvest rate, predation rate, and miscellaneous mortality rate are all pre-defined by the model user for each scenario within upper and lower bounds (Table 3). A random value for each parameter is drawn between the upper and lower bounds at each time step. To isolate the effects of changing moose harvest rate, we generated upper and lower bounds for R_t, P_t, and M_t and held them constant both within (through time) and across all scenarios (Table 3). To generate upper and lower bounds for parameters, we used data from the local moose management plan (CAB 2021) that estimates the conditions of both the moose population and forest stands within the area and defines moose management goals and measures on a three-year plan. We used

Table 3 Rates of changes in population (Eq. 1) for moose harvest scenarios.

Prescriptions	Scenarios			
	Business As Usual (BAU)	− 10% moose harvest rate	+ 10% moose harvest rate	+ 20% moose harvest rate
Reproduction rate (R)	25–40	25–40	25–40	25–40
Harvest rate (H)	20–30	18–27	22–33	24–36
Predation rate (P)	2.5–5	2.5–5	2.5–5	2.5–5
Miscellaneous Mortality rate (M)	2.5–5	2.5–5	2.5–5	2.5–5
Annual net impact on population	0	2–3	− 2–3	− 4–6

*Values were derived from the management plans of the moose management unit nr 1, Norra Dal, during the years 2018–2020 and 2021–2023 as approved by the County Administrative Board of Västra Götaland. www.lansstyrelsen.se. Prescription rates are given in percentage of population

CAB (2021) to determine the initial moose population size, as the population within the study area has been roughly stable since 2009 at an average of 8 moose per 1000 ha after harvest. To generate current harvest rates, we noted that an estimated 3.8 moose per 1000 ha were harvested annually from 2018 to 2020 or roughly 32% of the pre-harvest total population (Table 3, CAB 2021). However, the moose harvest strategy for 2021–2023 was to reduce harvest to 2.6 per 1000 ha or 19% of the population. Thus, we set the BAU moose harvest rate between 20 and 30% of the population. To set predation rates, we found that an estimated 3.4% of the pre-harvest moose population died as a result of predation and thus the predation rate was set between 2.5 and 5% of the population for each scenario. Finally, traffic accidents accounted for another 3.3% of the pre-harvest population and so the miscellaneous mortality rate was set between 2.5 and 5% of the population. Finally, we estimated the reproductive rate to balance the deaths attributable to harvest, predation, and miscellaneous mortality in the BAU moose harvest scenario, thereby helping to maintain a stable moose population over time. A lower value of 25% of the population offset the lower sum of mortality across all factors while an upper bound of 40% offset the upper sum of mortality across all factors (Table 3). The larger bounds for reproductive rate reflect a greater degree of uncertainty in this parameter estimate. However, the values we chose were supported by data showing that the average percentage of the total moose population made up of calves each year between 2009 and 2020 was 29%, with a high of 32% in 2011 and a low of 25% in 2018 (CAB 2021). We further assumed that some unknown level of calf mortality before population surveys would result in an underestimation of this number. In general, the parameters we selected were based on the best available data, along with an assumption that the goal of moose harvest under BAU is to remove ‘surplus moose’ that would not have died because of density-dependence, thereby maintaining a stable moose population over time. Finally, following demands from hunters to increase or maintain current moose population size and from forestry to reduce it, we generated three additional moose harvest scenarios: reducing the harvest parameters by 10% (18–27% of the population), increasing harvest parameters by 10% (22–33% of the population) and increasing it by 20% (24–36% of the population). All values for moose population parameters are given in Table 3, as well as expected changes in the moose population based on changing harvest rates assuming a constant carrying capacity.

Herbivores such as moose move to places where there is forage (Van Moorter et al. 2021). Thus, the ungulate population is spatially dynamic, responding to the spatial distribution of available forage biomass across the landscape on an annual time step. The total population is distributed each time step using moving window calculations of site preference (forage quality and quantity) within the 500-m neighborhood of each grid cell (site), resulting in a local site-level population density for each grid cell in each year. Site preference is the weighted average of the species preference values (Table 1) for each species present at a site multiplied by the total amount of forage biomass at a site. The local (site level) population density determines the amount of forage biomass removed from each cell at each time step based on the annual biomass requirements of the site level moose population. At each time step, biomass is removed from sites in an iterative process, starting by removing a predefined fraction (browse preference found in Table 1) of the most highly preferred species and moving to the next species until the forage biomass requirements of the local population are met. Biomass removal triggers a subsequent impact on annual net primary productivity (ANPP) in the following timestep. These effects are modelled by a linear increase in the proportion of ANPP reduced, beyond a threshold proportion of available forage biomass removed, and up to a maximum percent reduction at 100% removal of available forage biomass (see Table 1). Similarly, cohort mortality is also modelled as a linear increase in mortality probability with an increase in the proportion of available forage biomass removed, beyond a threshold proportion and up to a maximum mortality probability at 100% forage biomass removal.

Model outputs and analysis

We examined average moose population density and carrying capacity across the entire landscape to assess the effects of different moose and timber harvest strategies on moose population dynamics as they relate to the capacity of the landscape to support a moose population. In addition, we calculated the difference between landscape carrying capacity and moose population density as an index of how much larger the moose population could be, given available forage biomass. We also examined the amount of biomass removed by moose from pine. Biomass removed from pine included both direct consumption by moose and the loss of biomass due to cohort mortality directly caused by intense moose browsing. Finally, we examined average total aboveground live biomass for the following groups of species: pine, spruce, and deciduous species (pooled), as well as the sum of total biomass across all species. We ran in total 18 scenarios, the combinations of the 4 forest management scenarios and 4 moose harvest scenarios mentioned above as well as a scenario in which there was no forest management (NFM) in combination with the BAU moose harvest and a scenario in which there was no forest management and no moose harvest (NMH). Each of the 18 scenarios was run three times to verify that model behavior and results were consistent across replicates. We ran three replicates to balance the need to verify that model results were consistent and computing time. Finally, total aboveground live biomass, available forage biomass, landscape carrying capacity, and moose population densities were calibrated and validated in previous studies using similar model parameters as used here (De Jager et al. 2017a, b, 2019). For this study, we verified that these estimates approximated measurements for the study area under BAU scenarios.

Results

Moose population dynamics and carrying capacity

Under the current moose and forest management strategies for the area (BAU/BAU), moose population density increased from 8.0 moose per 1000 ha to a maximum of 10.8 moose per 1000 ha by year 2060, before declining to approximately 5.4 moose per 1000 ha by the end of the simulations at year 2110 (Table 4, Fig. 2 Panels A, F, K). Landscape carrying capacity increased from 8.3 moose per 1000 ha to 37.9 moose per 1000 ha by year 2060 before decreasing to 25.4 moose per 1000 ha by the end of the simulations (Fig. 2 Panels A, F, K). Thus, simulating the current management strategies in the area maintained a moose population of approximately 20 moose per 1000 ha below carrying capacity. In contrast, when there was no forest management in the landscape but the current moose harvest strategies were applied (BAU/NFM), the moose population ranged between a minimum of 3.8 and maximum of 7.9 moose per 1000 ha, while carrying capacity never exceeded 30 moose per 1000 ha, resulting in a moose population that was consistently closer to carrying capacity than with forest management (typically less than 20 moose per 1000 ha below carrying capacity) (Fig. 2, Panels E, J, O). Furthermore, the scenario with no moose harvest or forest management (NMH/NFM) resulted in an initial increase in the moose population to a maximum of 12 moose per 1000 ha, followed by a strong decline in the population after 30 years and continual decline for the remainder of the simulations to a low of 2.5 moose per 1000 ha. Further, landscape carrying capacity declined for the duration of the simulations, resulting in a moose population that was within 1–2 moose per 1000 ha of a very small carrying capacity (< 5 moose per 1000 ha) (Fig. 2 Panels E, J, O).

Within each forest management strategy (BAU, IB, IRT, YC), reducing the moose harvest rate by 10% tended to result in either similar or slightly larger moose population densities and either similar or slightly lower estimates of landscape carrying capacity when compared to BAU moose management (Table 4, Fig. 2). In contrast, increasing the moose harvest rate by 10 and 20% within each forest management strategy tended to result in smaller moose populations and larger estimates of landscape carrying capacity (Table 4, Fig. 2). Increases in landscape carrying capacity due to reducing moose harvest by 20% tended to be on the order of 2–8 moose per 1000 ha (Table 4).

Within each moose management strategy (BAU, − 10%, + 10%, + 20% harvest), BAU forest management (BAU), increased rotation time (IRT), and thinning the youngest cohorts (YC), often had overlapping estimates of moose population density and carrying capacity (Fig. 2). However, after 50 years in 2060, increasing the rotation time tended to produce lower moose population densities and lower landscape carrying capacities, while producing the opposite effect by the end of the simulations in 2110. Nevertheless, these forest management strategies had relatively little effect on moose population dynamics in comparison to the increased broadleaf strategy (IB). The increased broadleaf strategy resulted in very large estimates of carrying capacity (> 60 moose per 1000 ha) and larger moose population densities (Fig. 2, Table 5). Increased carrying capacity was on the order of 47–55 moose per 1000 ha under IB.

Production of total biomass

Total biomass across all species increased asymptotically from 6200 to 8200 g/m^2 (which equates to 6.2–8.2 tonnes/ha) in the absence of forest management (Fig. 3, Panel B). In contrast, the different forest management actions resulted

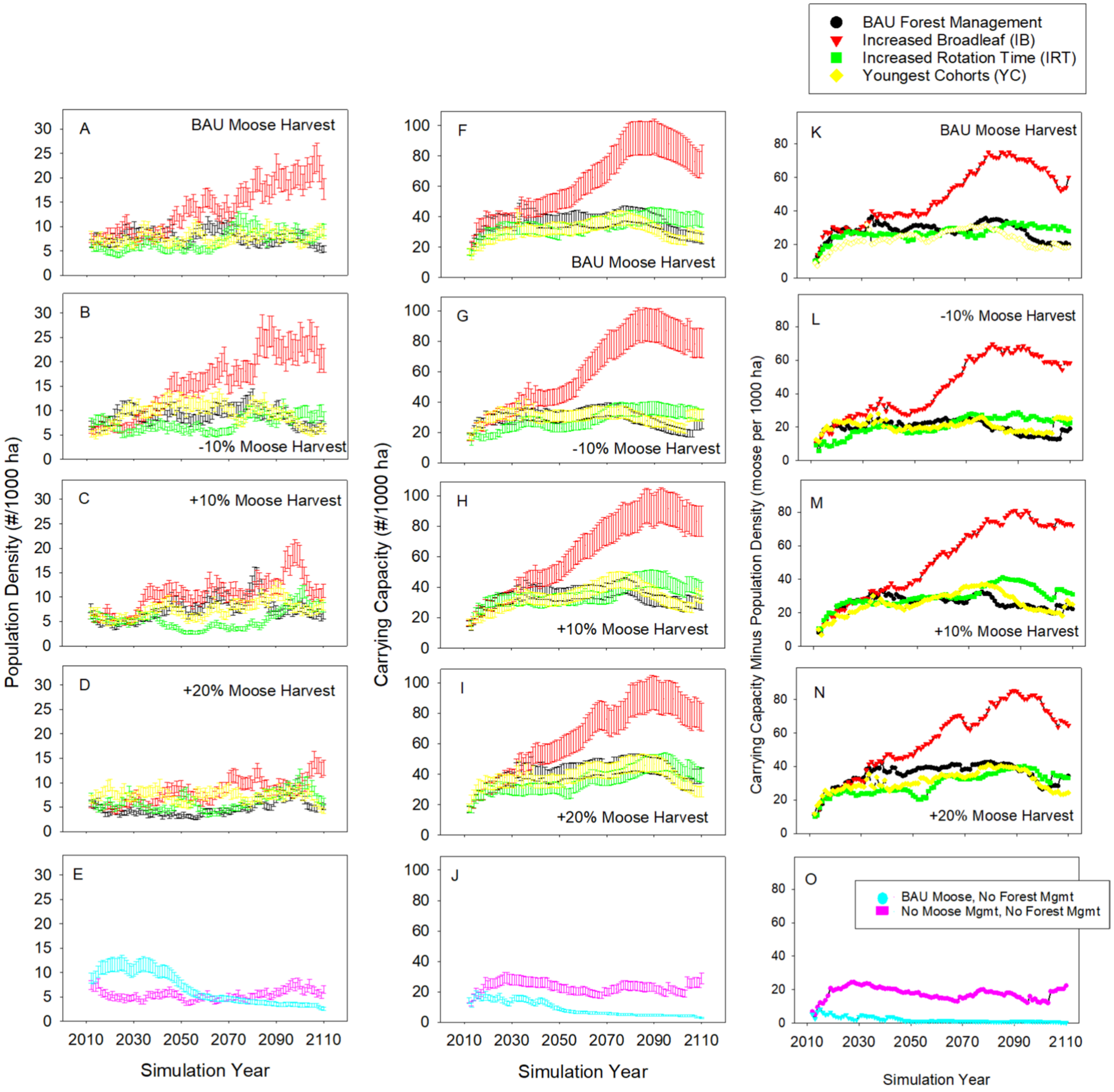

Fig. 2 Moose population density (±2 standard deviations, panels **A**-**E**), landscape carrying capacity (±2 standard deviations, panels **F**-**J**), and the difference between the two measures (panels **K**–**O**) for 18 different combinations of moose harvest and forest management strategies

into different temporal dynamics for total biomass, but ultimately, after 100 years, all scenarios resulted into approximately 8000 g/m^2. Initially (years 2030 to 2050), increased rotation time (IRT) generated the greatest estimates of total biomass, reflecting the effects of that management strategy on spruce (Fig. 4) and pine (Fig. 5) biomass. Later in the simulations (years 2060–2100) the increased broadleaf (IB) scenarios had the largest estimates of total biomass (Fig. 3), reflecting the effects of that management strategy on deciduous biomass production (Fig. 6). The different moose harvest scenarios had little to no effect on total aboveground live biomass.

Total aboveground live biomass of unbrowsed spruce increased from 2900 to between 4500 and 5500 g/m^2 depending on the scenario (Fig. 4). The increase was somewhat delayed in the scenarios that included forest management (Fig. 4A, C-E), but these scenarios ultimately resulted into slightly more spruce biomass than those without forest management. Changing the moose management strategy had little to no effect on spruce biomass.

Table 4 Moose population density and carrying capacity results for years 2060, 2110, as well as the minimum and maximum values for business-as-usual (BAU) moose harvest and four different forest management scenarios (BAU, business as usual; IB, increased broadleaf; IRT, increased rotation time; YC, thinning of the youngest cohorts). The starting value for moose population density was 8 per 1000 ha for all scenarios. Also given are difference values for each forest management scenario under different moose density scenarios relative to the same forest management scenario under BAU moose harvest to isolate the effects of changing moose harvest rates. Red boxes highlight lower values relative to BAU moose harvest while blue boxes highlight higher values

			Moose population density (per 1000 ha)				Landscape carrying capacity (per 1000 ha)			
Moose Harvest	Forest Management	Scenario	Year 2060	Year 2110	Min	Max	Year 2060	Year 2110	Min	Max
BAU	BAU	BAU/BAU	9.30	5.39	5.20	10.80	37.90	25.40	8.29	45.52
BAU	IB	BAU/IB	15.80	17.67	7.05	24.16	61.50	77.95	8.29	92.93
BAU	IRT	BAU/IRT	5.40	9.32	4.11	11.72	30.10	37.35	8.29	41.52
BAU	YC	BAU/YC	7.50	8.47	5.95	10.25	33.20	26.87	8.29	40.07
			Difference in moose density from BAU moose harvest				Difference in carrying capacity from BAU moose harvest			
			Year 2060	Year 2110	Min	Max	Year 2060	Year 2110	Min	Max
-10%	BAU	-10%/BAU	-0.50	1.11	0.76	2.14	-5.30	0.10	0.00	-10.19
-10%	IB	-10%/IB	0.10	2.64	-1.32	2.34	-3.70	0.66	0.00	-1.74
-10%	IRT	-10%/IRT	0.00	-0.53	1.02	-0.70	-5.10	-5.93	0.00	-5.34
-10%	YC	-10%/YC	3.10	-2.45	-1.23	2.67	-2.00	4.45	0.00	-2.39
+10%	BAU	+10%/BAU	-0.50	0.83	-1.40	3.62	-1.10	3.08	0.00	-4.33
+10%	IB	+10%/IB	-5.70	-6.40	-2.25	-4.70	5.00	5.42	0.00	1.29
+10%	IRT	+10%/IRT	-2.30	-1.42	-1.45	-0.62	3.50	1.50	0.00	4.61
+10%	YC	+10%/YC	-1.70	-0.07	-1.31	1.63	3.30	6.64	0.00	5.13
+20%	BAU	+20%/BAU	-5.20	-0.34	-2.53	-1.07	4.20	13.95	0.00	2.23
+20%	IB	+20%/IB	-8.70	-4.65	-2.97	-9.53	3.80	-0.49	0.00	0.65
+20%	IRT	+20%/IRT	-1.30	-3.24	-0.76	-0.33	4.80	1.82	0.00	6.83
+20%	YC	+20%/YC	0.40	-4.19	-1.67	-0.70	8.30	1.75	0.00	7.71

Total aboveground live biomass of pine was most strongly affected by forest management. Without forest management, pine biomass increased from 2200 to 2700 g/m^2 (Fig. 5, Panel B). But with forest management, pine biomass decreased from 2200 to between 1800 and 2000 g/m^2 depending on the forest management scenario. Increasing rotation time (IRT) resulted in the highest estimates of pine biomass throughout simulations and even resulted in a small initial increase in pine biomass to approximately 2600 g/m^2 before declining later. Thinning the youngest cohorts (YC) resulted into the lowest estimates of pine biomass, while the BAU and increased broadleaf (IB) strategies were similarly between the two other scenarios. Changing the moose harvest strategy had little to no effect on total aboveground biomass of pine.

Total aboveground live biomass of deciduous species remained stable at approximately 1000 g/m^2 for the scenarios that did not include forest management (Fig. 6, Panel B). BAU forest management, increased rotation time, and thinning only resulted into small declines in deciduous species biomass to a low of approximately 700 g/m^2 by the end of the simulations. In contrast to these results, the increased broadleaf scenario resulted into an increase in deciduous biomass to a high of approximately 2000 g/m^2. Changing the moose harvest scenario had little to no effect on total aboveground live deciduous biomass.

Moose browsing on pine

Irrespective of the forest management strategy and the moose harvest strategy applied, there was always some browsing of pine (Fig. 7). Estimates for business-as-usual moose and forest management were 2.8 g/m^2 on average for the duration of the simulations. Reducing moose harvest rates by 10% led to an increase in pine biomass removed to an average of 4–12 g/m^2 over the 100-year simulations depending on forest management scenario (Fig. 7 panel C). Increasing moose harvest rates by 10% (Fig. 7 panel D) and especially by 20% had the opposite effect (Fig. 7 panel E), i.e. reducing the amount of pine biomass removed. But effect sizes depended on forest management strategy. The increased broadleaf (IB) strategy led to relatively large increases in pine biomass removed to an average of 5–12 g/m^2 depending on the moose management strategy (Fig. 7).

Table 5 Moose population density and carrying capacity results for years 2060, 2110, as well as the minimum and maximum values for business-as-usual (BAU) forest management and four different moose harvest strategies (BAU, business as usual and reducing harvest rates by 10 percent and increasing them by 10 and 20 percent). The starting value for moose population density was 8 per 1000 ha for all scenarios. Also given are difference values for each moose harvest scenario under different forest management scenarios relative to the same moose harvest scenario under BAU forest management to isolate the impacts of changing forest management strategies. Red boxes highlight lower values relative to BAU moose harvest while blue boxes highlight higher values

			Moose population density (per 1000 ha)				Landscape carrying capacity (per 1000 ha)			
Moose Harvest	Forest Management	Scenario	Year 2060	Year 2110	Min	Max	Year 2060	Year 2110	Min	Max
BAU	BAU	BAU/BAU	9.30	5.39	5.20	10.80	37.90	25.40	8.29	45.52
-10%	BAU	-10%/BAU	8.80	6.50	5.96	12.94	32.60	25.50	8.29	35.33
+10%	BAU	+10%/BAU	8.80	6.22	3.80	14.42	36.80	28.48	8.29	41.19
+20%	BAU	+20%/BAU	4.10	5.05	2.67	9.73	42.10	39.35	8.29	47.75
			Difference in moose density from BAU forest management				Difference in carrying capacity from BAU forest management			
			Year 2060	Year 2110	Min	Max	Year 2060	Year 2110	Min	Max
BAU	IB	BAU/IB	6.50	12.28	1.85	13.36	23.60	52.55	0.00	47.41
-10%	IB	-10%/IB	7.10	13.82	-0.24	13.56	25.20	53.11	0.00	55.85
+10%	IB	+10%/IB	1.30	5.05	1.00	5.04	29.70	54.89	0.00	53.03
+20%	IB	+20%/IB	3.00	7.97	1.41	4.89	23.20	38.10	0.00	45.82
BAU	IRT	BAU/IRT	-3.90	3.93	-1.09	0.92	-7.80	11.95	0.00	-4.00
-10%	IRT	-10%/IRT	-3.40	2.29	-0.84	-1.92	-7.60	5.92	0.00	0.86
+10%	IRT	+10%/IRT	-5.70	1.68	-1.15	-3.33	-3.20	10.36	0.00	4.95
+20%	IRT	+20%/IRT	0.00	1.03	0.69	1.65	-7.20	-0.18	0.00	0.61
BAU	YC	BAU/YC	-1.80	3.08	0.75	-0.55	-4.70	1.47	0.00	-5.45
-10%	YC	-10%/YC	1.80	-0.48	-1.25	-0.02	-1.40	5.82	0.00	2.35
+10%	YC	+10%/YC	-3.00	2.18	0.84	-2.55	-0.30	5.02	0.00	4.02
+20%	YC	+20%/YC	3.80	-0.77	1.62	-0.19	-0.60	-10.73	0.00	0.04

Discussion

Our simulation modelling experiment highlights the importance of considering both ungulate and timber management in a managed forest landscape, thereby supporting suggestions to balance ungulate populations and forage supply across spatiotemporal frames (Vavra and Riggs 2010; Bjärstig et al. 2014; Apollonio et al. 2017; Girona et al. 2023b; Neumann et al. 2024). Our first major finding was that the current management strategies used in the study area maintain a moose population that was consistently below the carrying capacity of the landscape (i.e., the produced biomass). The current timber harvest strategies maintain a sustainable forage base for moose, and the current moose harvest strategy prevents the population from exhausting its food supply. When we removed moose and forest management from our model, the landscape was unable to generate enough forage to support the moose population over the long-term. In the absence of a functional predator population, management of the ungulate population to keep it from approaching carrying capacity would help suppress browsing damage. In addition, ungulate herbivore populations benefit from young forest stands created through timber harvest and browsing can prolong the time stands are within the height reach of herbivores. Thus, the current management regime seems to adequately balance management goals related to the production of timber and ungulates moving forward.

Our second major finding was that increasing or decreasing moose harvest rates had relatively predictable effects on landscape carrying capacity and the amount of biomass removed from pine but had almost no effect on total aboveground biomass. Increasing moose harvest rates generally led to smaller populations, larger carrying capacities (as more biomass was left on the landscape), and less removal of pine biomass. In contrast, decreasing moose harvest rates generally led to larger moose populations, lower landscape carrying capacities given the larger effects of browsing on forage production, and much larger amounts of biomass removed from pine. Yet changing moose harvest rates only affected the moose population and carrying capacity by a few moose per 1000 ha and these differences appeared to be insufficient to modify total aboveground biomass. In such a heavily managed landscape, small adjustments to the moose harvest strategies like those we simulated may not have large effects on forest production or composition.

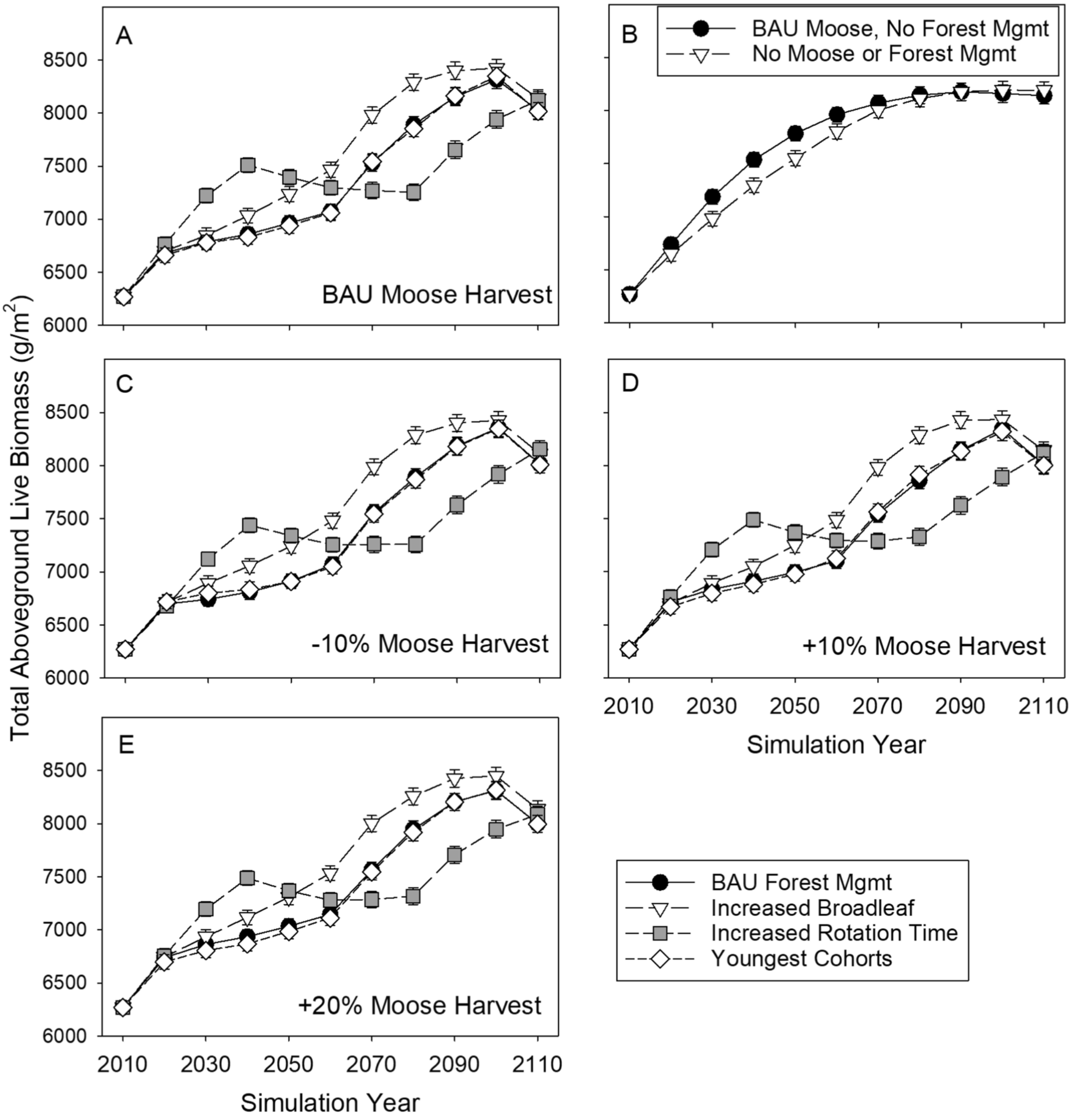

Fig. 3 Changes in total aboveground live biomass of all species (±2 standard deviations) during different simulations. Panel **A** shows the effect of different forest management strategies (see text and legend) while maintaining moose harvest at current levels (business as usual). Panels **C**–**E** similarly show the effect of different forest management strategies, but under a 10% reduction in moose harvest (**C**), a 10% increase in moose harvest (**D**), and a 20% increase in moose harvest (**E**). Panel **B** shows the effects of no forest management under both business-as-usual moose harvests and no moose harvest

Despite country-specific differences, management of ungulate-forest systems typically relies on indicators of ecosystem change to set deer harvest rates and to regulate browsing pressure. Examples of such indicators include animal performance, population abundance, tree species composition and the scarcity of certain plants, habitat quality and/or ungulate habitat impact (Morellet et al. 2007; Apollonio et al. 2010). In our system, one criterion that has been used to determine the most appropriate levels of moose harvest is the degree of damage moose cause to pine. When we increased moose harvest rates by 20%, we did find a reduction in the amount of biomass removed from pine. The Swedish Forest Agency (2022) uses the percentages of top shoots removed from pine as a way to track damage to pine. Although our model estimates total biomass removed from pine and not the percentage of top shoots removed,

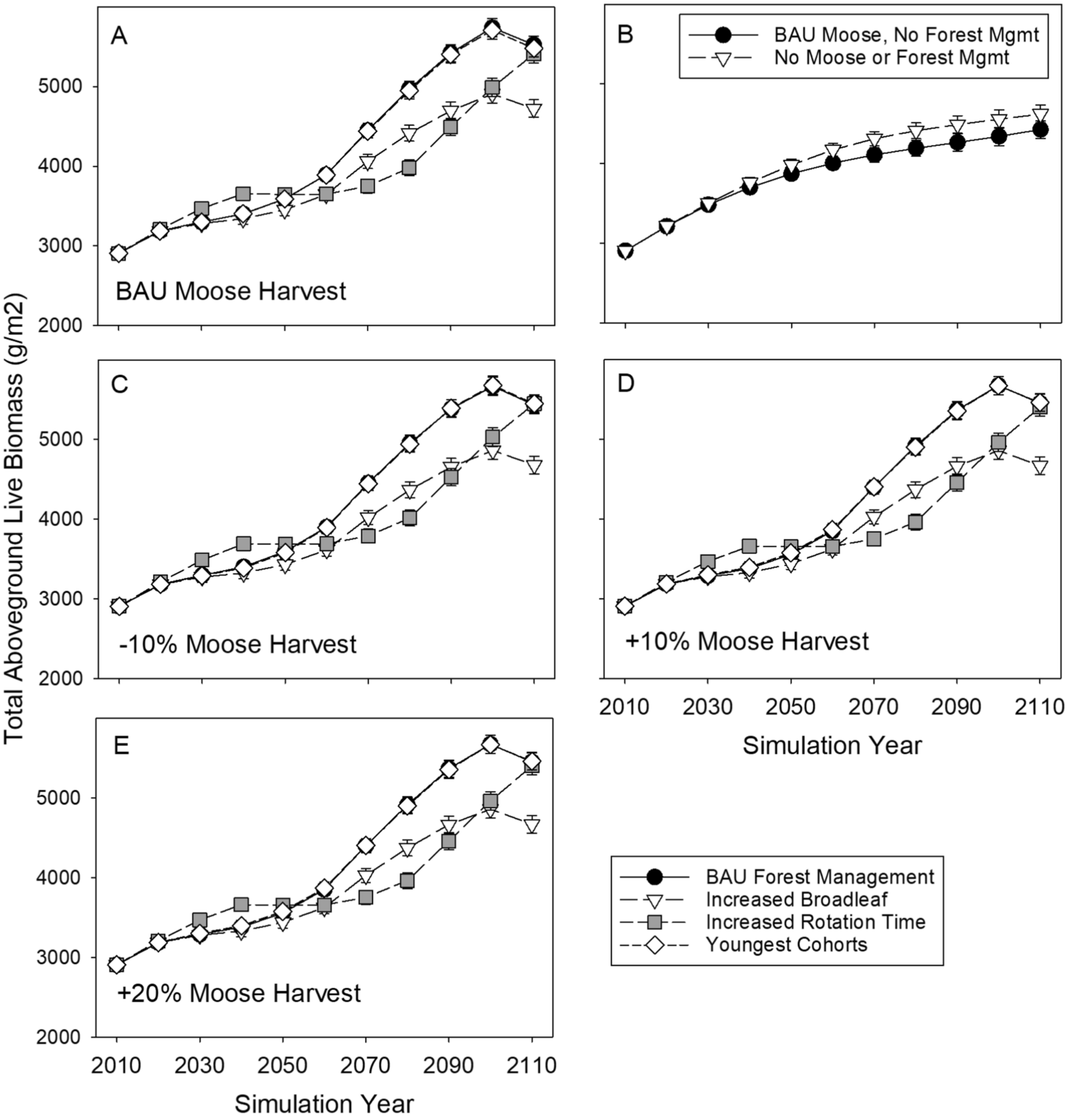

Fig. 4 Changes in total aboveground live biomass of spruce (±2 standard deviations) during different simulations. Panel **A** shows the effect of different forest management strategies (see text and legend) while maintaining moose harvest at current levels (business as usual). Panels **C**–**E** similarly show the effect of different forest management strategies, but under a 10% reduction in moose harvest (**C**), a 10% increase in moose harvest (**D**), and a 20% increase in moose harvest (**E**). Panel **B** shows the effects of no forest management under both business-as-usual moose harvest and no moose harvest

our results are meaningful in that more biomass removed from pine is expected to indicate a higher probability of top shoot removal. The following thresholds for percentage of top shoot removal are used to estimate damage in young production stands: tolerable ≤ 2%, serious 2– ≤ 5%, severe 5– ≤ 10%, and very severe > 10 (Swedish Forest Agency 2022). Within the moose management unit covering most of our study area, about 22% of all young pine trees showed browsing damage and the areal of forage-producing young forest is expected to increase by 11% during the coming three years (averaged values, inventories 2019–2023; Swedish Forest Agency 2023). Local moose management likely will increase harvest rates during the upcoming three-year management period for moose given the documented browsing levels and reported numbers. Our simulations suggest that increasing moose harvest rates will reduce the amount

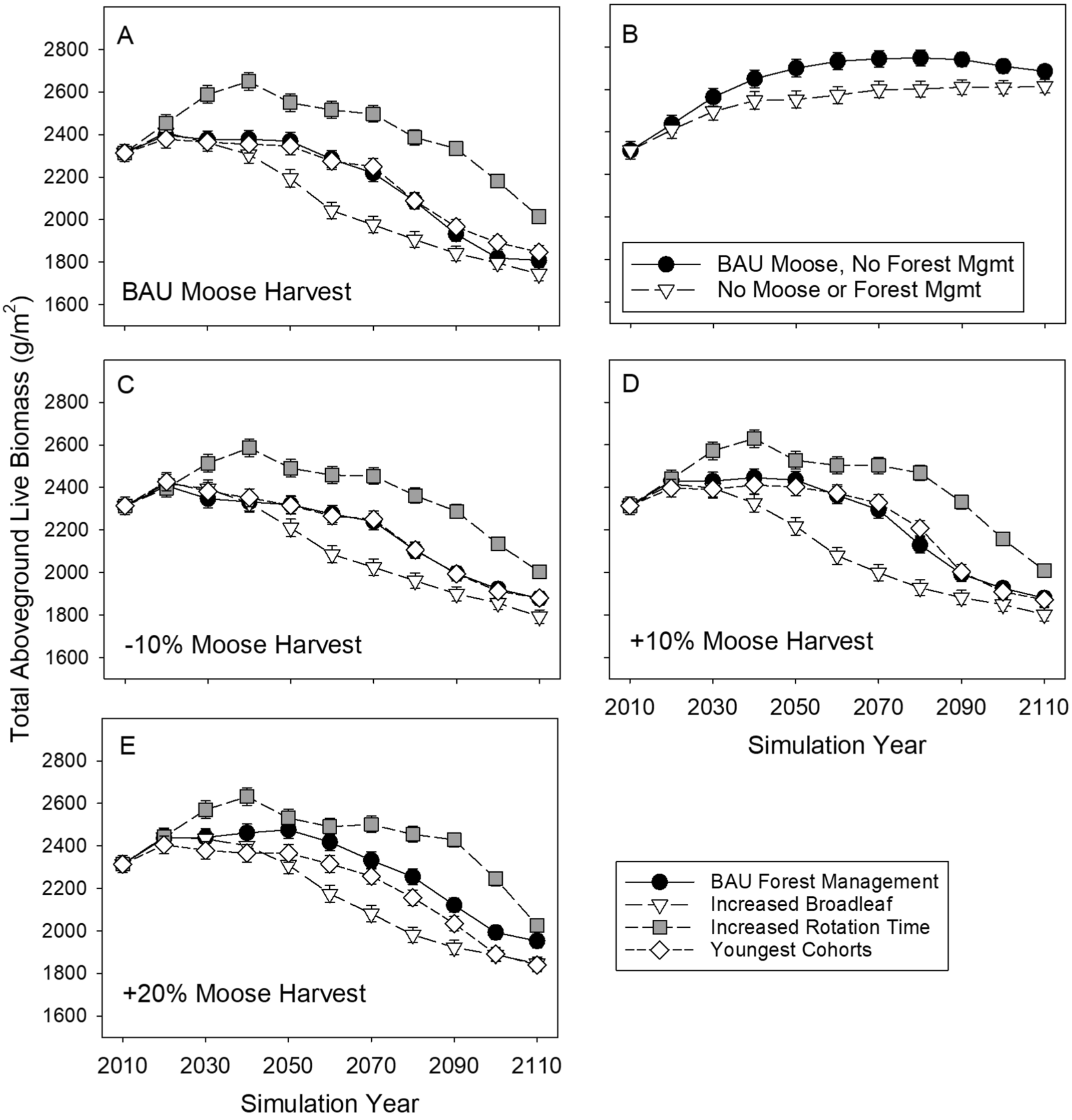

Fig. 5 Changes in total aboveground live biomass of pine (±2 standard deviations) during different simulations. Panel **A** shows the effect of different forest management strategies (see text and legend) while maintaining moose harvest at current levels (business as usual). Panels **C**–**E** similarly show the impact of different forest management strategies, but under a 10% reduction in moose harvest (**C**), a 10% increase in moose harvest (**D**), and a 20% increase in moose harvest (**E**). Panel **B** shows the impacts of no forest management under both business-as-usual moose harvest and no moose harvest

of pine biomass removed in all forest management strategies during the coming 20 years with a sharper and longer decrease with + 20% scenario and slower decrease with ‘thinning only’ and a quicker rebound with ‘increased broadleaf’ (Fig. 7). Despite difficulty in comparing estimates on future biomass/forage straight off, we can note that percentage increases suggested by our simulations and report are relatively similar. Interestingly, we found little difference in biomass increase during the first 10 years among management strategies, but more among tree species (Figs. 3–6; Swedish Forest Agency 2023). However, it is important to note that accepted levels of browsing damage may vary among stakeholders and may not always correspond to landscape carrying capacity. It has for instance been found that hunters in Sweden who do not own forests assessed the browsing damage on their primary hunting grounds as less

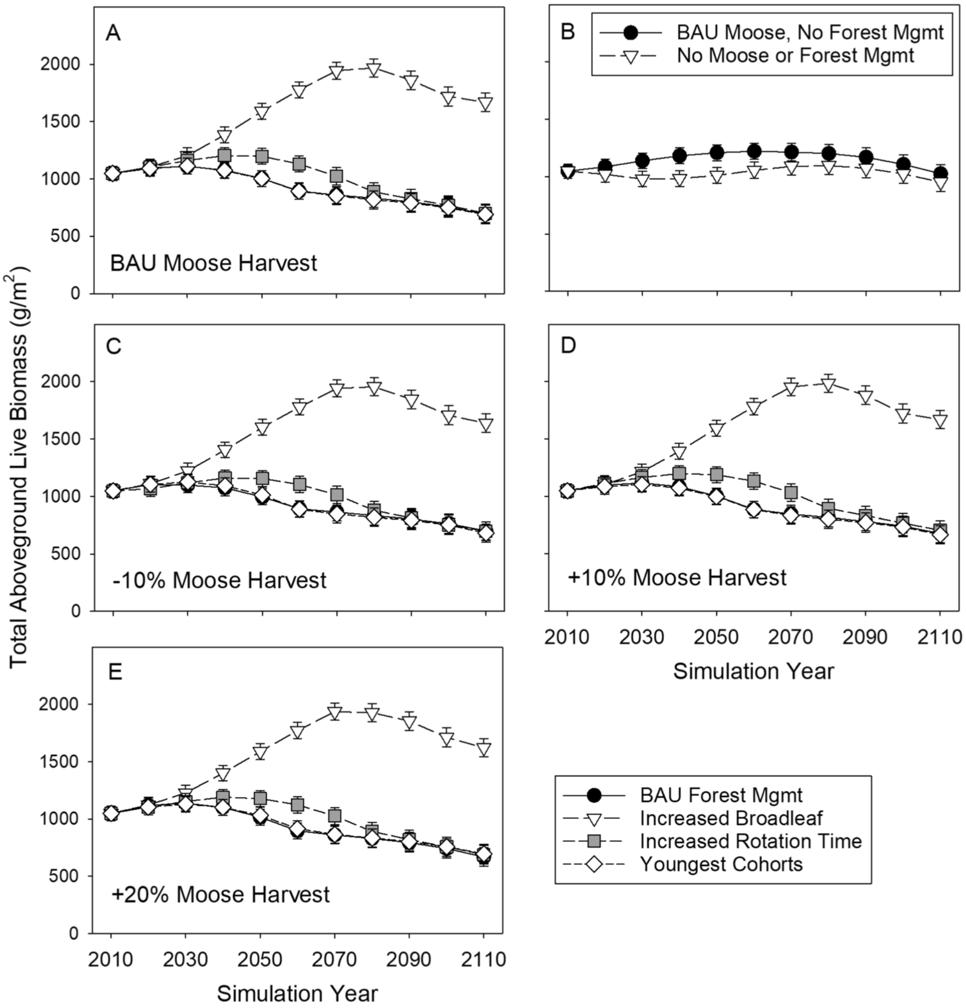

Fig. 6 Changes in total aboveground live biomass of all deciduous species (± 2 standard deviations) during different simulations. Panel **A** shows the effect of different forest management strategies (see text and legend) while maintaining moose harvest at current levels (business as usual). Panels **C**–**E** similarly show the effect of different forest management strategies, but under a 10% reduction in moose harvest (**C**), a 10% increase in moose harvest (**D**), and a 20% increase in moose harvest (**E**). Panel **B** shows the effects of no forest management under both business-as-usual moose harvest and no moose harvest

severe compared to non-hunting forest owners, who rated the browsing damage on their forest estates higher. Hunting forest owners rated browsing damage intermediately (Ezebilo et al. 2012). Browsing damage to pine across other parts of the globe reveal that damage rates vary largely, dependent on plant productivity (Danell et al. 1991), geography, and variations in weather conditions (Zamora et al. 2001). For example, a study in Scotland revealed that the probability that red deer (*Cervus elaphus*) or roe deer (*Capreolus capreolus*) browsed pine saplings less than 2 m tall was 9% (Palmer and Truscott 2003). In contrast, a study in the Mediterranean mountains showed browsing damage by goats and Iberian ibex (*Capra pyrenaica*) on 72% of the monitored saplings (Zamora et al. 2001).

Our third major finding was that alternative forest management strategies had varying effects on total standing tree biomass, moose population dynamics, and browsing on pine. Whereas total aboveground live biomass was hardly affected by the different moose harvest strategies, it was affected by forest management strategy, which may have implications for the ability of forests to sequester carbon (Dymond et al. 2016; Hof et al. 2017; Ameray et al. 2021). However, although the different forest management strategies led to different temporal dynamics for total biomass, after 100 years, at the end of the simulation, all scenarios resulted into approximately 8000 g/m^2. Forest management strategies in which the rotation time was increased to 100 years or only the youngest cohorts were thinned, had little effect on moose population dynamics according to our simulations. However, enlarging the proportion of broadleaf in the forest greatly increased the carrying capacity of the landscape for moose (from ~ 20 to > 60 moose per 1000 ha), with moose population densities that appeared to depend on the moose harvest rate. Because the increased broadleaf forest management strategy resulted into larger moose populations, it also typically had the highest estimates of pine biomass removed by moose. Thus, for this management scenario to be successful, even higher rates of moose harvest than we simulated here would be needed.

On an annual basis, moose have a varied diet and strive after balancing different food items (Spitzer 2019; Felton et al. 2020). Broadleaf species are frequently preferred by

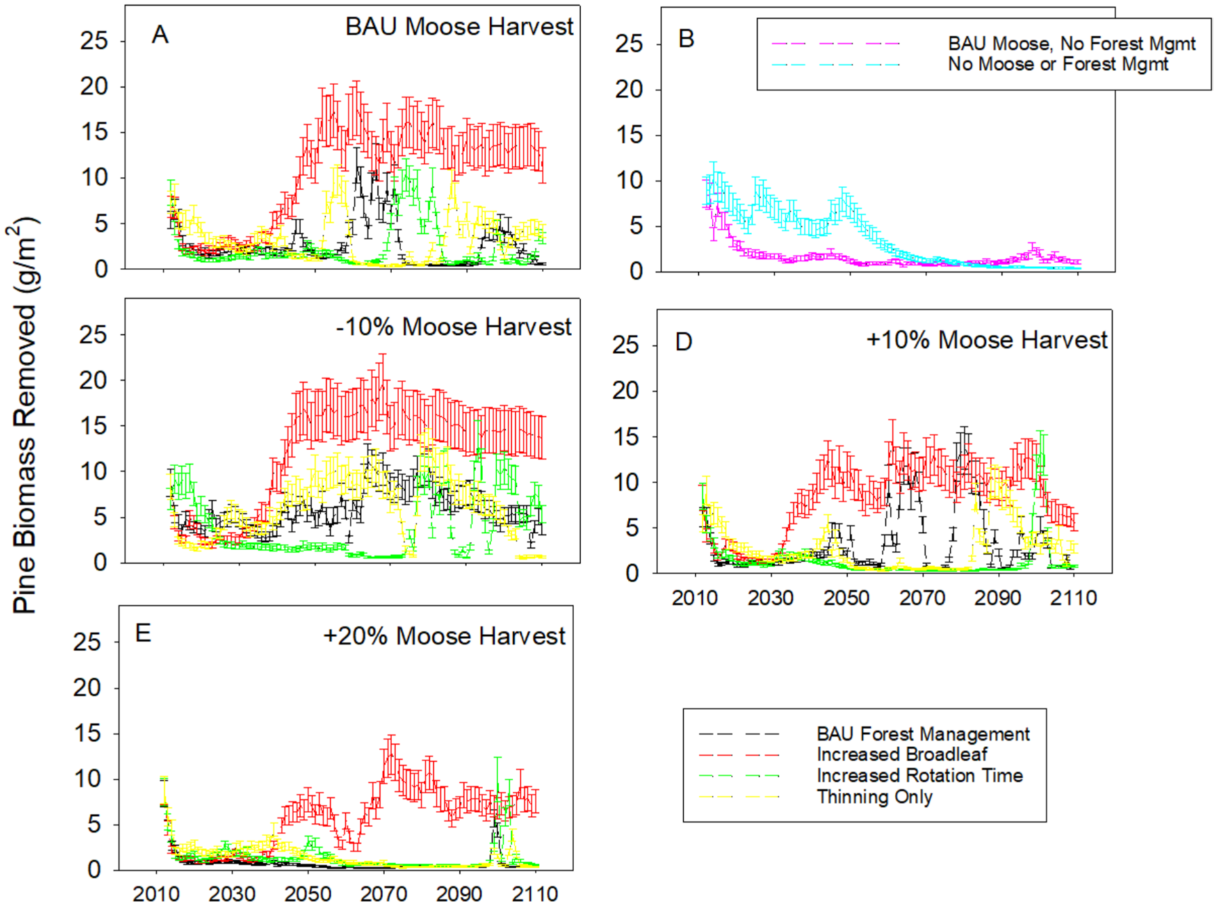

Fig. 7 Changes in the biomass of pine removed (±2 standard deviations) due to moose browsing during different simulations. Panel **A** shows the effect of different forest management strategies (see text and legend) while maintaining moose harvest at current levels (business as usual). Panels **C**–**E** similarly show the effect of different forest management strategies, but under a 10% reduction in moose harvest (**C**), a 10% increase in moose harvest (**D**), and a 20% increase in moose harvest (**E**). Panel **B** shows the effects of no forest management at all under both business as usual moose harvests and no moose harvest

moose (Hörnberg 2001), are a central food item during the summer growing season, and are thus important to moose recruitment (Felton et al. 2020). Importantly, access to broadleaf forage also has implications for browsing damage on pine (Felton et al. 2022). Compared to monocultures, species-rich forest landscapes might provide better conditions to satisfy the nutritional demands of herbivores more quickly, thereby reducing the browsing impact (e.g., mixed temperate forests, Ohse et al. 2017). In winter, pine is a key food item for moose (Shipley et al. 1998; Spitzer 2019) when animals switch to woody browse and are in a period of hypometabolism (Græsli et al. 2020). Increasing the proportion of broadleaf species in the landscape could be beneficial when the aim is to increase the size of the moose population (which occurred in our simulations). Higher levels of (old) broadleaved trees are generally associated with higher levels of biodiversity (Nilsson et al. 2001). Forest restoration strategies therefore also tend to include ways to increase the density of broadleaf trees in the boreal region (Hof and Hjältén 2018). However, our simulations do reveal that the browsing of pine, and thus possible damage to pine, may increase with broadleaf production, which could be undesirable to the forest industry beyond a certain threshold. Longer rotation times improve the field layer, including different *Ericacae* species (Petersson et al. 2019), which are important staple food items for moose year-round (Spitzer 2019), but which we were unable to simulate. Thus, an increased share of broadleaves on the landscape level, together with a good herbaceous field layer, may result in higher abundance of alternative forage available to moose, which may initially lower the browsing pressure and thus lessen damage on pine (Spitzer et al. 2021; Felton et al. 2022). Lengthening rotation times also comes with different economic consequences and risks for other damage (e.g., wind, snow, pest), which could be explored by coupling our simulations with an economic assessment.

Even if it is not possible to validate model results for future conditions,our simulations resulted in similar estimates of aboveground forest biomass, moose population densities, and carrying capacities as found in real landscapes and in previous applications of the same model platform to different systems (De Jager et al. 2017a). The only exception to this was the broadleaf harvest scenario, which resulted in substantially larger estimates of landscape carrying capacity than the other scenarios, and larger estimates than typically found in boreal forests. At the start of our simulations just 1% of the area of the landscape was in young broadleaf forests and the associated landscape carrying capacity was low (under 10 moose per 1000 ha). Young forest stands are known to support larger moose population densities as broadleaf species are highly preferred by moose (Månsson et al. 2007; Spitzer 2019). Thus, the expansion of young broadleaf stands in our model would be expected to increase the carrying capacity of the landscape. However, the magnitude of the increase projected here warrants some caution given how large population estimates became under this scenario. In addition, our simulations did not consider the occurrence of other browser species (e.g., roe deer). Roe deer and moose co-occur in most parts of the Swedish landscape (Neumann et al. 2020), and their diets can overlap, which can result in inter-specific forage competition (Hofmann 1989; Spitzer 2019; Spitzer et al. 2020). Specifically, this can reduce the availability of broadleaf forage for moose in landscapes with high roe deer densities. Moreover, high browsing pressure by other smaller herbivores, and thus general forage availability, may also affect the degree to which moose consume other forage than pine (Spitzer et al. 2021), thereby affecting browsing damage on economic valuable pine (Pfeffer et al. 2021).

The dynamics of a forest landscape are complex because many factors interact at multiple scales. Although modelling is a powerful tool to understand forest ecosystems and explore management options, it is always a simplification of reality. For example, we did not simulate herbaceous undergrowth, nor did we take the presence and browsing damage of other deer species into account or how predators like wolves (*Canis lupus*) affect moose distribution and browsing pressure in the area (Angelstam et al. 2017). Moose tend to browse largely on trees (Shipley et al. 1998; Hörnberg 2001; Felton et al. 2020); however, red deer and roe deer have larger proportions of non-woody species in their diet during summer (Spitzer 2019; Spitzer et al. 2020). Furthermore, in areas with higher densities of the smaller deer species, moose consume more pine and less *Vaccinium* species, indicating interspecific competition (Spitzer et al. 2021). Such competition may result in higher browsing damage (Pfeffer et al. 2021) and might have affected our results; this avenue could be pursued further. We also did not simulate the effect of natural disturbances like fire, windthrow, and pests, nor of different climate change scenarios because our primary aim was to understand the relation between browsing damage and forest management strategies. Including such effects in our simulations may have resulted in different outcomes as for instance storms and bark beetles (*Ips typographus*) mainly kill spruce trees (Komonen et al. 2011; Kärvemo et al. 2023), which can create gaps where deciduous trees generate (Drössler et al 2017). The increase in moose population in the Increased Broadleaf scenario compared to the other scenarios may thus have been overestimated. Importantly, climate-adaption measures to increase forest resilience applied by forest management need to consider the effect of browsing (Champagne et al. 2021). Here, modelling the effect of different strategies considering selective browsing by different deer species might be an important avenue to explore in future research. Specifically, our population distribution methods could be modified to consider variability in species preference by different ungulates or perhaps at a shorter-time step than a single year.

One important limitation to our study is that we did not take different and the most up to date climate change scenarios (CMIP6) into account. Climate change will not only affect the growth rate of the different tree species we simulated (Briceno-Elizondo et al. 2006), it may also affect species interactions and the populations dynamics and distribution of moose and other browsers and their predators (Hof et al. 2012; Holmes et al. 2021; Felton et al. 2024). Changed temperature and precipitation patterns affect herbivores directly and indirectly (Felton et al. 2024). Specifically, larger species that are more sensitive to heat stress (e.g., moose or red deer) might change their activity patterns, movement and space use (including habitat selection) to facilitate their thermoregulation (Felton et al. 2024), which in the end can modify animals' residence time and browsing pressure in a given forest (Neumann et al. 2024). We used the needed parameters previously generated for the area by Hof and Hjältén (2018) rather than generating new parameters due to the large amount of time such an undertaking requires (Furniss et al. 2022; Hof et al. 2024) and the near continuous updating of climate change scenarios. Furthermore, the scenario (RCP 4.5) used by them was a middle of the road scenario (IPCC 2013), similar to SSP2-4.5 (IPCC 2021), which was identified as one of the plausible scenarios (Pielke et al. 2022). Furthermore, we were mainly interested in assessing the effects of different browsing intensities and forest management strategies, rather than the effect of different climate change scenarios. Adding climate change scenarios would add yet another level of stochasticity, and with that, uncertainty to the modelling process as climate change is expected to have effects both on forest ecosystems as well as on ungulates like moose (Neumann et al. 2024). Yet, the effects of forest management on the future supply of ecosystem services in the boreal forest are thought to be much higher than the effects of climate change, although regional differences occur (Triviño et al. 2023; Robles et al. 2025).

Due to logistic reasons (computation time), we only simulated a restricted number of different moose harvest and forest management strategies. Some additional clear cut and age-related harvesting strategies could be simulated in the platform that we used, and others, such as ungulate-adapted slash piles and intensified soil scarification (Loosen et al. 2021), currently could not be simulated. Finally, we did not assess the economic consequences of the different strategies. A study by Nilsson et al. (2015) in which the effect of different browsing levels on the production and economic value of Scots pine was simulated, also showed minor effects of low browsing levels (2–5% browsing damage) on production. However, these minor effects on production did have substantial economic consequences. Including an economic analysis may therefore be an important next step.

Finally, when De Jager et al. (2017a) introduced the browsing extension to the Landis-II modelling framework, they conducted an extensive sensitivity and uncertainty analysis of the main model parameters. Their analyses showed that model outputs most closely connected to the ungulate population, such as biomass removed from the landscape, cohorts killed due to moose browsing, and forage biomass available tended to be most sensitive to variations in model parameters, whereas total biomass estimates tended to be insensitive to variation in model parameters. Although an extensive sensitivity analysis was beyond the scope of our study, our outputs such as forage biomass available and removed were more sensitive to differences in our management scenarios than total aboveground live biomass. Thus, further increases or decreases in animal harvest rates might be expected to drive similar changes as we observed here.

Conclusions

The aim of our study was to assess the effects of different management strategies on forest and moose dynamics to advance the debate on appropriate management strategies in forest ecosystems. We demonstrated that simulation modeling can be a useful tool for this purpose. Based on our simulations we can conclude that in this heavily managed landscape changes in moose harvest rates may have relatively minor effects on total aboveground live biomass and the degree to which moose browsing affects landscape distributions and the abundance of available forage biomass, but with varying levels of damage to commercially valuable species such as Scots pine. Similarly, some forest management strategies (increased rotation time and thinning younger cohorts) directly affected aboveground live biomass of select species but has little effect on moose population density and dynamics. The management strategy producing the largest effects on forest and moose dynamics consisted of increased production of broadleaved species. In such a heavily managed system that appears to be highly resilient to most changes in forest or moose management strategy, assessing stakeholder satisfaction would be beneficial. Our results will be helpful for management agencies and stakeholder groups to initiate discussions about future management strategies in the face of environmental change.

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Availability of data and material Data is provided within the manuscript. The LANDIS-II modelling platform is freeware, initialization parameters are available upon request.

Code availability The LANDIS-II modelling platform is freeware, initialization parameters are available upon request.

Declarations

Conflict of interest The authors declare no competing interests.

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