Received: 9 October 2024 | Revised: 22 September 2025 | Accepted: 25 September 2025

DOI: 10.1111/cobi.70198

Conservation Biology

CONTRIBUTED PAPER

Effects of ungulate browsing on forest assisted migration strategies to conserve ecosystem function

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Article impact statement: Climate-smart forest management aims to produce more resilient forests, but its success can be greatly affected by ungulate browsing.

[Correction added on January 24, 2026 after first online publication: The copyright line was changed.]

Abstract

Forest managers recognize that proactive management strategies, such as forest assisted migration (FAM) of tree species, intended to accelerate the pace of forest adaptation, may be necessary to maintain resilient forests and combat the stressors of climate change. However, the impact of interactions between climate change and ungulate browsers of trees, both of which have profound effects on the landscape, on the success of FAM efforts is unknown. We used a forest landscape model (LANDIS-II) to simulate assisted migration and browsing by ungulate (white-tailed deer [*Odocoileus virginianus*]) populations on a northern Wisconsin (USA) landscape under alternate climate futures. After accounting for effects of FAM strategy and climate change scenario, simulated ungulate browsing reduced species richness and the proportion of the landscape with tree species preferred by browsers and resulted in more of the landscape developing into novel forest communities that supported fewer ecosystem goods and services. Our results suggest that managers may need to select FAM species less preferred by ungulates or use seedling protection measures to mitigate the negative effects of chronically high ungulate populations in efforts to transition future forests to sustain ecosystem goods and services.

KEYWORDS

climate-smart forestry, forest assisted migration, forest conservation, LANDIS-II model, long-term study, *Odocoileus virginianus*, PnET-Succession, ungulate browse

INTRODUCTION

Climate change may affect the ability of forests to provide goods and services if extant tree species become maladapted to future conditions. Consequently, managers are considering silvicultural practices that shift tree composition and structure to adapt forests to the range of anticipated future conditions (Nagel et al., 2017). Such silvicultural "transition" (Millar et al., 2007) strategies seek to change forest composition through enrichment planting of nonendemic species (i.e., forest assisted migration [FAM]) so that forests become better adapted to future conditions (Gustafson, Kern, et al., 2023). The ability of FAM species to survive and compete when planted in new biomes is an active area of research globally (e.g., Mauri et al., 2023; Royo et al. 2023; Twardek et al., 2023), but uncertainty remains about how they will fare in the face of new competitors, pests, and weather extremes.

Ungulate browsing impacts on trees are an understudied aspect of FAM, and it is unknown whether FAM will be harmed or helped by ungulate browsing pressure (Champagne, Raymond, et al., 2021). Not only might ungulates negatively affect the ability of FAM to successfully recruit new tree species into future forests, but FAM tactics may also change the composition of forests in ways that negatively affect ungulate populations and the ecosystem services they provide (e.g., hunting [some species will benefit when ungulates reduce the presence of major competitors (e.g., De Vriendt et al., 2020; Stokely & Betts, 2020]). It is likely that the impact of ungulates will depend on which tree species are introduced under FAM. Reduction of uncertainties is important because FAM projects are costly and are unlikely to be undertaken without a high certainty of effectiveness at preserving forest ecosystem functions.

Landscape-scale studies of how ungulates and abiotic environmental conditions interact to affect forest dynamics are few.

Kramer et al. (2003) used the FORSPACE model to study the interaction of ungulates and fire on forest dynamics in a small landscape in the Netherlands. They found that ungulates and fire together are necessary to maintain open habitats. The ForClim gap model (Bugmann, 1996) has been used to simulate the interaction of climate change and ungulate herbivory to project changes in European forests. Those studies generally showed that a reduction in ungulate browsing pressure is not sufficient to offset the effects of climate change on forest composition (Cailleret et al., 2014; Didion et al., 2011). Both models simulate ungulate impacts simplistically because they use past ungulate effects on forest vegetation to predict future ungulate effects.

To fill some of the knowledge gaps concerning FAM and ungulates, we ran a landscape-scale (many square kilometers studied over centuries) simulation model to assess the importance of climate, aggressiveness of FAM strategies, and ungulate density for the conservation of ecosystem functions (Manning et al., 2018). The model used simulated the response of an ungulate population to availability of tree forage and the dynamic modification of tree vegetation by ungulates through time. We added to Gustafson, Kern, et al.'s (2023) methods the treatment factor ungulate browsing to evaluate the impact of ungulate browsing on the effectiveness of alternative FAM strategies designed to conserve specific goods and services (sawtimber, fall foliage colors, wildlife mast, and maple syrup) in the face of alternative climate futures. We addressed the following questions: will the FAM species that are preferred by ungulates achieve sufficient landscape abundance to conserve the goods and services provided by the species they replace (Question 1); will ungulates cause species and age class richness declines despite FAM strategies (Question 2); and will ungulates accentuate the effects of climate change on ecosystem goods and services (Question 3)?

We used the LANDIS-II forest landscape model because it uses process-based algorithms that are robust to novel conditions, such as climate change, and are tractable at landscape scales. In a similar study (Gustafson, Kern, et al., 2023), the mechanistic PnET-Succession extension of LANDIS-II was used to simulate 3 FAM strategies (differing in the distance between seed source and outplanting site) under 3 climate futures without ungulates in a subboreal landscape in northern Wisconsin (USA). Those simulations included most of the chronic disturbance regimes that significantly affect these forests, but one that could not be modelled at that time has the potential to disrupt any stand regeneration method (natural or artificial), namely, browsing by the dominant ungulate.

White-tailed deer (*Odocoileus virginianus*) are the dominant ungulate browser of trees in northern Wisconsin (Rooney & Waller, 2002). Their impact on the regeneration of many tree species is well documented at the plot and stand scale (Alverson et al., 1988), but consequences at landscape scale are less well known (Royo et al., 2017; Spake et al., 2020). Furthermore, because winters are expected to become milder and the number of hunters in Wisconsin is expected to decline (Winkler & Warnke, 2013), increased ungulate densities are a reasonable experimental treatment. Recent developments now allow process-based landscape modeling of ungulate browse impacts on forests through the simulation of vegetation effects on the ungulate population and of ungulate effects on the vegetation. Such an ungulate browsing disturbance extension (module) was developed for the LANDIS-II model, but its application thus far has been primarily for deer in northwestern Pennsylvania (USA) and for moose on Isle Royale (Michigan, USA) in Lake Superior (De Jager et al., 2020; De Jager, Drohan, et al., 2017; De Jager, Rohweder, et al., 2017). This browse extension provides the opportunity to conduct virtual landscape experiments to answer questions about the effect of ungulates on FAM strategies that seek to conserve ecosystem goods and services in the face of imminent climate change. For the present study, we made the browse extension compatible with the PnET-Succession extension to investigate possible interactions among ungulate browsing, climate change, and FAM strategies to improve understanding of how ungulates might affect such conservation efforts.

METHODS

Study area

Our simulation experiment was conducted in the 104,471-ha Laurentian mixed forest ecosystem in northeastern Wisconsin (USA) used by Gustafson, Kern, et al. (2023) (Figure 1). Forest types in the study area are strongly shaped by glacial landforms that created a sharp soil moisture gradient from mesic (west) to xeric (east), with lakes and lowland forest interspersed throughout (Sturtevant et al., 2009). Mesic forests (90% of landscape) are dominated by northern hardwood tree species (e.g., sugar maple, American basswood, and yellow birch [scientific names in Appendix S1]), and xeric forests (10%) are dominated by pine and oak (i.e., jack pine, red pine, red oak, and pin oak). Boreal species (e.g., quaking and big tooth aspen, paper birch, and balsam fir) are common in uplands and lowlands and typically include waterlogging tolerant species, such as black ash, white cedar, tamarack, and black spruce. A considerable portion (33%) of the current landscape is dominated by tree species that are moderately or highly preferred by deer (Figure 1; Appendix S1). Under anticipated climate change, boreal species in this landscape are vulnerable to declines, whereas other forest types may persist or increase (Janowiak et al., 2014). So, a range of FAM options may be applicable, but FAM is currently experimental; FAM management guides have not been developed. We assumed that the entire landscape was under a single management regime, even though this landscape has a mix of ownership types and a range of FAM strategies were applied across the entire landscape (see "Experimental design").

Experimental design

A landscape-scale factorial simulation experiment was conducted using the study area conditions as of 2010. Experiment simulations were run for 300 years (2010–2309) to allow legacies and ecological inertia to be overcome by the treatment effects.

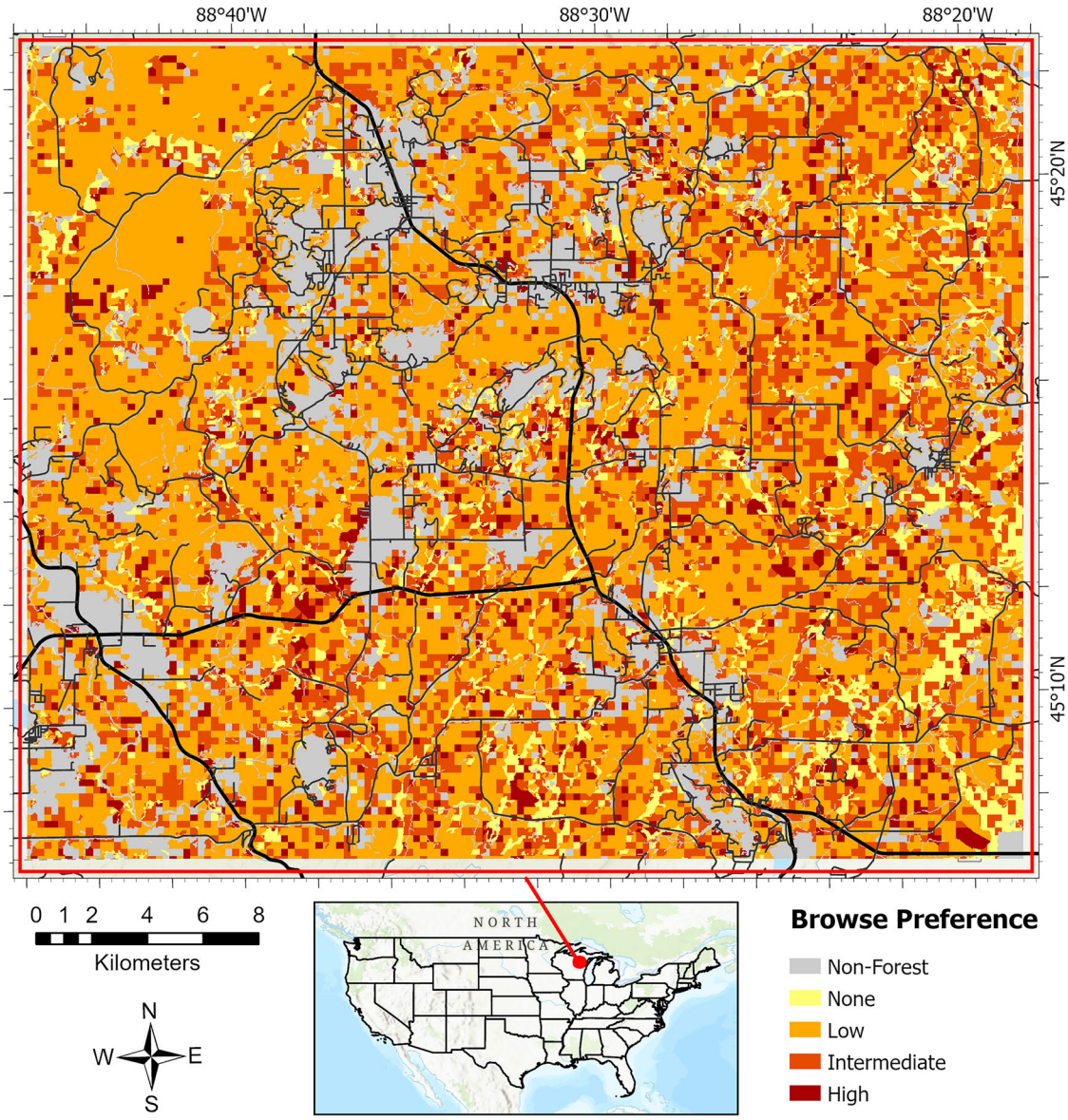

FIGURE 1 Study area (104,471 ha) in Oconto County, Wisconsin (USA) showing average deer browse preference for the tree cohorts in each cell at the start of simulations of forest dynamics (time = 0). Methods to estimate deer browse preference are in Appendix S14. Underlying soil types are in Gustafson, Kern, et al., 2023. Road data from https://data-wi-dnr.opendata.arcgis.com/datasets/.

We followed the experimental design of Gustafson, Kern, et al. (2023), which had 2 main factors (climate and assisted migration strategy), each with 3 treatment levels. That experiment included realistic natural disturbance regimes (wildfires, windstorms, and insect pests) that were simulated as background disturbances in all treatment combinations, but browsing by ungulates was not included. Because the existing LANDIS-II ungulate browsing extension (De Jager, Drohan, et al., 2017) did not have a compatible interface with the succession extension used in the prior study (PnET-Succession), we revised the ungulate browse extension interface to make it compatible. We ran the simulation experiment of Gustafson, Kern, et al. (2023) with an added third experimental factor with 3 levels: no deer, deer density at the current level of hunting pressure (current deer, ~7.72 deer/km^2), and higher deer density caused by a reduction in hunting pressure (future deer, ~8.55 deer/km^2) (Appendix S1). All deer population parameters (including hunting rate) functioned as constants throughout each simulation. We parameterized the future deer density factor level by arbitrarily reducing both hunting rate parameters (Appendix S2) by 50%. Deer densities may also rise in the future because of milder winters, but we did not model such causes, which meant reduced hunting pressure produced an arbitrarily higher deer density factor level. Model runs produced estimates of biomass removal via browsing at the 3 population levels, which were used specifically to quantify the impact of deer on the effectiveness of the FAM planting strategies.

The 3 climate factor levels were based on standard CO_2 Representative Concentration Pathways (IPCC, 2013): RCP 2.6 (little change in CO_2), RCP 6.0 (intermediate increase in CO_2), and RCP 8.5 (extreme increase in CO_2). The monthly climate projections for the climate treatments were generated by the General Fluid Dynamics Laboratory earth system model (GFDL-ESM2G, r1i1p1) (Dunne et al., 2012). To include increases in CO_2 beyond the year 2100, we used extrapolations of CO_2 to 2200 for each RCP scenario (Meinshausen et al., 2011), holding the final concentration constant until simulation end (2309). Climate (i.e., temperature and precipitation) projections provided by the GFDL Earth System Model have not been extrapolated beyond the year 2100, but temperature rise is expected to continue (Meehl et al., 2012). We extended the RCP 6.0 and 8.5 temperature projections by continually repeating the variability of the final 30 years (2071–2100) of projected temperatures but incrementing those values for an additional 100 years by using the trend of the first 100 years and a flat trend thereafter (details in Gustafson, Kern, et al. [2023]). Because precipitation had an insignificant trend under all climate scenarios, we did not extrapolate trends beyond year 2100 but repeated the last 30 years of the projected values.

The FAM strategy factor also had 3 levels, and each level increased the distance between the study area (outplanting site) and the source of the taxa that were planted. The aggressiveness of FAM strategies was considered proportional to the distance between the source and outplanting sites. Each of the 3 strategies was embedded in a set of standard silvicultural prescriptions designed for a climate-adaptive approach to forest transition with climate change (Appendix S3). That is, the harvest frequency, intensity, and extent varied by forest type in the same way across FAM strategies, and only the species planted differed by strategy. New cohorts were established by planting after every harvest event during the first rotation. Species planted (Appendix S4) were tailored to the forest type of the stand harvested and FAM strategy (Appendix S3). More cohorts of species targeted to more abundant forest types were ultimately planted than those targeted to less abundant forest types, following typical silvicultural practice. Methods that might be used to protect planted trees from browsers (e.g., repellents, barriers) were not simulated. The short-range migration strategy consisted of native species from south of (warmer than) the study area. These southerly provenances were generically parameterized to reflect the warmer climate south of the study landscape (approximately 40°N) by adding 1°C or 2°C to temperature-related parameter settings of the native provenances and leaving all other life-history and physiological parameters unchanged (Gustafson, Kern, et al., 2023). The medium-range migration strategy contained the FAM of nonendemic species whose native ranges are south of (and warmer than) the study area. The long-range migration strategy assisted the migration of species whose native ranges are even farther south of and much warmer than the study area. Long-range FAM species overlap with or occur farther south than species used in the medium-range migration strategy (details in Gustafson, Kern, et al. [2023]).

Model description

We used LANDIS-II version 7.0 (Scheller et al., 2007), a forest landscape model simulating forest succession based on the processes of forest development (seed dispersal, tree establishment, growth) and degeneration (disturbance, competition, senescence) through time. The LANDIS-II consists of a library of modules (extensions). Specific extensions can be activated to simulate specific ecological processes. In LANDIS, landscapes are represented as a grid of spatially interacting cells (typically 0.1–2.25 ha) on which species composition and vertical structure are assumed to be homogeneous, and these cells are spatially aggregated into biophysical units (ecoregions) with homogeneous soils and climate. In each cell, forest composition is represented as age cohorts of one or more tree species whose competition is a function of their vital attributes (e.g., growth capacity, shade tolerance, drought tolerance, longevity, seed dispersal, ability to sprout vegetatively) and conditions on the cell. This produces stochastic successional pathways driven by abiotic conditions, competition, and disturbance (Mladenoff, 2004). Independent disturbance extensions (including silvicultural activity) simulate processes that remove some or all of cohort biomass as a function of disturbance type and severity.

Our experiment was implemented using the PnET-Succession version 5.1 (Gustafson & Miranda, 2022; Gustafson, Sturtevant, et al., 2023) succession (growth and competition) extension of LANDIS-II because PnET-Succession has direct links between climate drivers (CO_2 concentration, temperature, and precipitation) and tree species cohort net primary productivity based on physiological first principles (Aber et al., 1995). The PnET-Succession also accounts for life-history traits that were necessary for our study (e.g., waterlogging tolerance, temperature tolerance). A mechanistic approach is critical when evaluating climate change effects because phenomenological modeling approaches use the past to predict the future, and future climate is expected to fall well outside the domain of the empirically studied past (Gustafson, 2013). Tree cohorts (and their propagules) compete for light and water in each grid cell, and their competitiveness is determined by how their life-history traits interact with the abiotic environment. This competition interacts with disturbances to determine successional trajectories. Additional details about PnET-Succession in the context of this study are in Gustafson, Kern, et al. (2023).

Modeling details

The input maps were gridded representations (cell width 30 m) of the study area. The abiotic environment was represented as biophysical units based on soil types in SSURGO (Soil Survey Staff, 2013) soil map polygons. These polygons simplify the abiotic environment to 6 major biophysical types. Climate was assumed to be homogeneous across the generally flat study area. Initial forest conditions (species and age classes) were based on maps produced by Janowiak et al. (2014) with the imputation methods of Wilson et al. (2012) to assign forest inventory

and analysis (FIA) plot attributes to each 250-m cell based on MODIS satellite imagery. These maps indicating presence of tree species in 10-year age cohorts were resampled to 30-m resolution to match other simulation input layers. Experiment simulations were run for 300 years (2010–2309) to allow initial conditions and ecological inertia to be overcome by the treatment effects. Variability among model runs at the landscape scale (resulting solely from establishment, growth, and disturbance stochasticity) was relatively low, so each experimental combination was replicated only 4 times ($n = 4$).

The PnET-Succession species parameters (e.g., Appendix S5) were calibrated (Gustafson, Kern, et al., 2023) to growth curves generated using the Lakes States variant of the FVS model (Dixon & Keyser, 2008), which uses local FIA (U.S. Forest Service Forest Inventory and Analysis) data to predict stand growth as a function of site conditions. The FAM strategies (and associated silvicultural practices) were simulated using the LANDIS-II biomass harvest extension version 4.7 (Gustafson et al., 2000) with the parameters in Gustafson, Kern, et al. (2023). An assumption on which LANDIS-II is based is that each cohort (including those established by planting) represents a uniform distribution of stems across the cell, although only mean cohort biomass density is tracked (Gustafson, Sturtevant, et al., 2023).

To conduct the experiment in the context of realistic natural disturbance regimes, we included wildfires, windstorms, and insect pests as background disturbances in all treatment combinations. Wildfire was simulated using Base Fire version 4.0 (Scheller & Domingo, 2017) calibrated against records of wildfires in the region as described in Gustafson et al. (2020). Ignition rates increased proportionally for the 2 most severe climate change scenarios. Cohort damage caused by microburst wind events was simulated using Base Wind version 3.1 (Scheller & Domingo, 2011) parameterized with data in Rich et al. (2007). Tornadoes and derechos were simulated using Linear Wind version 2.0 (Gustafson, Miranda, et al., 2018) calibrated to data in Hjelmfelt (2007) for the upper Great Lakes region and adjusted for climate change based on findings of Emanuel (2005) and Knutson et al. (2010), as described in Gustafson et al. (2020). The major insect pests of the study area include defoliators and borers. Defoliators (forest tent caterpillar [*Malacosoma americanum*], spongy moth [*Lymantria dispar*]) were simulated using Biomass Insects version 3.0 (Foster, 2011) and calibrated for the study area by Lucash et al. (2018). Emerald ash borer (EAB) (*Agrilus planipennis*) was simulated using the base biological disturbance agent extension version 4.1.0 (Sturtevant et al., 2019). We assumed that EAB would move into the area as anticipated, rapidly depleting the living biomass of all ash species, including black ash, which dominates many of the lowland forests of the study area (Gustafson et al., 2025). We followed the EAB methods of Gustafson, Sturtevant, et al. (2018) but decreased the likelihood of disturbance from 1.0 to 0.5, applied every 10 years, to simulate mortality of all ash cohorts as an exponential decline that reduced ash occupancy to about 15% of its initial abundance by 20 years, with complete extirpation by 100 years. Harvest (and replanting) of wetland hardwood stands (currently dominated by black ash) was accelerated (doubled) in the first 20 years to increase the conversion of such stands to FAM non-ash types before EAB killed the ash in an attempt to keep water levels in check so that other tree species could survive.

Deer browsing impacts on temperate forests in North America are widely believed to have direct consequences for short- and long-term forest dynamics, so we simulated such impacts with the Biomass Browse version 2.1 extension (De Jager, Drohan, et al., 2017). For a complete description of how browsing is implemented in the Landis-II framework, including detailed explanation of parameter estimates, see De Jager, Drohan, et al. (2017). Appendix S1 provides values for parameter estimates we used in this study. The browse extension was run with an annual time step. First, the extension uses a set of parameter estimates that determine the fraction of total cohort biomass available to foraging ungulates for each cohort (forage availability). Next, the extension removes a fraction of available forage depending on browser population size (user defined at time Step 1 and then fluctuating annually) and the preference of the population for different tree species. Preference values (0–1) are user-defined fractions of available forage biomass expected to be removed by the ungulate population and do not change over time in the extension. The extension implements the impacts of forage removal on the growth and survival of tree cohorts in the next time step, again with user-defined parameters that define the sensitivity of species to lost tissue. Such reductions in cohort growth or survival influence successional dynamics in the LANDIS-II framework like other disturbances, with consequences for the amount of available forage in subsequent time steps and subsequent herbivore population densities.

We generated deer population parameters (e.g., Appendix S1) with the best available data, including deer population and reproductive estimates for the region and estimates of hunter, predator, and traffic-related mortality (details in Appendix S14). In the model, mortality prevents the deer population from reaching the maximum possible density, a density that is determined by the total forage availability across the entire landscape and the annual forage requirements of the deer population (De Jager, Rohweder, et al., 2017). The estimated deer reproductive and mortality rates for the region (Appendix S1) created a population that was approximately 40% of the maximum possible population as determined by the forage availability in our landscape (not shown). Therefore, the population is estimated to remove approximately 40% of the total forage available across the landscape in any given time step (year). Stochasticity in population parameters creates minor variability from 1 year to another. When we simulated a 50% reduction in hunting pressure, the population rose to about 50% of the maximum population density. Thus, simulated deer populations were removing approximately 40% of total available forage across the entire landscape under the current deer scenario and 50% under the future deer scenario.

These landscape-level deer dynamics determine the total biomass removed from the landscape, but cell-level forage selection (cohorts actually removed) can vary greatly from site to site depending on the local deer population and the relative preference of deer for all the species present on the cell. At each

time step, the deer population is spatially distributed (among cells) as a function of the quality and quantity of the forage available in each cell and creates local variation in deer density and related impacts to the plant community. Forage quantity in each cell is determined by the presence of forage species with deer preference value >0 when below a maximum age threshold that defines susceptible cohorts. Forage quality is determined by the species preference values (Appendix S1). Forage biomass is removed (in the extension) sequentially (by tree species) in each cell, starting with the most highly selected species. A fraction of that species' available forage is removed up to the maximum fraction defined by the preference parameters in Appendix S1. If more forage biomass is required to meet the demand by the deer associated with the cell, biomass is removed from the next most preferred species, and so on. If the local population forage requirements are still not met after forage is removed from all preferred species, 100% of available forage is removed successively from the most highly preferred species to the least (excluding species with a preference value of 0) until the requirement is met. Because of the way the ungulate population is distributed, the local population cannot exceed total forage biomass at a site; therefore, no more than 100% of forage biomass can be removed from a site. In this way, significant local variation in forage biomass removal occurs at each time step, and yet the total forage biomass removed equals that required by the landscape-wide deer population.

Finally, the impacts of forage biomass removal on cohort growth and survival are simulated according to the fraction of available biomass removed. Growth and survival impacts are implemented once a threshold fraction of available forage biomass is removed from cohorts and increases linearly as the fraction of available forage biomass increases up to a user-defined maximum impact (Appendix S1).

Analyses

We evaluated the ecosystem goods and services studied by Gustafson, Kern, et al. (2023) to see if the presence of ungulate browsing changed the outcomes without ungulates. We compared the response variables simulated with deer browse (with 2 levels of hunting mortality) with those simulated without deer browse (population = 0). The effects of the silvicultural treatments on selected ecosystem goods and services were evaluated by quantifying (and comparing) the areal extent of specific combinations of species providing specific ecosystem goods and services (Appendix S6). In addition to the ecological goods provided by timber harvest, we evaluated the abundance of tree species used for maple syrup production (Appendix S6). Similarly, ecosystem services were quantified by the area of the landscape occupied by species providing non-extractive forest benefits for wildlife and aesthetics, namely, mast or other food type and fall foliage colors (Appendix S6). We assumed that if functional forest type extent was maintained during the simulation of experimental treatments, then the associated ecosystem goods and services would also be conserved.

We relied primarily on visual comparison of temporal trends in outcomes across experimental factors rather than on significance tests as advocated for modeling experiments by White et al. (2014). However, a Bayesian factor analysis (Morey & Rouder, 2024) was conducted using R (package anovaBF) (R Core Team, 2023) to assess the importance of each treatment factor on selected response variables at year 300.

RESULTS

Deer dynamics

The browse extension appropriately simulated reciprocal dynamics between the deer population and tree forage. The ratio of forage consumed:forage available varied little by climate and FAM treatments, and the future deer scenario always produced a (barely) significantly higher ratio than the current deer scenario (not shown), indicating that the population consumed a consistent fraction (about half) of the available forage regardless of the treatment factors. Without deer on the landscape, total forage initially increased slightly but then declined to a lower equilibrium (not shown), indicating that factors other than deer also reduce available forage (e.g., maturation, succession). Deer also generally increased the area of non-preferred species (none, generally conifers) at the expense of low-preference species (Figure 2). The high abundance of highly preferred species with the medium-range FAM strategy reflects both the preference values of those species and the ability of highly preferred species to thrive under all climates. Severe climate change appeared more likely to produce more open (no cohorts) sites, and deer exacerbate this trend.

Vegetation response

Simulated deer browsing of approximately 40% of available forage biomass (current deer) increased the area of the landscape occupied by unpreferred (low and none) species and decreased the area occupied by preferred species, especially when climate changes were less than severe (RCP 2.6 and RCP 6) and with no harvest and short-range FAM (Figure 2). Whatever effect deer had on the abundance of deer-preference classes under little or intermediate climate change, it was exacerbated by severe climate change, with some variation associated with planting strategy. Reducing hunting pressure (future deer) increased deer browsing from 40% to 50% of available forage biomass (not shown) but produced minor effects on ecosystem goods and services compared with the current deer scenario (see below). To enhance the clarity of the presentation of results, we omitted future deer density results from most graphs and tables because those outcomes were generally close to current deer results, as reduced hunting of deer did little to increase deer density.

Biomass accumulation varied by both growth rate of the species and its tolerance (and its competitors' tolerance) to the climate (Appendices S8 and S9). Similar to Gustafson, Kern,

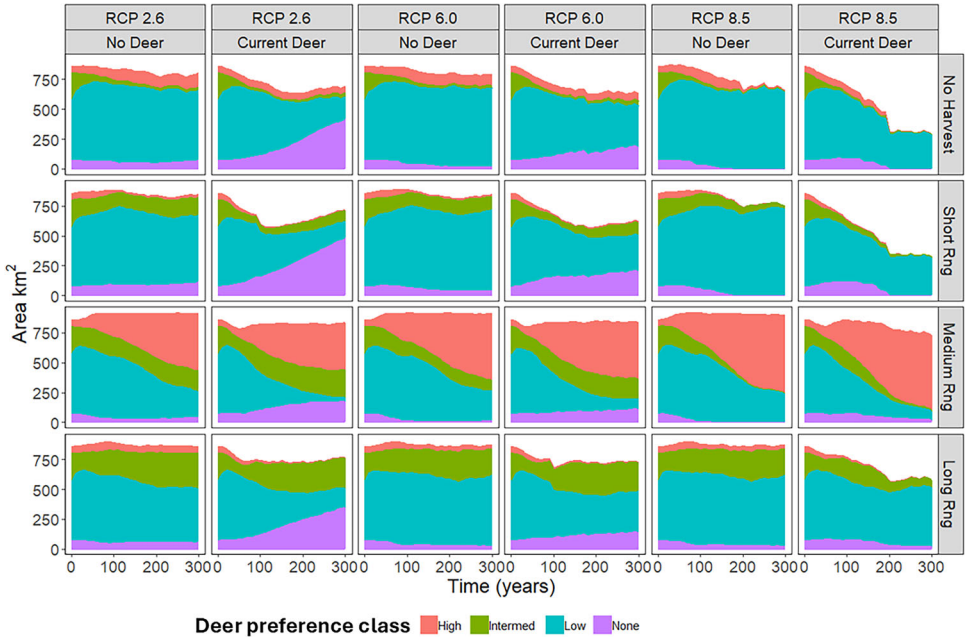

FIGURE 2 Area dominated by tree species (by deer preference class) through time relative to 6 climate and forest assisted migration strategies (see "Experimental design" section). The current deer factor level refers to ungulate population density resulting from current hunting levels.

et al. (2023), no native species thrived under severe climate change (RCP8.5), although some maintained a presence, and only red maple, elm, and white cedar thrived under intermediate climate change (RCP6.0). A species' response to deer was mostly related to its deer preference value (by definition) but was also sometimes dependent on the preference value of the species' competitors (in each grid cell). Some species (e.g., black spruce, tamarack) did markedly better in the presence of deer (Appendix S8), presumably because one or more potential competitors were limited by deer. In medium-range FAM, many native species that are preferred by deer were replaced by FAM species under moderate to severe climate change (Figure 3). There was a steady decline throughout the simulation for the first 200 years and then a drop when the climate was intolerable for the northern hardwoods.

Deer browsing decreased species and age-class richness under all scenarios (Figure 4); deer had the greatest impact under the RCP2.6 climate (all FAM strategies) and the medium range FAM strategy (all climates). The future deer scenario produced almost no difference from the current deer scenario in species or age-class richness. Deer browsing interacted with climate to cause forest composition to shift dramatically, resulting in a large decline of current forest types in all scenarios (Figure 5).

Effect of deer on ecosystem goods and services

Deer browsing resulted in more landscape cells having no cohorts (temporarily open) under all climate and FAM strategy combinations (Figure 5) and altered the number of cells providing specific ecosystem goods and services (Appendix S7). Deer increased the abundance of pulpwood species at the expense of sawtimber species (Appendix S10). Deer generally reduced the abundance of species with brilliant fall colors and increased the abundance of species with no fall colors (Appendix S11). Climate change had a greater negative effect on the abundance of maple syrup trees than did deer, but both had substantial effects (Appendix S12). The effect of deer on mast species depended on the FAM species planted, and deer were particularly detrimental to the hard mast species under medium-range FAM strategy (Appendix S13).

Factor analysis

The factor analysis showed that FAM strategy factors produced the greatest individual (not interaction) effect on most of the response variables tested (Table 1). The climate effect strength increased through time (not shown). The deer factor had a very strong effect on most response variables, driven primarily by the difference between the no deer level and the current and future deer (not shown) density levels. The interaction between deer and every other factor was also extremely strong. Specifically related to whether ungulates cause species and age class richness to decline despite FAM, both richness response variables were most significantly affected negatively by the deer factor. The biomass of FAM species was affected more by management strategy than deer, likely because the productivity of the species planted varied more than their temperature tolerance or deer preference. Surprisingly, the biomass of native species (considered threatened by climate change) was least affected by climate, perhaps because biomass cannot be reduced to a value lower than zero. Climate tended to have the least effect, but it

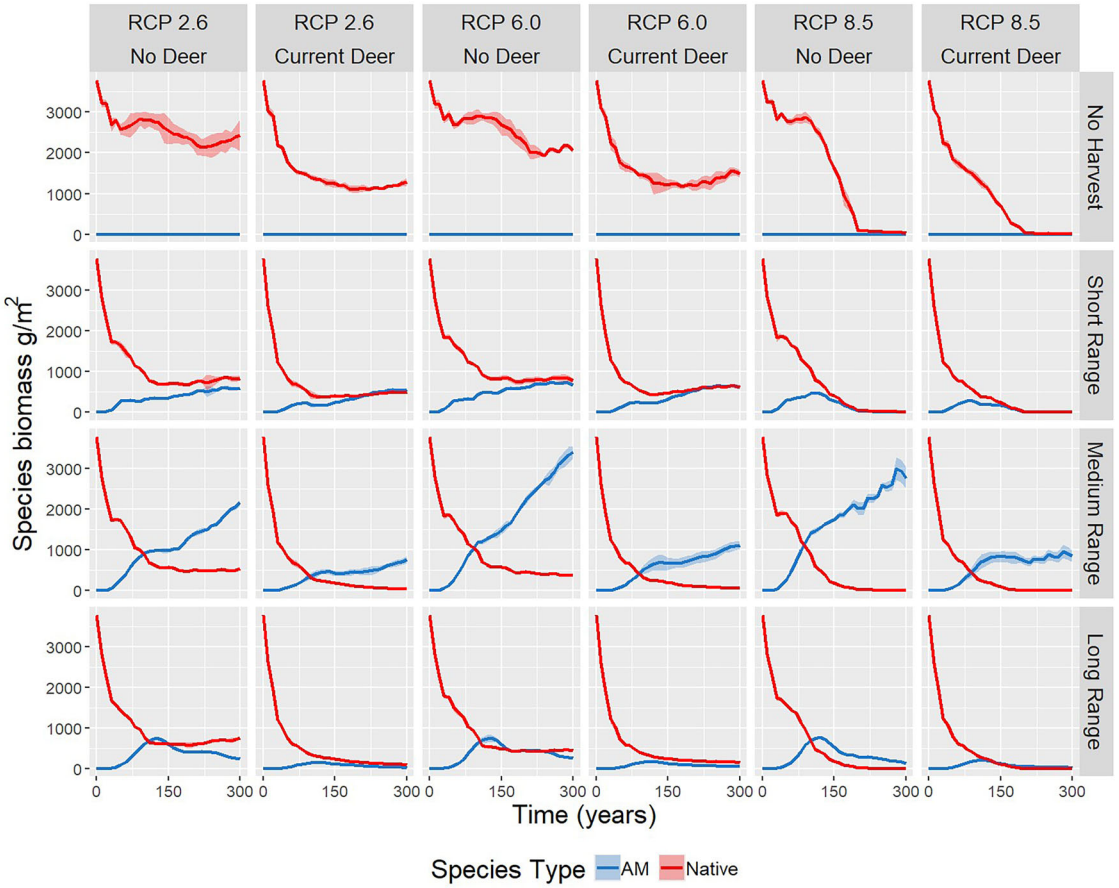

FIGURE 3 Across 0.1-ha cells in Oconto County, Wisconsin, mean total tree biomass of only cohorts highly preferred by deer (Appendix S1) by climate and forest assisted migration strategy (shading, 95% confidence intervals, which are generally less than the width of the lines; strategies and ungulate population density defined in Figure 2's legend).

nevertheless was always highly significant. For all response variables, there was very strong evidence for an interaction between deer and the other 2 factors.

DISCUSSION

The ability of natural forests to sustain the ecosystem goods and services currently provided is thought to be at risk because of climate change. The amount of risk is uncertain because of inherent uncertainty in climate projections (Qian et al., 2016) and because of empirical uncertainty in how climate change will directly affect tree growth, competition, and mortality and indirectly affect forest dynamics by modifying the disturbance regimes that drive forest succession (Gustafson, 2013; Nagel et al., 2017). Forest managers are compelled to implement forest stand management actions today with the goal of ensuring forest landscape sustainability in a different (and distant) tomorrow. Yet, the considerable uncertainty about the effectiveness of past practices in the face of changing conditions combined with the many unknowns about the effectiveness of proposed climate-smart forestry practices puts forest managers in a difficult position. We aimed to reduce some of the uncertainty surrounding the interaction of assisted migration climate-smart strategies and natural disturbances, particularly browsing by ungulates. Our results showed that although white-tailed deer caused a marked decline in many ecosystem goods and services, they did not fully eliminate them. The results of this study compared with Gustafson, Kern, et al. (2023) highlight the importance of including browse selection in simulation studies. Some FAM species were helped by deer (via control of its competitors), but most were harmed. Thus, measures to manage the impact of ungulates (both negative and positive) on the effectiveness of FAM tactics appear prudent.

The effects of deer varied by tree species, and although perhaps not catastrophic for these ecosystems, they were nonetheless a significant degrading factor. Current deer densities resulted in clearly worse outcomes than no deer for most ecosystem attributes, but future deer densities were only slightly more degrading than current deer densities. Climate change may be a greater threat to these ecosystems than deer, although climate change (and FAM) was favorable to deer in our simulations by introducing some species that are preferred by deer. Question 1 was whether FAM species preferred by deer (silver maple, Atlantic cedar, yellow poplar, black tupelo, southerly big-tooth aspen provenances, scarlet oak, black willow) would achieve suf-

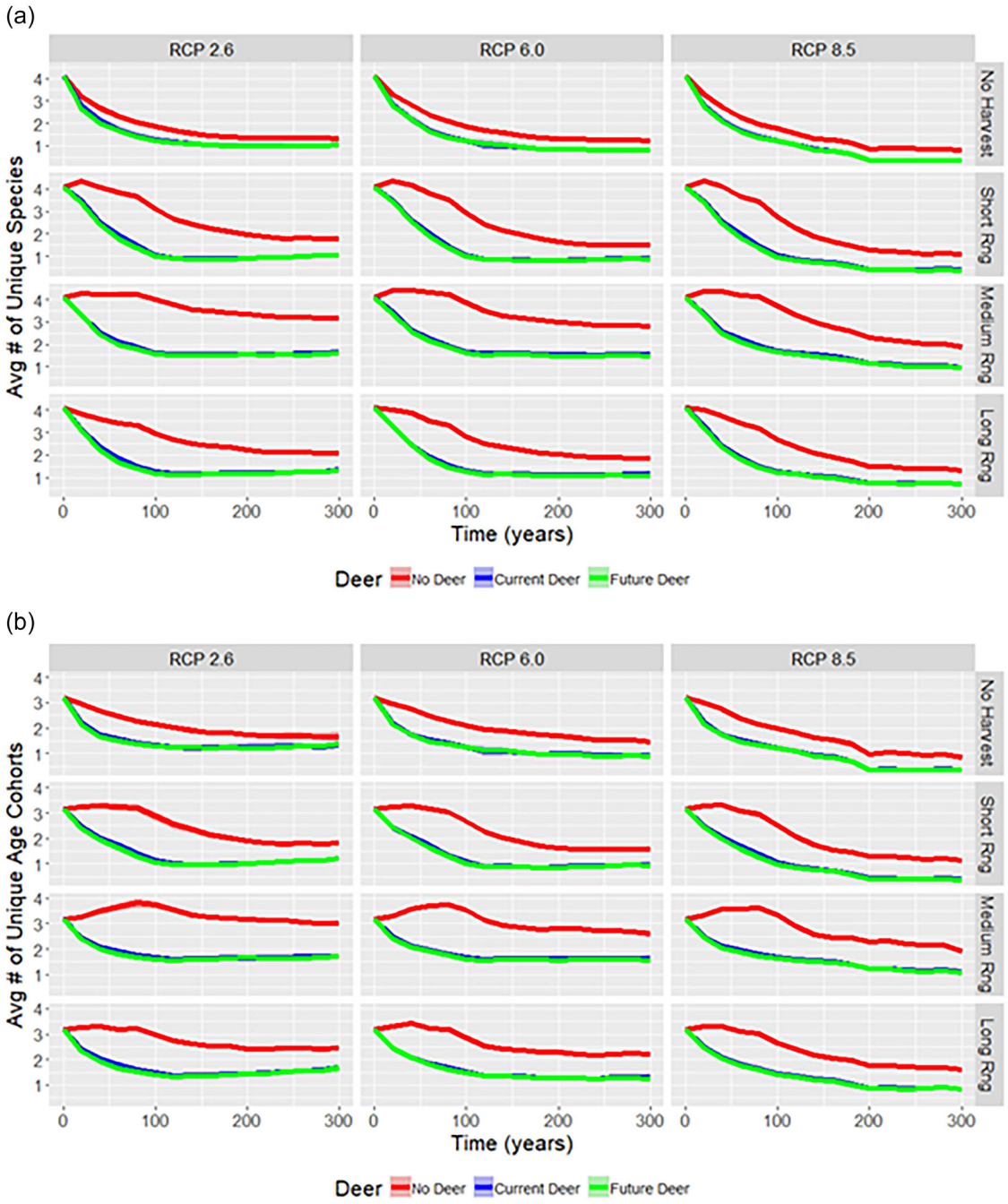

FIGURE 4 Mean number per cell of (a) tree species and (b) 10-year age-class tree species richness in Oconto County, Wisconsin, through time under 3 climate scenarios and 4 forest assisted migration (FAM) strategies (shading, 95% confidence intervals, which are generally less than the width of the lines; strategies defined in Figure 2's legend).

ficient landscape abundance under climate change to conserve their associated goods and services, and these species did.

Preferred browse species gained a presence, but their abundance did not always reach that of the native species they were meant to replace. For example, whereas big-tooth aspens-S (species notation used in Appendix S1) appeared to conserve aspens in the short-range FAM strategy, yellow poplar was unable to replace the native aspens in the long-range FAM strategy (Figure 5). Question 2 was whether deer will cause richness to decline by differentially reducing preferred species and age classes, and such a decline was apparent, although we could not identify the mechanism that caused this.

Question 3 was whether deer will accentuate climate change effects on ecosystem goods and services, and this association was also found. Forest's capacity to produce timber, mast for wildlife, fall color, and maple syrup had an increasingly negative impact on ecosystem functions with deer and under increasingly higher emissions scenarios, although not with a uni-

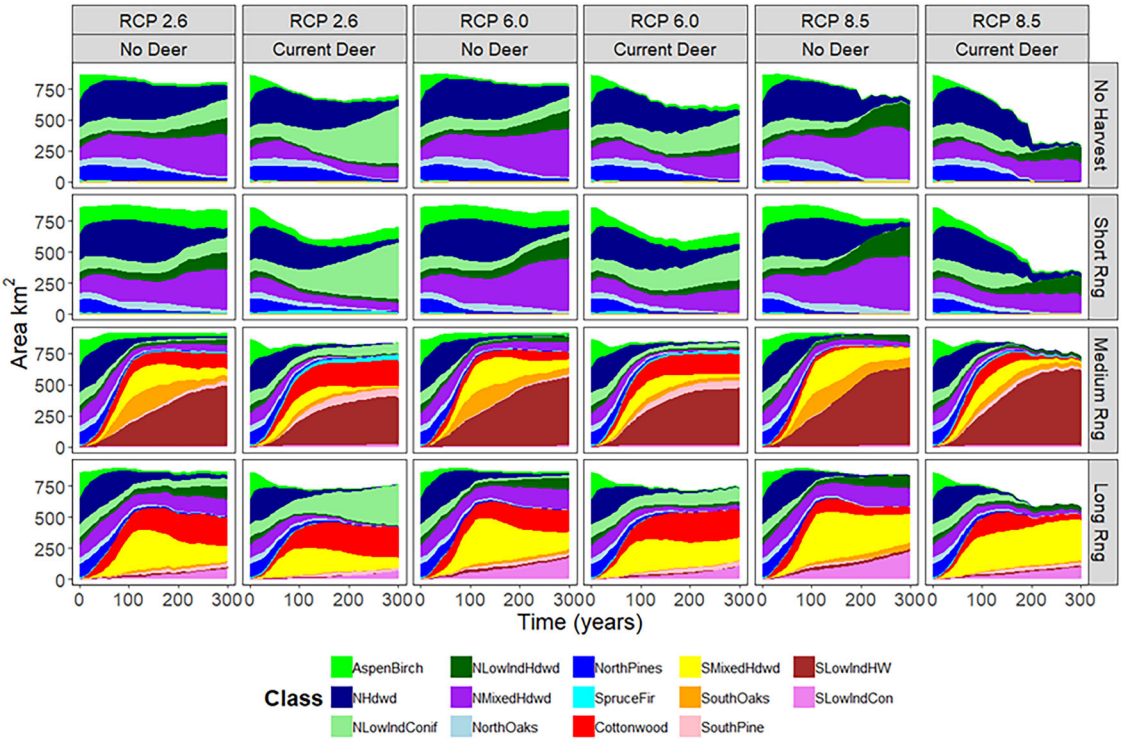

FIGURE 5 Area of each forest type by climate scenario with or without (current) simulated deer browsing (whitespace, sites with no tree cohorts; NHdwd, northern hardwood; NLowLndConif, northern lowland conifers; NLowlnHdwd, northern lowland hardwoods; NMixedHded, northern mixed hardwoods; NorthOaks, northern oaks; NorthPines, northern pines; SMixedHdwd, southern mixed hardwoods; SouthOaks, southern oaks; SouthPine, southern pines; SLowlndHW, southern lowland hardwoods; SLowlndCon, southern lowland conifers; strategies and ungulate population density defined in Figure 2's legend).

form response to the treatments for colors and syrup. Level of deer impacts (Question 3) were less clear because future deer densities did not produce clearly worse outcomes than current deer densities for most measures of ecosystem goods and services through time (not shown). However, current deer densities resulted in clearly worse outcomes than no deer for some ecosystem attributes (Appendices S10–S13). Current deer densities reflected a deer population that sustained relatively high hunting rates, and the no-deer scenario was a theoretical minimum simulated for comparison purposes. Future deer densities generally reflected the fact that despite the presence of chronic wasting disease in the state since 2002 and high harvest rates (>300,000 deer/year), the statewide deer population has continued to increase (https://widnr.widen.net/s/dkh5cwc8gv/deerpopulation2022).

Our results suggest that FAM can at least partially conserve ecosystem goods and services under multiple climate change scenarios, even with ungulate browsing. They also suggest that without FAM, the conservation of the modeled ecosystem goods and services may be impossible under expected climate futures. The FAM strategies had a large effect on most response variables, and the interaction of FAM strategies and climate was generally high. However, deer clearly had a negative effect on the abundance of forest vegetation (Figure 5) and reduced the potential production of commodities, degrading the efficacy of FAM for meeting such conservation objectives. Deer are widely considered a keystone herbivore (i.e., if removed, the ecosystem would change dramatically) in this region (Waller & Alverson, 1997). Our simulated deer had a clear impact on forest composition over time, although this may also reflect a continuous trend of increasing deer density that may have already produced legacy effects. The combined effects of climate change and sustained deer browsing appear to be a threat to the sustainability of ecosystem goods and services in sub-boreal forests in the upper Great Lakes region. Our results also produced general insights that may be applicable to other forest–ungulate landscape dynamics in other ecosystems.

Caveats

We simulated 300 years into the future even though there is considerable uncertainty about many of the inputs beyond even 50 years. We did this because of the ecological inertia of forests resulting from the longevity of trees. Trees rarely die directly from climate stress, but establishment and competition of young cohorts is the process that will determine future forest composition. Fewer than 100 years is simply too little time to evaluate the effects of the treatments given this inertia. The model as configured here explicitly simulates climate and disturbance effects, with succession being an emergent property. Thus, the model produces projections of expected future ecosystem states given the inputs but does not predict a future state.

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TABLE 1 Results of factorial analysis of variance computed using Bayesian methods to estimate relative experimental factor effects while accounting for the effects of other experimental factors in a study of forest assisted migration (FAM).[a]

Response variable	Forest assisted migration (FAM) strategy	Climate	Deer density	FAM strategy × deer	Climate × deer density
Total biomass (%)	$1.97 \pm 0.00\%$	$1.123406 \times 10^{10} \pm 0.00\%$[b]	$8.240124 \times 10^{6} \pm 0.00\%$[b]	$1.779329 \times 10^{7} \pm 2.53\%$[b]	$3.447441 \times 10^{26} \pm 3.43\%$[b]
Biomass of native spp.	$1.138877 \times 10^{11} \pm 0.00\%$[b]	$2.828300 \times 10^{2} \pm 0.01\%$[b]	$7.569200 \times 10^{2} \pm 0.00\%$[b]	$8.294582 \times 10^{17} \pm 1.32\%$[b]	$2.876402 \times 10^{5} \pm 1.45\%$[b]
Biomass of FAM spp.	$4.67203 \times 10^{35} \pm 0.00\%$[b]	$0.85 \pm 0.01\%$	$0.44 \pm 0.02\%$	$1.498108 \times 10^{37} \pm 3.24\%$[b]	$1.092696 \times 10^{46} \pm 1.67\%$[b]
Species richness	$9.060488 \times 10^{6} \pm 0.00\%$[b]	$3.53374 \times 10^{3} \pm 0.01\%$[b]	$2.630168 \times 10^{6} \pm 0.00\%$[b]	$7.984241 \times 10^{20} \pm 2.14\%$[b]	$6.836663 \times 10^{11} \pm 2.05\%$[b]
Age richness	$3.51100 \times 10^{5} \pm 0.00\%$[b]	$1.33028 \times 10^{5} \pm 0.01\%$	$4.123967 \times 10^{14} \pm 0.71\%$[b]	$7.349187 \times 10^{17} \pm 1.22\%$[b]	$2.508615 \times 10^{13} \pm 0.98\%$[b]

[a]Only the last simulated year (300) is included in the analysis (of 4 replicates). Table values are Bayes factor effect strength with proportional error given.
[b]Very strong effect of the factor. Thresholds for factor effect strength: 1–3, negligible evidence; 3–20, positive evidence; 20–150, strong evidence; >150, very strong evidence (Morey & Rouder, 2024).

For some tree species, we were forced to make assumptions about preferences by white-tailed deer because empirical data were not available. Such assumptions involved a decision about which known species was most similar to the unknown species in terms of palatability to deer.

In areas of elevated ungulate populations, managers can take strategic actions, over time and space, to minimize browse impacts across a landscape. For example, managers may use temporary fencing (Bergquist et al., 2009), impediments (e.g., slash piles) (Loosen et al., 2021; van Ginkel et al., 2021), or other targeted efforts (e.g., repellents) (Redick & Jacobs, 2020) where regeneration goals focus on browse-sensitive species and during periods when trees are at browse-accessible size (i.e., seedling and sapling phases). Our simulations did not account for potential strategies, such as these, to protect FAM plantings from deer, so the results should be interpreted as worst-case scenarios.

Our results do not reflect uncertainty in climate projections or initial conditions (i.e., inputs were the same [except for random number seed] for each replicate). The error estimated in our results reflects the uncertainty associated with stochasticity in the model, namely, establishment, growth, competition (of tree cohorts), and disturbances (events and their location and intensity).

Our model also does not include non-tree vegetation and supplemental food sources (e.g., agriculture, backyard feeding) or non-tree deer forage (e.g., shrubs and herbs). Such food sources could increase deer density, reduce demand for tree forage, or some combination. In a study of adjacent crop fields and forests, the type of crop planted in the field influenced the browse pressure on saplings in the nearby forest (Widén et al., 2024). Because we did not model effects of forage species that are not trees, our simulations could be considered a worst-case scenario of only tree-based forage available to browsers.

It is also possible that climate change could lead to changes in deer range and deer behavior in different seasons. For example, as winters become milder, there may be less impetus for deer to migrate to areas that offer protection from hash winter conditions, resulting in a more dispersed presence of deer across the landscape in the winter, when they are most likely to forage on trees. Our model does not simulate deer range shifts or movement to thermal cover.

Management implications

Our findings emphasize the significant interaction that ungulate browsing can have with forest management practices (Table 1). Although climate-smart practices focus on managing for more resistant or resilient forests, the outcome of silvicultural actions can be greatly affected by ungulate browsing. Understanding the cumulative effects of ungulate browsing on FAM and other climate-smart forestry practices is imperative for making informed decisions about how to position forests for the best outcomes in the future. Of the climate adaptation strategies, FAM offers considerably more opportunity to affect future species composition through the selection of species and stock for planting. This offers an opportunity for selecting species that

are also adapted to browse pressure (Champagne, Royo, et al., 2021). In this study, the tree species for FAM plantings were not selected with browser preference as a selection criterion. However, our findings suggest that perhaps the impact of ungulates could be somewhat mitigated by making browser preference a selection criterion. Additional mitigation measures at multiple scales would likely be important, considering the complex factors that determine ungulate habitat and behavior (e.g., forage, cover, predators, roads, crops, and gardens, among others, interacting over space and time) (Beguin et al., 2016; Redick & Jacobs, 2020; Tremblay et al., 2007). Although our results suggest that climate effects may be greater than ungulate effects (on trees) on this landscape, deer nonetheless represent a significant negative force that perhaps could be mitigated by forest or deer management. We did not explore all the management options, but we did quantify some consequences of a subset of options and of the developing trend toward fewer hunters. An important take-home message from our study is that ungulate browsing can affect the overall success of FAM (or the magnitude of its impacts), suggesting that managers can (and should) take that into account. It appears that under a high-emissions climate future, a thoughtful FAM approach is probably necessary.

We conclude that ungulates have a negative effect on the ability of FAM to conserve ecosystem goods and services; ungulates do not appear to significantly alter functional type composition and abundance in our study area, although they do have a substantial effect, especially for highly preferred tree species; and additional study is needed to determine whether selecting FAM species with low preference by ungulates might significantly mitigate the negative effects of chronically high ungulate populations. Our results also suggest that methods to mitigate browsing damage may be required in the future to sustain forest ecosystem function in locations where ungulate densities are very high.

AUTHOR CONTRIBUTIONS

Eric J. Gustafson: Conceptualization; methodology; software; writing—original draft. **Nathan R. DeJager**: Methodology; writing—review and editing. **Amanda M. McGraw**: Methodology; writing—review and editing. **Christel C. Kern**: Conceptualization; methodology; writing—review and editing. **John M. Kabrick**: Conceptualization; methodology; writing—review and editing.

ACKNOWLEDGMENTS

We thank B. Miranda for coding changes to the browse extension and J. Suvada and J. Fowler for technical assistance with analyses. We also thank C. Wilson, A. Royo, M. Lucash, and 3 anonymous reviewers for critiques that helped us improve the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gustafson, E. J., DeJager, N. R., McGraw, A. M., Kern, C. C., & Kabrick, J. M. (2025). Effects of ungulate browsing on forest assisted migration strategies to conserve ecosystem function. *Conservation Biology*, e70198. https://doi.org/10.1111/cobi.70198