Trading off nature for nature-based solutions: The bioeconomics of forest management for wildlife, timber, and carbon

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Abstract
Nature-based solutions are attracting interest for their potential to enlist ecological processes as cost-effective and safe ways to capture and store carbon in forest ecosystems. Such solutions often need to be implemented in landscapes in which there are longer established values for other ecosystem services including wildlife and timber production. Here we develop an integrative model that illustrates the inherent trade-offs that will arise among the competing values for landscape space and how to resolve them. The analysis characterizes boreal forest ecosystem dynamics involving interactions among the main trophic compartments of an intact boreal ecosystem, aka “nature.” The model accounts for carbon accumulation via biomass growth of forest trees (timber), carbon loss due to controls from moose herbivory that varies with moose population density (hunting), and soil carbon inputs and release, which together determine the carbon sink strength of the ecosystem. We link the ecological dynamics with an economic analysis by assigning a price to carbon stored within the intact boreal forest ecosystem. We then weigh these carbon impacts against the economic benefits of timber production and hunting across a range of moose population densities. Combined, this carbon-bioeconomic program calculates the total ecosystem benefit of a modeled boreal forest system, providing a framework for examining how different forest harvest and moose densities influence the achievement of carbon storage targets, under different levels of carbon pricing. The analysis shows that promoting nature-based solutions merely for carbon storage may result in loss of a key part of “nature” via loss of the trophic structure and key functional controls in the ecosystem.

KEYWORDS
bioeconomic modeling, ecosystem dynamics, financing carbon capture, wildlife control over ecosystem functioning
INTRODUCTION

Nature-based solutions are attracting interest for their potential to enlist ecological processes as cost-effective and safe ways to mitigate and adapt to climate change, with the co-benefit that they could help to reverse biodiversity loss and protect ecosystems, along with their functions and services (Girardin et al., 2021; Miles et al., 2021; Mori, 2020; Osaka et al., 2021; Pörtnér et al., 2023; Seddon et al., 2021; Smith et al., 2022). This is considered a win–win for protecting biodiversity and the climate. Indeed, the UN Convention on Biological Diversity Post-2020 Global Diversity Framework (CBD/WG2020/3/3, 2022) and the IPCC Sixth Assessment (IPCC, 2022) actively promote nature-based solutions as being vital to reduce the risk of exceeding 2°C while sustaining both nature and human livelihoods.

Nature-based solutions are now attracting attention as financial investment opportunities in the form of carbon offsets to enhance atmospheric CO₂ uptake and storage in ecosystems (Busch et al., 2019; Chami et al., 2022; Girardin et al., 2021; Kooijman et al., 2021; Seddon et al., 2021). Carbon offset payments are further seen as ways to incentivize the protection of nature (i.e., species, ecosystems, and ecosystem services) as part of a broader effort to create a sustainable nature-based economy. Forest ecosystems, especially, are considered to have high potential for investment due to their capacity to capture and store large amounts of atmospheric CO₂ in plant biomass and in soils (Bastin et al., 2019; Busch et al., 2019; Fargione et al., 2018; Griscom et al., 2017; Houghton & Nassikas, 2018; McCarney et al., 2008; Salvatori & Pallante, 2021). Such investments are viewed as potentially having ancillary benefits for conservation by protecting habitat for a diversity of wildlife species (Buote et al., 2020; Littlefield & D’Amato, 2022; McCarney et al., 2008; Rittenhouse & Rissman, 2012).

However, treating wildlife conservation merely as an ancillary benefit overlooks the functional role of wildlife species in controlling forest ecosystem processes (Brodie & McIntyre, 2019; Kielland & Bryant, 1998; Osuri et al., 2016; Pastor et al., 1998; Peres et al., 2016; Ramírez et al., 2021; Seagle, 2003; Sobral et al., 2017), including controlling the amount of carbon that is captured and stored (Berzaghi et al., 2019; Brodie & Gibbs, 2005; Osuri et al., 2016; Peres et al., 2016; Sobral et al., 2017; Wilmers & Schmitz, 2016). Hence, not accounting for these functional roles could lead to nature-based solutions failing to meet their carbon storage targets (Schmitz et al., 2023; Schmitz & Leroux, 2020), let alone overlooking the considerable economic value that comes from their functional controls over carbon capture and storage (Bello et al., 2021; Berzaghi et al., 2022; Brodie, 2018; Macias-Fauria et al., 2020).

We introduce here an approach for undertaking bioeconomic analyses of dynamic “nature” in support of nature-based carbon offsets. By dynamic nature, we mean both the species composition and functional interactions among species within and between trophic compartments of ecosystems that control ecosystem processes including carbon cycling. We illustrate our approach using boreal forests of the northern hemisphere as a case example. Boreal forests represent the largest forest biome globally and, after tropical forests, perhaps hold the largest global carbon stores (Gauthier et al., 2015).

A dynamic boreal ecosystem can be minimally described as interactions among several key trophic compartments—soils, primary producers (trees), browsers of trees (moose), and predators of moose (wolves and humans) (Yona et al., 2019). These key ecosystem components influence boreal forest carbon dynamics via several natural control processes. Plants increase their biomass carbon by converting atmospheric CO₂ to new biomass, that is, net primary productivity (NPP). As a key consumer of plant biomass, moose control NPP, and hence carbon capture and storage as biomass. The degree of control over NPP varies with moose abundance and browsing intensity (Petersen et al., 2023; Wilmers & Schmitz, 2016). Wolves and humans in turn suppress moose populations. They thereby may indirectly augment carbon capture and storage by increasing NPP (Wilmers & Schmitz, 2016; Yona et al., 2019). As well, soil reservoirs store dead organic matter because cool soil conditions of intact boreal forests limit microbial decomposition rates and hence soil CO₂ release (Schmitz et al., 2003). Hence, boreal soils, perhaps even more than trees, play a large role in the total carbon balance of the boreal ecosystem (Bradshaw & Warkentin, 2015).

Despite helping to augment carbon capture and storage, wolves are being culled in many parts of the boreal forest to meet specific values for conserving other threatened wildlife species that are vulnerable to wolf predation (Hebblewhite, 2017; Maher et al., 2020). This reflects a willingness of managers to overlook the need to take a holistic perspective that considers the functional roles of animals in their entirety. In a more holistic context, the release from predation pressure could cause moose populations to increase and heavily browse growing trees, thereby changing tree species composition and biomass across the landscape (De Jager et al., 2017). Heavy browsing, especially of regenerating trees, reduces forest canopy height and closure and causes soil warming (Bonan, 1992; Kielland & Bryant, 1998; Schmitz et al., 2003), resulting in lower humidity, warmer and drier soils, and hence CO₂ release via increased soil microbial respiration.
(Crowther et al., 2016) or increased frequency and intensity of forest fires (Schmitz et al., 2003). Thus, failing to account for moose effects when taking measures to conserve other wildlife in this ecosystem could lead to conflicts with carbon offset investments. In addition, large-scale and widespread timber extraction is an essential source of economic and social welfare of local communities (Yona et al., 2019). Rising moose abundances, consequent to wolf culling, could reduce timber production as well (Schmitz, 2005; Wam et al., 2005). But moose cannot be eliminated from the landscape entirely to avoid negative impacts on timber production or carbon storage. This is because the species is valued by local communities for providing hunting opportunities and provisioning and social and cultural services (Bélisle et al., 2021; Natcher, 2009; Timmerman & Rogers, 2005; Wam et al., 2005).

Hence, sustaining a boreal nature-based economy for these different values requires treating the three sectors—wildlife, timber, and carbon—in a functionally integrated way, yet they currently are not (Chapin & Whiteman, 1998; McCarney et al., 2008; Yona et al., 2019). Here we illustrate how to undertake such an integrative, ecologically informed functional examination to reveal the economic benefits and opportunity costs of explicitly managing the interplay and trade-offs among the different trophic compartments of the boreal ecosystem. This entails consideration beyond mere existence value of moose (Krutilla, 1967) to account for their functional role as drivers of economic return via impacts on timber production, via impacts on forest carbon uptake and storage in tree and soil biomass, and via hunting revenue. While the additional provisioning and cultural services (Bélisle et al., 2021; Natcher, 2009; Timmerman & Rogers, 2005; Wam et al., 2005) could also be considered in bioeconomic analyses (e.g., Ansuategi et al., 2019; Armstrong et al., 2017; Enriquez & Finnoff, 2021), our focus on moose foraging and hunting impacts on ecosystem carbon capture and storage is intended to highlight the underappreciated fact that moose management can change the direct impact of moose on whole ecosystem functionality and hence on key regulatory and provisioning ecosystem services of boreal forests.

Our analysis considers the three-way interaction between (1) managing for forest carbon sequestration and storage in tree and soil biomass versus (2) managing for tree biomass carbon removal from timber harvest versus (3) managing for tree biomass carbon removal and alteration of soil processes arising from changes in moose abundance, and hence browsing impacts. The key insight from our analysis is that rising carbon prices can incentivize significant alteration of dynamic nature via large reductions in moose population density to ensure the maximization of the benefit of the nature-based solution. This arises because a carbon market can quickly provide an income stream that becomes far larger than any revenue from hunting or other ecosystem service values for moose. This can in turn create issues about the fairness of wealth distribution among local communities living within boreal forests.

The insights we offer have potentially significant, broadscale implications given that geographically boreal forests of northern Canada and Russia cover 10% of the Earth’s land area. While our examination here focuses on boreal forest ecosystem dynamics, the principles can be generalized to other forests ecosystems, and indeed other ecosystems globally. Hence, our analysis, while examining a case study, is also intended to offer conceptual insight into ways of integrating climate policy with wildlife and forest and ecosystem management more broadly.

THE MODEL

Previous analyses of the interplay between boreal forest timber, carbon, and moose have either treated moose and other wildlife indirectly, focusing on the ancillary benefits arising from conserving and enhancing wildlife habitat while managing for tree biomass carbon (e.g., McCarney et al., 2008), or directly as a consumer of harvestable timber production (Wam et al., 2005). Here we expand the scope of analysis using an ecosystem dynamics model that accounts for moose functional control not only over timber production but also over carbon uptake and storage in tree biomass and in soils. The modeling explores two baseline scenarios for forest harvesting and associated forest productivity (carbon capture) and standing timber biomass carbon: a “nonharvested” system (i.e., no timber is harvested) and a “harvested forest” system (i.e., timber is harvested). For each scenario, we consider how moose will impact forest productivity and timber biomass carbon at varying moose harvest (hunting) levels. Together timber × moose harvesting scenarios create different conditions on which to apply a carbon market. The analyses reveal how ecosystem functioning in the presence and absence of timber and moose harvest alter the carbon content of the forest ecosystem. This allows an examination of how different carbon prices could alter the abundance and trophic structure of the ecosystem.

The following presents a conceptual overview of our modeling. Details of model calibrations and numerical implementation are presented in Appendix S1. A key element of our approach is that we solve for the “social planner’s” solution in different scenarios. One can interpret this as the manager’s solution that seeks to optimize the overall net benefits among the sectors considered.
While this means we do not account for strategic incentives among sectors that might arise (i.e., moose hunting, timber harvesting, and the carbon market), it does enable us to focus on trade-offs that arise with coordinated management of the ecological and forest management system as a whole.

The ecological system

The structure of our model boreal ecosystem is characterized as interactions among four functional trophic levels—soil, primary producers (trees), browsers of trees (moose), and hunters of moose (wolves or humans)—that comprise a food chain in which each trophic level controls the others’ population (Schmitz, 2005). To model forest carbon dynamics, we modify a simple dynamical systems model describing trophic interactions (Schmitz, 1992) to dynamically link forest tree production with the moose population and soil organic matter pool. Tree biomass, moose density, and soil carbon pool size are treated as dynamic state variables. We treat hunter abundance as a fixed control variable, in light of management that sets fixed hunter harvest levels of moose or the abundance of wolves present in the ecosystem. Our analysis models biomass dynamics in tonnes of biomass per square kilometer (t/km²) in the ecological systems and then converts biomass to biomass carbon (in tonnes of biomass carbon per square kilometer, tC/km²) in the economic system. The ecosystem dynamics are described by three fundamental equations:

\[
\begin{align*}
\frac{dT}{dt} &= F_T(T) - FM(T)M - HT - \rho T \\
\frac{dM}{dt} &= [eFM(T) - dm - \Lambda M]M - HM \\
\frac{dOM}{dt} &= \rho T + dmM + \pi HT - m_S OM.
\end{align*}
\]

where \(T\) is standing tree biomass (in tonnes of biomass per square kilometer), \(M\) is moose density (in animals per square kilometer), \(OM\) is the soil organic matter pool (in tonnes of biomass per square kilometer), and all other terms are defined as follows. \(F_T(T)\) represents the net biomass growth rate of trees or NPP (NPP = carbon uptake – carbon respiration [in tonnes of biomass per square kilometer per year] before other sources of biomass loss). These other losses include moose consumption of tree biomass \(FM(T)\) (in tonnes of biomass per square kilometer per animal per year), which varies functionally with tree biomass at a per capita rate, timber harvesting rate \(HT\) (in tonnes of biomass per square kilometer per year), and loss of dead biomass to the OM pool \(\pi HT\) (in percentage per square kilometer per year). Changes in moose population abundance results from consumption and assimilation of plant biomass to meet physiological needs for maintenance and reproduction \(FM(T)\), where \(e\) (in percentage) is the efficiency by which moose-consumed plant biomass is assimilated and converted into per capita moose growth and reproduction, \(dm\) is the per capita natural mortality rate of moose (in percentage per square kilometer per year), \(\Lambda M\) is a rate cost of density-dependent interactions among members of the moose population (in percentage per square kilometer per animal per year), and \(HM\) (in animals per square kilometer per year) is the hunter harvest rate of moose. OM dynamics are a function of buildup due to detrital inputs from trees \(\rho T\), death and decay of moose \(dmM\), debris inputs from timber harvesting \(\pi HT\), and loss due to soil respiration \(m_S OM\). Together the different components of the ecological dynamics enable the calculation of the net amount of forest carbon biomass accrued in the ecosystem per time (net ecosystem productivity or NEP).

Forest management system

We consider two scenarios for timber harvesting. The first assumes a “nonharvested” system (i.e., no timber is harvested) such that \(HT = 0\). This scenario assumes an average stand age of 100 years (McCarthy & Weetman, 2006; McLaren & Peterson, 1994). The second scenario, the “harvested forest” system (i.e., timber is harvested), assumes that a constant fraction of the standing tree biomass is harvested in each time period, where the fraction harvested depends on an assumed rotation length of \(r\) years. We express annual timber harvest as a function of the standing biomass and the assumed rotation length such that \(HT = HT(T; r)\). The assumption of a fixed rotation length is a simplification of practices in the forestry sector, but one that enables us to focus primarily on the ecological interactions. We assume that forests are composed of spruce and pine and harvested as even-aged stands, in accordance with common boreal forestry practices (Asante et al., 2011). For boreal stands harvested without a carbon market, a harvest rotation of 80 years tends to be the ideal mature stand age for clear-cutting (Asante et al., 2011). Thus, a rotational harvest management program that removes and regenerates 1/80th of the entire forest area each year within an 80-year time frame ensures steady annual revenues (Asante et al., 2011). This program leads us to model dynamics for 80 uneven-aged forest plots, aged in discrete
1-year increments. We use the TIPSY forest biomass simulator and Chapman Richards functions (Asante et al., 2011) to estimate annual timber harvest for the 1/80th rotational harvest program in the absence of moose.

The economic system

Analytical approach

In what follows, we assume that moose hunting harvest level, and in turn moose density, is the choice variable such that for any choice of $M$, we can define the steady-state conditions. We then compare steady-state conditions between incremental changes in moose abundance rather than on the transitional dynamics from one steady state to another or following disturbances such as wildfires. We define a steady state as a condition where the standing tree biomass and moose population are constant. That is, Equations (1) and (2) are equal to zero. We do not assume that Equation (3) will equal zero, reflecting the more realistic possibility for organic matter to continually increase over time, even if $T$ and $M$ are constant. This means that setting $dT/dt = dM/dt = 0$, along with one of the timber harvesting conditions (non-harvested or harvested), establishes a system of two equations and three unknowns: $T$, $M$, and $H_M$.

A steady state is therefore fully defined by the functions $\bar{T}(M)$ and $\bar{H}_M(M)$, which are implicitly defined by Equations (1) and (2). As described above, a nonharvested forest imposes the constraint $H_T = 0$, whereas the harvested forest sets $H_T = H_T(\bar{T}(M); r)$. Finally, note that given a steady state, $dOM_t/dt$ changes over time depending on the steady-state values and an initial value of OM. This is discussed further below.

Baseline equilibria

We establish two baseline conditions before introducing the possibility of payments for carbon sequestration. The first assumes that the forest is nonharvested and the chosen level of $M$ is intended to maximize the net financial benefits of moose hunting alone. The second assumes the forest is harvested and considers the dual objective of choosing $M$ to maximize the combined net financial benefits to hunting and timber harvesting. These become the baselines upon which we subsequently add a carbon market.

We first specify the net financial benefits (i.e., benefit minus costs) of each activity. Let $NB_{H_H}(H_M)$ denote the net benefits of moose hunting and let $NB_{H_T}(H_T)$ denote the net benefits of timber harvesting. Assuming the forest is nonharvested and the level of moose density is chosen with only human hunters in mind, the steady state, chosen level of moose density will satisfy

$$M^o = \arg \max_M \left\{ NB_{H_H}(\bar{H}_M(M)) : H_T = 0 \right\},$$

where the constraint clarifies that timber harvest must equal zero. Now assuming the level of moose density is chosen to maximize the net benefits to both hunters and timber harvesters, the solution will satisfy

$$M^* = \arg \max_M \left\{ NB_{H_H}(\bar{H}_M(M)) + NB_{H_T}(\bar{H}_T(M)) \right\}.$$  

The maximand in Equation (5) differs from Equation (4) because it includes the net benefits of timber harvesting, which is no longer restricted to zero. In particular, the second optimization accounts for the way that moose density affects the steady-state timber harvest. Because $\bar{H}_T(M)$ always decreases with $M$ (that is, a larger moose population means less harvestable timber in the steady state), accounting for the timber harvest in moose management will always create an incentive for lower moose density, that is, $M^* > M^o$. The net benefit of moose harvesting is also density dependent; the benefit per moose generally increases as moose density decreases (see additional details in Appendix S1).

Biomass carbon

Central to our analysis is the introduction of payments for carbon sequestration in trees and soils. We therefore need a measure of the carbon content in $T$ and OM. Our basic characterization of forest ecosystem dynamics abstracts considerable detail found in many current carbon cycle models that explicitly account for variation in the carbon content of trees due to fluxes and storage among finely divided ecosystem biomass compartments (e.g., wood, leaves, roots) and due to varying availability of soil nutrients and water. Furthermore, current carbon cycle models characterize carbon flux at explicitly physiological levels including photosynthesis, and plant and soil respiration (Holmberg et al., 2019; Piao et al., 2013; Zaehle et al., 2014). While such mechanisms can be embedded in Equations (1) and (3) (Schmitz & Leroux, 2020), specifying this level of detail would add unnecessary complexity given the purpose of analysis here, which is to illustrate how to examine trade-offs that account for the dynamical role of animals on carbon exchange and storage, rather than estimate actual carbon
storage for a particular region. We therefore approximate, as a first approximation, that carbon photosynthetically fixed in trees is a constant fraction $\alpha = 0.5$ of live biomass $T$ and dead organic matter $OM$ from trees (Houghton et al., 2009; Jain et al., 2010). In natural ecosystems, the amount of soil carbon storage varies spatially. However, for the purposes of this analysis, we do not consider spatial variations in our modeled ecosystem. Instead, we assume a starting condition of 34,000 tC/km² to reflect average values found across boreal forest landscapes (Watson et al., 2000).

Carbon payments

We consider a market for carbon sequestration where payments are based only on the additional carbon stored due to changes in the control variable $M$. We assume a price of carbon dioxide denoted as $PC$, which is translated into a price of carbon via $\delta PC$. As noted previously, carbon is stored in two places relevant for our analysis: trees and soils in quantities $\alpha T$ and $\alpha OM$, respectively.

Carbon payments for storage in trees are assumed to take the following form:

$$f(M; \bar{M}) = \frac{\delta P_C \alpha}{r} \left( \hat{T}(M) - \hat{T}(\bar{M}) \right),$$

where $M$ is any chosen level of moose density, and $\bar{M}$ is a corresponding baseline for comparison, before the introduction of a carbon price (see below). The carbon payments are therefore structured to compensate for the difference in standing carbon between two steady states, where the payment is put on an annual basis depending on the assumed rotation length $r$. This means that the forest carbon market is structured to pay for storage over the length of a rotation, for which we have annualized the payments.

Carbon payments for the additional increment of soil carbon are similarly structured to compensate for the difference arising between two steady states. But at equilibrium, there is no change in steady-state standing biomass ($dT/dt = 0$ in Equation 1), while soil carbon may be continuously accruing ($dT/dt \neq 0$ in Equation 3). Therefore, although payments for forest carbon ($f(M; \bar{M})$) compensate for a discrete change in the total storage level, soil carbon payments represent a change in the rate of soil accumulation. This difference occurs because soil carbon can continuously accrue across timber generations, while a shift in the steady-state standing biomass carbon only occurs once across the timber rotation generation.

Defining this payment similarly requires quantifying the annual changes in soil carbon across the timber rotation period, given the spatial heterogeneity of carbon additions and decomposition across the rotation. We define this payment by first solving for $OM_t$ for any period $t = 1, 2, ..., r$ given an initial rate of soil carbon accumulation $OM_0$:

$$OM_t(M; OM_0) = \rho \hat{T}(M) + d_MM + \pi \hat{H}_T(M) - m_S OM_t-1$$

which determines the amount of loss due to decomposition during the rotation in relation to existing OM storage rate (note: higher levels of starting OM leads to more carbon lost during forest harvesting, and more loss potential if high moose populations trigger decomposition). Now, given assumptions about the initial values of $OM_0$ and a baseline steady-state equilibrium, we define the soil carbon payment as follows:

$$k(M; \bar{M}) = \frac{\delta P_C \alpha}{r} \sum_{t=1}^{r} [OM_t(M; OM_0) - OM_t(\bar{M}; OM_0)].$$

The summand adds up the difference in organic matter accrual over all $r$ time periods (by taking the difference between the change in each period from the baseline over $r$ years), multiplying by $\alpha/r$ converts the total difference into an average, annual carbon difference, and $\delta P_C$ translates the quantity into a carbon payment for the change in the rate of OM storage. This average annual carbon accrual across $r$ rotation plots means that payments for soil carbon are structurally different from forest carbon payments; $k$ represents annual average additional carbon storage between $M$ and $\bar{M}$, while $f$ utilizes $r$ to annualize payments for the one-time change in $T$ storage between $M$ and $\bar{M}$.

Equilibria with carbon payments

We now consider how the nonharvested and harvested steady-state equilibria change with the introduction of a carbon payment. With our setup, the first step is to consider how the conditions differ for the optimally chosen level of moose density.

The non-harvested forest level of moose density with a carbon payment will satisfy

$$M* = \arg \max_{M} \{NBt_{H0} \left( \hat{H}_M(M) \right) + f(M; M') + k(M; M') : H_T = 0 \}.$$  

where Equation (9) differs from Equation (4) because the carbon payments enter the maximand, and importantly,
the baseline condition upon which the payments are calibrated to the solution $M^*$ in Equation (4). To the extent that greater moose density leads to less standing carbon and less accumulated soil carbon, we would expect moose densities to be lower with the carbon payment, that is, $M^* < M^*$. Moreover, using the different terms in Equations (4) and (9), we can solve explicitly for the carbon payments (for trees and soil) and the change in net benefits to moose hunters.

The choice of moose density with a harvested forest and carbon payments will satisfy

$$M^{**} = \max_M \left\{ NB_{H_M} \left( \bar{H}_M(M) \right) + NB_{H_T} \left( \bar{H}_T(M) \right) + f(M; M^{**}) + k(M; M^{**}) \right\}.$$ (10)

In this case, and in parallel, Equation (10) differs from Equation (5) because the carbon payments are included, and the baseline condition for calibrating the payments to the solution $M^{**}$ in Equation (5). It follows from Equation (10) that the numerical analysis introduced added incentives, compared with Equation (9), to reduce moose density for purposes of greater benefits from timber harvesting.

Deriving analytical solutions for the bioeconomic system is challenging given the number of equations involved and their inherent nonlinearities. We therefore conduct the analyses numerically. Our approach involves examining carbon dynamics across gradients of moose population density as managed through moose hunting. The numerical analysis thus examines carbon dynamics in terms of steady-state conditions that permit expressing each of the endogenous variables ($T$, $M$, and OM) as functions of the other variables and moose and timber harvesting levels to conduct a carbon accounting of the boreal ecosystem. A detailed explanation of the model functions and numerical analyses is presented in Appendix S1.

**RESULTS**

The numerical analysis reveals that under nonharvested forest conditions (intact nature), the levels of standing tree biomass, NEP, and timber harvested all decrease in a sigmoid manner with increasing moose density (Figure 1). This nonlinear trend between moose abundance and the three response variables is a consequence of an interplay between two intra-moose population controls that together determine the levels of moose impacts (Appendix S1: Equations S2 and S5). One control comes from density-dependent negative feedback on moose population growth with rising moose density (i.e., logistic moose population growth), and a second control comes from a saturating rate of moose biomass consumption with increasing tree biomass (i.e., a saturating Type II moose functional response). However, the dominance of each control changes across the moose density gradient. At low densities (<0.5 moose/km²), moose are unable to cause heavy damage to plants because their per capita functional response is saturated and there are too few animals to cause heavy damage. At high densities (>1.0 moose/km²), moose are unable to increase damage to plants because of strong intrapopulation competition for plant biomass. The strongest moose impacts, and hence greatest change in ecosystem carbon, occur at intermediate densities between 0.5 and 1.0 moose/km².

**FIGURE 1** Modeled relationships between increasing moose density and carbon stock (standing biomass of trees) and carbon loss or gain (harvested timber, and the carbon sink capacity [net ecosystem productivity, NEP]) of a boreal forest ecosystem. The nonlinear relationship arises from an interplay between density-dependent logistic moose population growth and a saturating moose consumption rate on forest vegetation (a Type II moose functional response). The dominance of each factor varies across the moose density gradient. At low densities (<0.5 moose/km²), moose are unable to cause heavy damage to plants because their per capita functional response is saturated and there are too few animals to cause heavy damage. At high densities (>1.0 moose/km²), moose are unable to increase damage to plants because of strong intrapopulation competition for plant biomass. The strongest moose impacts, and hence greatest change in ecosystem carbon, occur at intermediate densities between 0.5 and 1.0 moose/km².
moose density from 0.5 to 1.0 animals/km², which is at the lower end of recorded moose densities for boreal forests (Jensen et al., 2020; Petersen et al., 2023), is sufficient to reduce carbon storage in soil organic matter by 25%. This modeled reduction in carbon storage is consistent with previous empirical estimates (Schmitz et al., 2014; Wilmers & Schmitz, 2016) and remote sensing analyses of forest productivity in relation to moose densities across North American and Scandinavian boreal forests (Petersen et al., 2023).

The ecological control by moose on forest standing tree biomass, NEP, and timber available for harvest leads to nonlinear relationships between carbon pricing and the optimal level of moose density for nonharvested ($M^*$) and harvested ($M^{**}$) forest scenarios in Equations (9) and (10). In the absence of a carbon payment (the Y-intercept of each curve), moose density is solely driven by benefits from hunting (Figure 2, red lines) and the combination of benefits from hunting and timber harvest (Figure 2, blue line). In the absence of carbon pricing, optimal moose density in the harvested scenario is between 0.33 and 0.66 times lower than the nonharvested scenario due to balancing the trade-off in benefits from moose and timber harvesting.

Adding a carbon market would encourage lowering moose densities to maximize forest carbon storage. The amount of decline in density needed to maximize carbon storage varies in a negative exponential manner with rising carbon prices, with the trend in decline remaining similar for different initial harvested optimal moose equilibrium density ($M^* = 1.0$, and $M^* = 0.5$). This need for a rapid managed decline in moose density results from the high marginal change in forest carbon impact of moose browsing at population densities between 0.5 and 1.0 moose/km², weighed against the comparatively low marginal benefit of the additional sustained moose harvest yield. The analysis reveals that as the carbon price increases, the benefit-maximizing moose population density in non-harvested and harvested forests converges to a very low moose density between 0.1 and 0.2 moose/km² because carbon benefits progressively outweigh benefits from the other sectors. That is, rising carbon prices encourage large reductions in moose population density to ensure the maximization of carbon storage in the ecosystem. Indeed, carbon prices as low as $5/\text{tCO}_2$ would already encourage a major 50% reduction in optimal moose density (Figure 2). Moose density between 0.1 and 0.2 moose/km² represents the point beyond which further moose population reduction would have limited impact on ecosystem carbon storage (see Figure 1), that is, moose are no longer a functionally significant player in the ecosystem.

In the nonharvested forest, the reductions in optimal moose density with increasing carbon price translates into a nonlinear saturating increase in total carbon stored in tree biomass and annual soil OM carbon accumulation with increasing carbon price. It increases only slightly and linearly in the harvested forest (Figure 3). This saturation results from constraints imposed by underlying ecosystem dynamics. But the absolute difference in carbon storage in trees between nonharvested and harvested cases results from less carbon stored in the average younger-aged trees comprising stands in the 80-year rotation of the harvested forest. The difference in annual OM storage results primarily from the decomposition that occurs in younger forest plots triggered by forest harvesting. The small increase in carbon storage with
There is growing interest to account for the economic value of nature-based solutions that capture and store carbon in ecosystems (Chami et al., 2022). This includes financially accounting for carbon benefits accrued via the conservation of animals to preserve their functional roles that control the carbon cycle in ecosystems (e.g., frugivory and dispersal of seeds from carbon dense trees; Bello et al., 2021; Berzaghi et al., 2019; Brodie, 2018; trampling and foraging to restore and protect plant production in the arctic steppe and carbon in permafrost; Macias-Fauria et al., 2020). In some cases, valuing the animal effects involves a straightforward calculation of the additional carbon accrued with every unit of the animal population increase (Bello et al., 2021; Macias-Fauria et al., 2020). In other cases, animal effects on carbon storage may vary nonlinearly with animal abundance (Berzaghi et al., 2019; Brodie, 2018) such that over a range of low to intermediate density, animals could have neutral or beneficial effects, with a switch to negative effects at high density (Berzaghi et al., 2019; this study). Hence, considering wildlife conservation to meet the dual goals of mitigating biodiversity loss and climate mitigation must go beyond a focus merely on protecting and restoring species, and explicitly include consideration of their density-dependent population ecological effects on ecosystem processes (Figure 1).

Our analysis highlights potential risks associated with promoting forest production merely as a nature-based solution for carbon capture and storage (Bastin et al., 2019; Fargione et al., 2018; Griscom et al., 2017; Houghton & Nassikas, 2018). This need to consider risks will be especially critical whenever new carbon offset programs are superimposed onto landscapes in which there are longer established values for other ecosystem services. For instance, in boreal forest ecosystems, this could include forest production of timber for extraction (Holmberg et al., 2019; McCarney et al., 2008; Wam et al., 2005; Yona et al., 2019), provisioning, and cultural services provided by wildlife tourism and hunting (Bélisle et al., 2021; Holmberg et al., 2019; Timmerman & Rogers, 2005) and conservation of threatened wildlife species (Drever et al., 2019). The consideration of the functional roles of animals in these ecosystem services may require reconciling trade-offs because of the different ecosystem service values provided by any given animal species (Brodie, 2018).

Our analysis for moose reveals that failing to anticipate and reconcile such conflicts may result in loss of a key part of “nature” vis-à-vis loss of the trophic structure and key functional controls within the ecosystem in order to maximize carbon storage. The risk of this outcome increases
with increasing prices of carbon. This is because maximizing ecosystem carbon storage with increasing carbon prices would necessarily incentivize reducing moose population size substantially due to moose limitation of forest biomass production and hence carbon uptake and biomass storage capacity. This reduction could become especially profound in the nonharvested scenario, where moose population sizes have not yet been optimized to support timber production (Figure 2).

Regardless of scenario, superimposing a carbon market onto a harvested or nonharvested forest landscape could collapse the moose hunting economy. This is because even at a low carbon price, the benefit for moose hunting would become increasingly negative as carbon price increases (Figure 4) because moose populations must be reduced to such an extent that sustaining hunting comes at a net cost. Consequently, the welfare of a community dependent on the recreational and cultural services provided by moose could become increasingly jeopardized by carbon offset investments. This provides a specific example in which managing natural systems primarily to reduce atmospheric CO₂ emissions might have perverse effects on natural systems themselves and raise questions about distributional fairness (Honegger et al., 2021). But moose population management is typically accomplished through hunting, and so without hunting, it may be challenging to meet carbon storage goals of offset investments due to the need to implement carbon management initiatives predicated on reducing the density of browsing species.

The solution to meeting the multiple objectives of management for wildlife, timber, and carbon sequestration is to utilize hunting not just for game or recreation, but as part of a nature-based solution via a new means to enhance carbon sequestration (Yona et al., 2019). Doing so requires moving away from setting hunting levels using classic population-based maximum sustained yield (MSY) bioeconomic concepts to more holistic forest ecosystem dynamic bioeconomic concepts that set moose sustained yield to reach ecologically meaningful densities for carbon capture and storage (Schmitz et al., 2023). The determination of what is ecologically meaningful requires balancing moose density-dependent impacts on tree production and soil carbon deposition (Figure 1) against carbon gains accrued in tree biomass and soil (Figure 3). For the conditions (diminishing returns curves) specified in our modeling scenarios, ecologically meaningful becomes
a density between 0.2 and 0.4 moose/km², which is much lower than the classic population-based MSY of 1 moose/km² (Appendix S1).

The much lower moose density leads to a loss of economic return to the hunting economy. But the amount of that loss, which increases with increased carbon price, can be imputed as the minimal cost of sustaining an intact forest for moose carbon and timber production. This implies that rather than hunters paying for the opportunity to hunt moose, carbon offset investments should pay hunters for the service provided to sustain the nature-based climate solution along with other ecosystem services. That is, hunting can be viewed as a control on ecosystem dynamics much like the control exerted by wolves. Hence, an alternative way to value wolves is to quantify the economic benefit they provide as part of carbon offset programs via their control over moose populations (Schmitz et al., 2014). This could conceivably be imputed in the same way as the determination of the economic value of moose hunting.

Our ecosystem model is a basic caricature of ecosystem dynamics. As such, it does not include an explicit account of biogeochemical processes in terms of carbon and nutrient dynamics that are characteristic of conventional models of ecosystem service production and carbon dynamics (Holmberg et al., 2019; Piao et al., 2013; Zaehle et al., 2014), as well as models that account for animal effects on biogeochemical processes driving carbon cycling (Rizzuto et al., 2024). This was done because our primary intention was to motivate new modeling developments by illustrating how an integrative approach can help us devise creative alternative solutions for climate change mitigation. Thus, our modeling results do not offer estimates of carbon sequestration on which to base specific on-the-ground management decisions. Rather, our modeling approach offers insights on how to go about providing an integrative way to illustrate and quantify the trade-offs among different values and ecosystem services offered by forest ecosystems. Accurately accounting for carbon dynamics in nature-based solutions will require the development of new kinds of management models to capture the harvest and carbon implications of ecosystem co-uses. These models will need to explicitly blend classic animal and plant population density and production concepts with ecosystem trophic dynamic models that account for biogeochemical cycling, production, and net ecosystem carbon storage. Moreover, solutions for such models will need to move away from considering steady-state conditions, as is done in conventional forest management, to focus on transitions between steady states to anticipate the outcomes of management for multiple different ecosystem values within a single ecosystem. Such new ways of analyzing the models will help to appropriately value different ecosystem components to avoid the perverse outcomes encountered in our current modeling in which implementing well-intentioned nature-based climate solutions could end up destroying dynamic nature.

AUTHOR CONTRIBUTIONS
Jonah Ury, Matthew J. Kotchen, and Oswald J. Schmitz conceived and designed the study. Jonah Ury lead the model development and analyses in consultation with Matthew J. Kotchen and Oswald J. Schmitz. Jonah Ury, Matthew J. Kotchen, and Oswald J. Schmitz wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Code and data (Schmitz et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.j0zpc86p1.

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REFERENCES


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