

In review

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. Our 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), and carbon loss due to controls from moose herbivory that varies with moose population density (hunting), and soil carbon inputs and release, which together determine net ecosystem productivity (NEP), a measure of carbon sink strength of the ecosystem. We examine how controls on carbon dynamics are altered by forest management for timber harvest, and by moose hunting. 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 modelled 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 key insight is that implementing nature-based solutions to maximize carbon capture and storage can end up destroying nature in the absence of an integrative whole ecosystem perspective that considers wildlife, carbon and timber together. Moreover, these perverse effects of carbon pricing on the

destruction of nature become more of a concern in non-harvested systems because harvested systems already have an incentive to lower the moose population.

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 (Mori 2020, Osaka et al. 2020, Girardin et al. 2021, Miles et al. 2021, Seddon et al. 2021, Smith et al. 2021). 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) 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, Girardin et al. 2021, Kooijman et al. 2021, Seddon et al. 2021, Chami et al. 2022). 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 owing to their capacity to capture and store large amounts of atmospheric CO₂ in plant biomass and in soils (McCarney et al. 2007, Griscom et al. 2017, Fargione et al. 2018, Houghton and Nassikas 2018, Bastin et al. 2019, Busch et al. 2019, Salvatori and Pallante 2021). Such investments are viewed as potentially having ancillary benefits for conservation by

protecting habitat for a diversity of wildlife species (McCarney et al. 2007, Rittenhouse and Rissman 2012, Buote et al. 2020, Littlefield and D’Amato 2021).

However, treating wildlife conservation merely as an ancillary benefit overlooks the functional role of wildlife species in controlling forest ecosystem processes (Pastor et al. 1988, Kielland and Bryant 1998, Seagle 2003, Osuri et al. 2016, Peres et al. 2016, Sobral et al. 2017, Brodie and McIntyre 2019, Ramirez et al. 2021) including controlling the amount of carbon that is captured and stored (Brodie and Gibbs 2005, Wilmers and Schmitz 2016, Osuri et al. 2016, Peres et al. 2016, Sobral et al. 2017, Berzaghi et al. 2019). Hence not accounting for these functional roles could lead to nature-based solutions failing to meet their carbon storage targets (Schmitz and Leroux 2020, Schmitz et al. 2023), let alone overlooking the considerable economic value that comes from their functional controls over carbon capture and storage (Brodie 2018, Macias-Fauria 2020, Bello et al. 2021, Berzaghi et al. 2022).

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. 2018). 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, i.e., 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 (Wilmers and Schmitz 2016, Petersen et al. 2023). Wolves and humans in turn suppress moose populations. They thereby may indirectly augment carbon capture and storage by increasing NPP (Wilmers and Schmitz 2016, Yona et al. 2018). 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 and Warkentin 2015).

But in many parts of the boreal forest, wolves are being culled to meet values for conserving other threatened wildlife species that are vulnerable to wolf predation (Hebblewhite 2017, Maher et al. 2020). Once released from predation pressure, moose populations can increase and heavily browse growing trees, thereby changing tree species composition and biomass across the landscape (Jaeger et al. 2017). Heavy browsing, especially of regenerating trees, reduces forest canopy height and closure and causes soil warming (Bonan 1992; Kielland and 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. 2018). 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. This is because the species is valued by local communities for providing hunting opportunities and provisioning and social and cultural services (Timmerman and Rogers 2005, Wam et al. 2005, Natcher 2009, Bélisle et al. 2021).

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 and Whiteman 1998, McCarney et al. 2007, 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. Our analysis considers the three-way interaction between (i) managing for forest carbon sequestration and storage in tree and soil biomass vs (ii) managing for tree biomass carbon removal from timber harvest vs (iii) 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 the destruction 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, broad scale implications given that geographically boreal forests of northern Canada and Russia cover 10 percent 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 via 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. 2004). 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 following presents a conceptual overview of our modeling. Details of model calibrations and numerical implementation are presented in the Appendix S1.

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. The ecosystem dynamics are described by three fundamental equations:

$$\frac{dT}{dt} = \mathcal{F}_T(T) - \mathcal{F}_M(T)M - H_T - \rho T \quad (1)$$

$$\frac{dM}{dt} = [\varepsilon \mathcal{F}_M(T) - d_M - \Lambda M]M - H_M \quad (2)$$

$$\frac{dOM_t}{dt} = \rho T + d_M M + \pi H_T - m_S OM. \quad (3)$$

where T is standing tree biomass, M is moose density, OM is the soil organic matter pool, and all other terms are defined as follows. $\mathcal{F}_T(T)$ represents the net biomass growth rate of trees or net primary productivity (NPP = carbon uptake – carbon respiration) before other sources of biomass loss. These other losses include moose consumption of tree biomass $\mathcal{F}_M(T)$, which varies functionally with tree biomass at a per capita rate, timber harvesting rate H_T , and loss of dead biomass to the OM pool as natural detrital inputs at rate ρT . Changes in moose population abundance results from consumption and assimilation of plant biomass to meet physiological needs for maintenance and reproduction $\varepsilon \mathcal{F}_M(T)$, where ε is the efficiency by which moose-consumed plant biomass is assimilated and converted into per capita moose growth and reproduction, d_M is the per capita natural mortality rate of moose, ΛM is a rate cost of density-dependent interactions among members of the moose population, and H_M is the hunter harvest rate of moose. OM dynamics are a function of buildup due to detrital inputs from trees ρT , death and decay of moose $d_M M$, debris inputs from timber harvesting πH_T , and loss due to soil respiration $m_S OM$.

Forest management system

We consider two scenarios for timber harvesting. The first assumes a non-harvested system (i.e., no timber is harvested) such that $H_T = 0$. The second 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 $H_T = H_T(T; r)$. Assuming 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 assumed 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 $1/80^{\text{th}}$ of the entire forest area each year within an 80-year time frame ensures steady annual revenues (Asante et al. 2011). This program led to us to model dynamics for 80 uneven-aged forest plots, aged in discrete one-year increments. We used the TIPSy forest biomass simulator and Chapman Richards functions (Asante et al. 2011) to estimate annual timber harvest for the $1/80^{\text{th}}$ rotational harvest program in the absence of moose.

The economic system

Analysis 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. We define a steady state as a condition where the standing tree biomass and moose population are constant. That is, Eqs. 1 and 2 are equal to zero. We do not assume that Eq. 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 $\hat{T}(M)$ and $\hat{H}_M(M)$, which are implicitly defined by Eqs. 1 and 2. As described above, a non-harvested forest imposes the constraint $H_T = 0$, whereas the harvested forest sets $H_T = H_T(\hat{T}(M); r)$. Finally, note that given a steady state, $\frac{dOM_t}{dt}$ 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 non-harvested 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 $NB_{H_M}(H_M)$ 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 non-harvested and the level of moose density is chosen with only human hunters in mind, the steady state, chosen level of moose density will satisfy

$$M^\circ = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) : H_T = 0 \right\}, \quad (4)$$

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

$$M^{\circ\circ} = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) + NB_{H_T} \left(\hat{H}_T(M) \right) \right\}. \quad (5)$$

The maximand in (5) differs from (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 $\hat{H}_T(M)$ 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, i.e., $M^\circ > M^{\circ\circ}$.

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 (Piao et al. 2013, Zaehle et al. 2014, Holmberg et al. 2019). While such mechanisms can be embedded in Eqs. 1 and 3 (Schmitz and 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 assume, 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).

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 P_C , and this is translated into a price of carbon via δP_C . As noted previously, carbon is stored in two places relevant for our analysis: trees and soils in quantities αT and αOM , respectively.

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

$$f(M; \bar{M}) = \frac{\delta P_C \alpha}{r} \left(\hat{T}(M) - \hat{T}(\bar{M}) \right), \quad (6)$$

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 were similarly structured to compensate for the difference arising between two steady states. But at equilibrium, there is no change steady state standing biomass ($\frac{dT}{dt} = 0$ in Eq. 1), while soil carbon may be continuously accruing ($\frac{dT}{dt} \neq 0$ in Eq. 3). Therefore, whereas payments for forest carbon ($f(M; \bar{M})$) compensate for a discrete change in 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 $t = 1, 2, \dots, r$ given an initial rate of soil carbon accumulation OM_0 :

$$OM_t(M; OM_0) = \rho \hat{T}(M) + d_M M + \pi \hat{H}_T(M) - m_S OM_{t-1}. \quad (7)$$

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 lead 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:

$$k(M; \bar{M}) = \frac{\delta P_{C\alpha}}{r} \sum_{t=1}^r [OM_t(M; OM_0) - OM_t(\bar{M}; \overline{OM}_0)]. \quad (8)$$

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

α/r converts the total difference into an average, annual carbon difference, and δP_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 non-harvested 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

$$M^* = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) + f(M; M^\circ) + k(M; M^\circ) : H_T = 0 \right\}. \quad (9)$$

where (9) differs from (4) because the carbon payments enter the maximand, and importantly, the baseline condition upon the payments are calibrated is the solution M° to (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, $M^* < M^\circ$. Moreover, using the different terms in (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

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

In this case, and in parallel, (10) differs from (5) because the carbon payments are included, and the baseline condition for calibrating the payments is the solution $M^{\circ\circ}$ in (5). It follows that (10)

introduces added incentives, compared to (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. Detailed explanation of the model functions and numerical analyses is presented in Appendix S1.

RESULTS

The numerical analysis reveals that under non-harvested forest conditions (intact nature), the levels of standing tree biomass, NEP, and timber harvested all decrease in a sigmoid manner with increasing moose density (Fig. 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 levels of moose impacts (Appendix S1 Eq. S2, 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 moose densities (high plant biomass) moose are unable to cause heavy damage to plants because their consumption of plant biomass is saturated. At high moose

densities (low plant biomass) moose again are unable to increase damage to plants because of strong intra-population competition for plant biomass. Hence, the strongest moose impacts occur at intermediate moose densities when there is a transition between the dominance of one control to the other. Accordingly, over low but increasing moose densities, moose will have neutral to minor negative impacts on high forest biomass and NEP. As moose densities rise to intermediate densities, the system over time will undergo a quasi-threshold change in which plant biomass and NEP decline rapidly (Fig. 1). This is followed again by neutral or minor negative impacts on low forest biomass and NEP high moose densities. This modeling reveals that a rise in moose density from 0.5 to 1.0 animals per 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 percent. This modeled reduction in carbon storage is consistent with previous empirical estimates (Schmitz et al. 2014, Wilmers and 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 non-harvested (M^*) and harvested (M^{**}) forest scenarios in Eqs. 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 (Fig. 2, red lines) and the combination of benefits from hunting and timber harvest (Fig. 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 non-harvested 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 ($M^{\circ} = 1.0$, and $M^{\circ} = 0.5$). 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 to 1.0 moose per 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 converge to a very low moose density between 0.1 and 0.2 per 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 per tCO₂, would already encourage a major 50% reduction in optimal moose density (Fig. 1). Moose density between 0.1 and 0.2 per km² represents the point beyond which further moose population reduction would have limited impact on ecosystem carbon storage (Fig. 1), i.e., moose are no longer a functionally significant player in the ecosystem.

In the non-harvested 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 (Fig. 3). The absolute difference in carbon storage in trees between non-harvested 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 increasing carbon price in the harvested forest arises because the system is already optimized for both moose and timber harvesting before the introduction of carbon prices. This stems from the moose population decreasing less in the harvested forest as carbon price increases than in the non-harvested forest. Hence, perverse effects of carbon pricing on the destruction of nature become more of a concern in non-harvested systems because harvested systems already have an incentive to lower the moose population.

The financial benefits of moose hunting and carbon storage vary inversely with increasing carbon price (Fig. 4). The decline in moose population density with increasing carbon pricing (Fig. 2) results in greater tree and soil carbon benefits (a function of both the increasing level of carbon storage and the increasing price per unit of carbon stored), and a reduction in moose hunting benefits. The differences in the amount of benefit between the non-harvested and harvested forest results from moose populations shifting more substantially in the un-harvest forest case (Fig. 2), with a concomitant larger reduction in hunting benefits and a greater change in forest carbon composition than in the harvested forest (Fig. 4).

DISCUSSION

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 [Brodie 2018, Bello et al. 2021, Berzaghi et al. 2022]; trampling and foraging to restore and

protect plant production in 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). However, in other cases, animal effects on carbon storage may vary nonlinearly with animal abundance (Brodie 2018, Berzaghi et al. 2019) 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 (Fig. 1).

Our analysis highlights potential risks associated with promoting forest production merely as a nature-based solution for carbon capture and storage (Griscom et al. 2017, Fargione et al. 2018, Houghton and Nassikas 2018, Bastin et al. 2019). 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. In boreal forest ecosystems for instance, this could include forest production of timber for extraction (Wam et al. 2005, McCarney et al. 2007, Holmberg et al. 2019, Yona et al. 2019), provisioning and cultural services provided by wildlife tourism and hunting (Timmerman and Rodgers 2005, Holmberg et al. 2019, Bélisle et al. 2021) 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 the destruction of “nature” vis à vis loss of the trophic structure and key functional controls within the ecosystem to maximize carbon storage. The risk of this outcome increases with increasing prices of carbon. This is because maximizing ecosystem carbon storage necessarily requires reducing moose population size due to moose limitation of forest biomass production and hence carbon uptake and biomass storage capacity.

In turn, the economic benefit of moose hunting becomes negative even at a low carbon price (Fig. 4). It becomes increasingly negative as carbon price increases 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 becomes increasingly jeopardized by carbon offset investments. This provides a specific example where 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 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 and Sylvén 2023). The determination of ecologically meaningful requires balancing

moose density-dependent impacts on tree production and soil carbon deposition (Fig. 1) against carbon gains accrued in tree biomass and soil (Fig. 3). For the conditions (diminishing returns curves) specified in our modeling scenarios, ecologically meaningful becomes a density between 0.2 and 0.4 moose per square kilometer, which is much lower than the classic population-based MSY of 1 moose per square kilometer (Supplemental Appendix).

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 to offset carbon 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 (Piao et al. 2013, Zaehle et al. 2014, Holmberg et al. 2019) as well as models that account for animal effects on biogeochemical processes driving carbon cycling (Rizzuto et al. 2023). 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 support of nature-based solutions that will be implemented in forest ecosystems in which other timber production and wildlife values will require the development of new kinds of management models. 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 outcomes of management for multiple different ecosystem values within a single ecosystem. Such new ways of analyzing the models will help to appropriate value different ecosystem components to avoid the perverse outcomes encountered in our current modeling in which implementing well-intentioned nature-based climate solutions end up destroying dynamic nature.

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AUTHOR CONTRIBUTIONS

JU, MJK and OJS conceived and designed the study. JU lead the model development and analyses in consultation with MJK and OJS. JU, MJK and OJS wrote the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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Figure Legends

Fig. 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 (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 per km^2) moose are unable to cause heavy damage to plants because their consumption of plant biomass is saturated. At high densities (> 1.0 per km^2) moose are unable to increase damage to plants because of strong intra-population competition for plant biomass. The strongest moose impacts, and hence greatest change in ecosystem carbon, occurs at intermediate densities between 0.5 - 1.0 moose per km^2 .

Fig. 2. Examination of how increasing carbon prices influences the optimal density of moose in a non-harvested and harvested forest scenario to maximize the net benefits among forest harvesting, moose hunting and carbon storage. The solid and dashed red lines represent different moose management scenarios in which moose populations are reduced from a high density case (maximum sustained yield: dashed line) or reduced from a lower-density starting population (half of MSY population: solid line). Regardless, maximizing net benefits from investments in the nature-based solution (ecosystem carbon storage) and timber management for harvesting incentivizes large reductions in moose population densities and hence loss in their attendant control over the forest ecosystem. That is, investments in nature-based solutions and timber encourage reducing or eliminating a key functional control of forest ecosystem dynamics, i.e., trading-off nature for nature-based solutions.

Fig. 3. Modeled relationship between the price of carbon offsets and the amount of carbon stored in tree biomass and soils of a boreal ecosystem. Carbon storage in tree biomass and soil eventually saturates with increasing carbon price due to the decreasing marginal reduction in moose density (M) as carbon price increasing (Fig. 1), as well as limitations on carbon uptake imposed by natural ecological processes.

Fig. 4. The cumulative relationship between carbon price and the additional net economic benefit of investment in nature-based boreal forest carbon capture and storage. Maximizing the return on investment incentivizes the destruction of “nature” by reducing moose populations to low levels. This leads to an increasing negative return for a cultural ecosystem service—moose hunting—with increasing carbon prices.

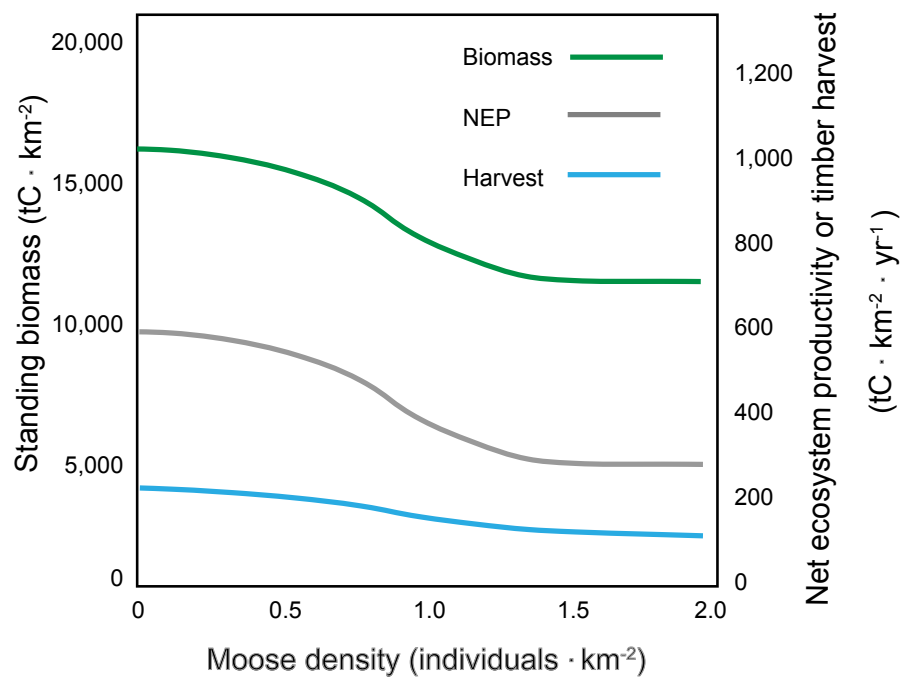


Figure 1

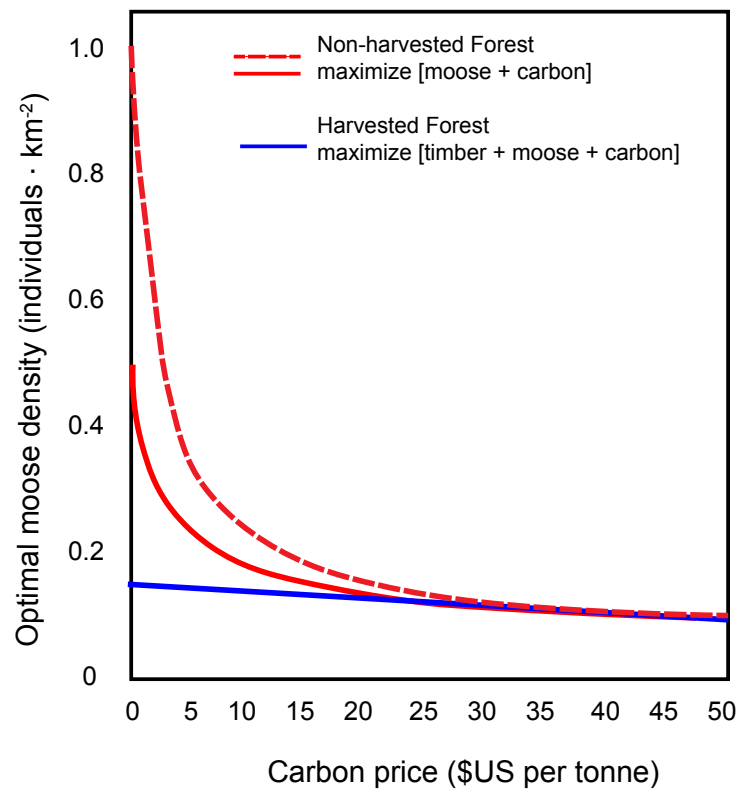


Figure 2

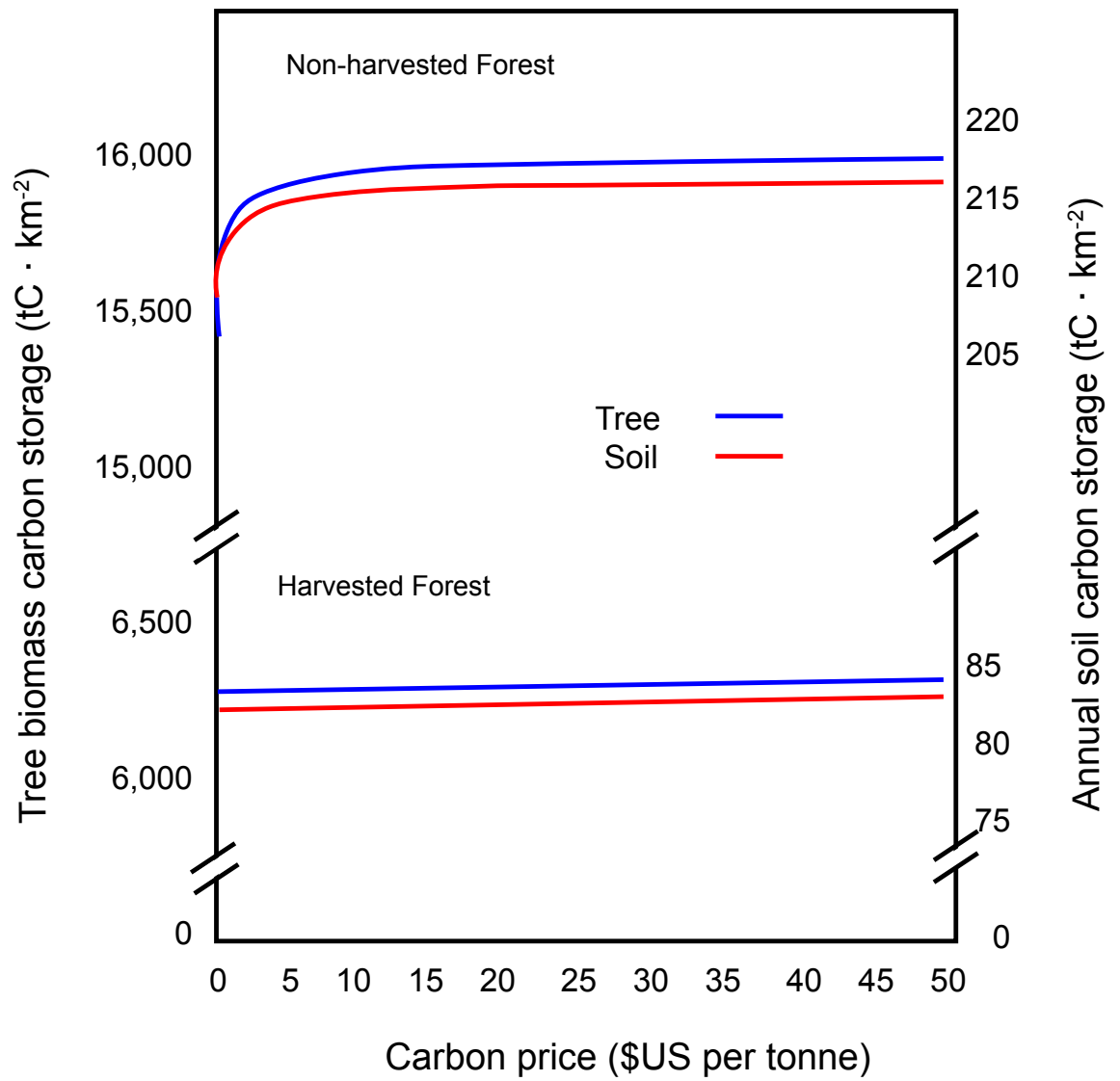


Figure 3

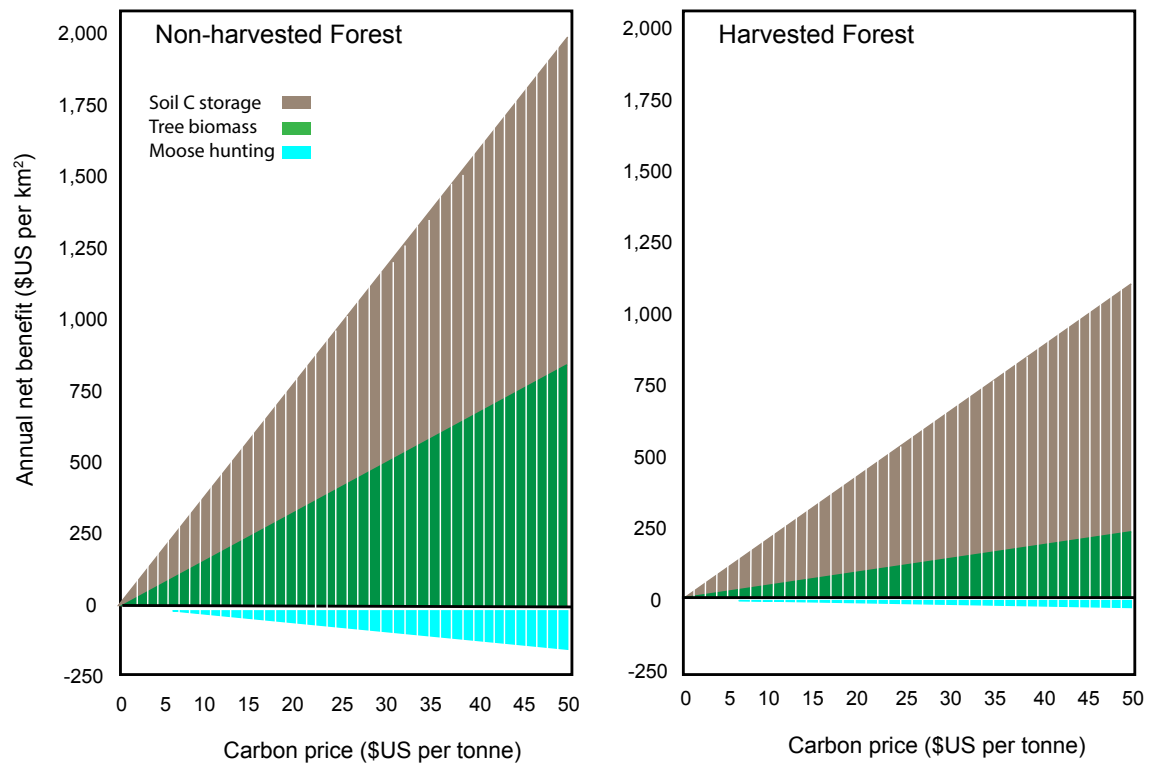


Figure 4

APPENDIX S1

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

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Overview

The following narrative presents the equations and assumptions that describe the systems and system dynamics of the bioeconomic boreal forest model. The narrative further details how the models were analyzed to produce the results presented in the main text. All model parameters and functions and their literature sources are presented in Table S1. Our analysis examines the interrelationships between three main components of the bioeconomic system: the ecological system, the forest growth and yield system, and the economic system. The ecological system relates the interplay among net ecosystem productivity—aka the carbon sink potential of an ecosystem—tree biomass (T), moose population abundance (M), moose hunting (H_M), forest harvesting (H_T) and dead organic matter pools (OM). The Forest growth and yield system characterizes merchantable timber yield (H_{TY}), harvestable biomass, and their impacts on OM . The economic system links the two, by applying prices to H_M , H_T and carbon storage. The following sections describe these different components of the overall model in detail.

The Ecological Systems Model

As described in the main text, the foundational structure for this analysis is built on a dynamical systems model describing trophic interactions (Schmitz 1992) modified to explicitly link forest tree production with moose population and soil organic matter dynamics:

$$\frac{dT}{dt} = \mathcal{F}_T(T) - \mathcal{F}_M(T)M - H_T - \rho T \quad (S1)$$

$$\frac{dM}{dt} = [\varepsilon \mathcal{F}_M(T) - d_M - \Lambda M]M - H_M \quad (S2)$$

$$\frac{dOM}{dt} = \rho T + d_M M + \pi H_T - m_S OM \quad (S3)$$

where T is standing tree biomass, M is moose density, OM is the soil organic matter storage pool, and all other terms are defined as follows. $\mathcal{F}_T(T)$ represents the net biomass growth rate of trees or net primary productivity (NPP = carbon uptake – carbon respiration) before other sources of biomass loss. These other losses include per capita moose consumption of tree biomass $\mathcal{F}_M(T)$, which varies functionally with tree biomass, resulting a total rate of tree biomass loss to moose that varies with moose density M ; timber harvesting H_T at a constant rate; and loss of biomass as dead organic matter inputs to the OM storage pool at rate ρT . Changes in moose population abundance results from consumption and assimilation of plant biomass to meet physiological needs for maintenance and reproduction $\varepsilon \mathcal{F}_M(T)$, where ε is the efficiency by which moose-consumed plant biomass is assimilated and converted into per capita moose growth and reproduction, d_M is the per capita natural mortality rate of moose, ΛM is a rate cost of density-dependent interactions among members of the moose population, and H_M is the harvest rate of moose by either natural predators or humans. We treat harvest rate of moose as a fixed control variable, given management that sets fixed levels of moose harvest by humans or sets the abundance of dominant predators (wolves) present in the ecosystem. The OM dynamics is a function of buildup due to detrital inputs from trees ρT , death and decay of moose $d_M M$, debris inputs from timber harvesting πH_T , and loss due to soil respiration $m_5 OM$.

Expanding on that described in the main text, we now describe the functional relationships in more detail. We assume that forest growth is bounded due to plant competition for nutrients and therefore exhibits biomass growth of the form (Schoener 1973, Tilman 1982, Schmitz 1992):

$$\mathcal{F}_T(T) = \left(\left[\frac{RS_N}{T} \right] - m_T \right) T \quad (\text{S4})$$

where S_N is the supply rate of nutrients to the ecosystem, R is plant biomass production per unit of nutrient uptake (effectively rate of photosynthesis per unit of nutrient uptake). Accordingly, RS_N is gross production of plant biomass (GPP), and $m_T T$ is the loss rate of plant biomass due to plant respiration, such that $RS_N - m_T T = \text{NPP}$.

The ability of moose to consume trees saturates with increasing tree biomass owing to physical constraints on biting and chewing imposed by the size of a moose's mouthparts (Spalinger and Hobbs 1992, Gross et al. 1993). This saturating per capita consumption rate can be described by a type-II consumer functional response:

$$\mathcal{F}_M(T) = \left[\frac{\phi T}{1 + \beta T} \right], \quad (\text{S5})$$

where ϕ represents the moose search rate for forage and β represents forage processing time.

This very basic characterization of forest ecosystem dynamics abstracts considerable detail found in many current carbon cycle models that explicitly account for variation in 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 (GPP), and plant and soil respiration (Piao et al. 2013, Zaehle et al. 2014). Such mechanisms can be embedded in Eqs. S1 and S3 by expressing these processes in terms of their respective rate functions (Schmitz and Leroux 2020). But expressing dynamics at this level of detail is beyond the purpose of the analysis here, which is to illustrate how to frame an economic trade-off analysis that accounts for the role of animals on carbon exchange and storage in an integrated way when reconciling competing interests. We therefore approximate this processes by assuming that any biomass accrual as T or loss of tree biomass as OM contains 50% carbon (Houghton et al. 2009, Jain et al. 2010), such that $\alpha = 0.5$.

The Forest Growth and Yield Model

We examined two primary scenarios in the forest growth and yield model: the “non-harvested forest” where no timber harvest takes place (i.e., $H_T = 0$), and the “harvested forest” where some level of timber harvesting takes place (i.e., $H_T > 0$). This distinction explicitly determines the fate of plant biomass (and implicitly biomass carbon) in the ecological systems model, and hence the influence on the workings of a forest-carbon market. All equations in the forest growth and yield model delineated below operate in units of carbon mass; hence we convert the ecological biomass dynamics to biomass carbon by multiplying tree biomass by $\alpha = 0.5$.

Forest harvesting, H_T , results in the permanent removal of carbon from the ecosystem as merchantable timber at rate H_{TY} , and the deposition of carbon in the OM pool of the ecosystem as woody debris arising from harvesting at rate H_{TOM} . In classic forest management, timber yield is accounted in terms of volume of wood. For the purposes of carbon accounting, and for consistency with the ecological model, we assess timber harvest in terms of biomass carbon. Hence, carbon in

merchantable timber yield, H_{TY} , and in organic matter debris H_{TOM} are determined by the following equations:

$$H_{TY} = (1 - \pi) * \alpha H_T \quad (S6)$$

$$H_{TOM} = \pi * \alpha H_T = \alpha H_T - H_{TY} \quad (S7)$$

where H_{TY} represents the timber yield in tons of carbon (tC)/(time), and $1 - \pi$ is the proportion of the timber harvest biomass H_T that is merchantable lumber, which is a function of forest age and tree composition. The H_{TOM} Eq. specifies that all non-merchantable biomass carbon is in the form of debris inputs from timber harvesting, πH_T , which stays in the ecosystem and is subject to decomposition.

OM carbon flows in the harvested (h) and non-harvested (nh) scenarios follow directly from the ecological systems model:

$$OM_{nh} = \alpha \rho T - m_S OM \quad (S8)$$

$$OM_h = \alpha \rho T + H_{TOM} - m_S OM \quad (S9)$$

with litterfall rate, ρ , based on the quantity of standing biomass, T , and a per unit of OM mass decomposition rate, m_S .

The Economic Program

The economic program is constructed to evaluate the optimal levels of moose harvesting, the key choice variable, at various carbon prices. The optimum is defined as the moose population level that maximizes the combined net benefits of timber harvesting, moose hunting, and carbon capture and storage for a range of carbon prices. Our analysis compares differences between steady-state magnitudes rather than the rate of change from one steady state to another. We define a steady state as a condition where the standing tree biomass and moose population are constant. That is, when Eqs. S1 and S2 are equal to zero, consistent with resource harvesting theory. We do not assume that Eq. S3 will equal zero, reflecting the more realistic possibility that the organic matter pool can build-up continually over time, even if management holds T and M at steady state in the forest ecosystem. For any choice of M , a steady state is defined by the functions $\hat{T}(M)$ and $\hat{H}_M(M)$, which ultimately obey dynamics defined by Eqs. S1 and S2 of the ecological system.

These steady states are evaluated in terms of the net benefits of each activity to the system: moose harvesting, $NB_{H_M}(H_M)$, timber harvesting, $NB_{H_T}(H_T)$, forest carbon stored in trees, f , and forest carbon stored in organic matter, k . Net moose and timber harvesting benefits are a function of gross harvest benefits minus costs. Forest and organic matter carbon storage benefits are a function of a market for carbon sequestration where payments are based only on the additional carbon stored and a price on carbon, P_C . The following elaborates on each of these benefit pools.

Moose Hunting

We assume moose net benefits arise merely from moose hunting which can be expressed as:

$$NB_{H_M}(H_M) = B(H_M) - \kappa(H_M) \quad (S10)$$

where H_M is the steady-state hunting yield for a given managed moose population size in a given-aged forest, $B(H_M)$ is the benefit to hunters from moose hunting, and $\kappa(H_M)$ is the cost to moose hunters as a function of moose hunting level. To maintain a steady-state hunting yield, moose harvests H_M must equal their population growth rates implying $\frac{dM}{dt} = 0$ with moose harvest. As such, steady-state moose yield can be described in terms of the ecological dynamical system as:

$$H_M = ([\varepsilon M(T) - d_M - \Lambda M]M)_M. \quad (S11)$$

For the purposes of calibration, we consider the objective of moose hunting in isolation of other objectives. We assume first that the objective to choose the level of moose hunting is to maximize the net benefits of moose hunting, excluding the effects on timber or other aspects of the system, such as organic matter storage and carbon. The moose benefit is evaluated using hunters' willingness to pay (WTP) as a proxy for economic benefit to hunters. For our purposes the "partial equilibrium" benefits of moose hunting can be therefore written as $B(H_M) = WTP_M * H_M$, where WTP_M is the willingness to pay for moose hunting at a given moose population level.

We model the costs $\kappa(H_M)$ as an increasing and convex function, where $\kappa'(H_M) > 0$. We assume this cost takes the functional form $\kappa(H_M) = \frac{\psi}{2} H_M^2$ so that the marginal cost is linear $\kappa'(H_M) = \psi H_M$. The net benefit (Eq. S10) is estimated as the maximized solution that satisfies $WTP = \psi H_M$. Rather than solve this problem, we assume this is the problem already being solved by wildlife managers, and therefore we take an estimate of WTP and an observed level of H_M to back out a calibrated value of ψ , which in turn gives us the full cost function. By linking to observed values of H_M , the cost function incorporates the manager's revealed preferences,

accounting for market and non-market values. Note that NB_{H_M} should be a concave function with a maximum value at the observed level of H_M .

Timber Harvesting

The steady state net benefits of timber harvesting are expressed as:

$$NB_{H_T}(H_T) = H_{TY}(T(M); r) * P_T - C_H(H_T) \quad (S12)$$

where P_T is the timber unit sale price, C_H is the harvest cost as a function of harvest rate, and r is the timber rotation period (therefore $\frac{1}{r}$ is the area proportion of standing biomass harvested each year). For the purposes of this analysis—assessing tradeoffs between moose and other ecosystem services—we assume r to be a constant rotation period, resulting in a constant fraction of standing biomass harvested each year. With r constant, H_{TY} is a fully defined function of M because Eqs. S1 and S2 are assessed in steady state. As such, steady-state timber yield can be described in terms of the ecological dynamics as:

$$H_T = \mathcal{F}_T(T) - \mathcal{F}_M(T)M - \rho T \quad (S13)$$

Substituting Eqs. S13 into S12 using H_T for H_{TY} in Eq. S6 yields the complete timber harvest net benefit equation.

$$NB_{H_T}(r) = (\mathcal{F}_T(T) - \mathcal{F}_M(T)M - \rho T) * \frac{(1-\pi)*\alpha}{\lambda} * P_T - C_H(H_T) \quad (S14)$$

This equation remains a function of the fraction of biomass harvested, because r determines the level of steady-state standing biomass, T . Given moose harvesting determines the level of standing biomass as well (Eq. S1), the net benefit function also depends on moose management. Maximizing this expression with respect to the choice variable H_M tells how to manage moose when the objective is to solely maximize the net benefits of timber harvesting.

Carbon Payments

We consider a market for carbon sequestration where payments are based only on the additional carbon stored. We assume a price of carbon dioxide denoted P_C , and this is translated into a price of biomass carbon via δP_C . As noted previously, carbon is stored in two places relevant for our analysis: trees and soils in quantities αT and αOM , respectively.

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

$$f = f(M; \bar{M}) = \frac{\delta P_C \alpha}{r} (\hat{T}(M) - \hat{T}(\bar{M})), \quad (S15)$$

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

Carbon payments for the additional increment of soil carbon were similarly structured, assuming the same r time horizon and paying only for the difference accumulated between two steady states. Before defining this payment, however, we solve for OM_t for any period $t = 1, 2, \dots, r$ given an initial value OM_0 :

$$OM_t(M; OM_0) = \rho \hat{T}(M) + d_M M + \pi \hat{H}_T(M) - m_S OM_{t-1}, \quad (S16)$$

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

$$k = k(M; \bar{M}) = \frac{\delta P_C \alpha}{r} \sum_{t=1}^r [OM_t(M; OM_0) - OM_t(\bar{M}; \bar{OM}_0)] \quad (S17)$$

The summand adds up the difference in organic matter accrual over all r periods, multiplying by α/r converts the total difference into an average, annual carbon accrual, and δP_C translates the quantity into a payment. This average annual carbon accrual across r rotation plots means that carbon 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. Our analysis first establishes two baseline conditions to represent the equilibrium moose populations before the introduction of carbon payments for sequestration, as described further in main Manuscript (Eq. 4 and 5). The first baseline (Eq. S18) is for the non-harvested forest and maximizes the net benefits of moose hunting alone. The second baseline (Eq. S19) is for the harvested forest when moose density is chosen to maximize the net benefits to both hunters and timber harvesters.

$$M^\circ = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) : H_T = 0 \right\}. \quad (\text{S18})$$

$$M^{\circ\circ} = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) + NB_{H_T} \left(\hat{H}_T(M) \right) \right\}. \quad (\text{S19})$$

Because $\hat{H}_T(M)$ is always decreasing in M , accounting for the timber harvest in moose management will always create an incentive to lower moose density, i.e., $M^\circ > M^{\circ\circ}$.

Eqs. S20 and S21 consider how the non-harvested and harvested steady state equilibria change with the introduction of a carbon payment. In particular, we consider how the conditions differ for the optimally chosen level of moose density. The level of moose density with a carbon payment in the unharvested forest case will satisfy:

$$M^* = \arg \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) + f(M; M^\circ) + k(M; M^\circ) : H_T = 0 \right\}. \quad (\text{S20})$$

This baseline condition is used to estimate carbon payment increments relative to M° in (S18). Because higher moose density leads to less standing carbon and less accumulated soil carbon, we expect $M^* < M^\circ$, that is, moose densities to be lower with the carbon payment. By comparing Eq. S18 to S20, we can solve explicitly for the carbon payments (for trees and soil) and the change in net benefits to moose hunters.

For a harvested forest, the choice of moose density with carbon payments will satisfy:

$$M^{**} = \max_M \left\{ NB_{H_M} \left(\hat{H}_M(M) \right) + NB_{H_T} \left(\hat{H}_T(M) \right) + f(M; M^{\circ\circ}) + k(M; M^{\circ\circ}) \right\}. \quad (\text{S21})$$

The baseline condition for calibrating the payments is the solution $M^{\circ\circ}$ in (Eq. S19). It follows that by introducing carbon payments, (Eq. S21) introduces added incentives to reduce moose density for purposes of greater benefits from timber harvesting.

Together, the moose cost and benefit equations can be used to determine the optimal moose density for the ecosystem. This optimal point occurs where the marginal moose cost equals the marginal moose benefit, where MC_m and MB_m are the marginal cost and marginal benefit, respectively:

$$MC_m = MB_m \quad (\text{S22})$$

$$\frac{dC_m}{dt} = \frac{dB_m}{dt}$$

$$\frac{d(FB_{M=x} - FB_{M=0})}{dt} = \frac{d(WTP_{M=x})}{dt}$$

Bioeconomic Analysis

Deriving analytical solutions for the bioeconomic system is challenging given the number of equations involved and their inherent nonlinearities. For the purposes of this study, we instead opted to conduct the analyses numerically. Our approach involves examining carbon dynamics across gradients of moose population density as managed through moose hunting. Like our Economic Program, the numerical analysis thus examines carbon dynamics in terms of steady-state conditions for Eqs. S1, S2, and S3. These steady states permit expressing each of the 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, within a set of bounded conditions.

Empirical relationships

We derive the empirical relation between net ecosystem productivity (NEP) and moose population density based on measurements from moose exclosure experiments (McInnes et al. 1992). These experiments suggest that boreal NEP without moose present results in 421 tC uptake km⁻² year⁻¹, declining to 401.7 tC km⁻² year⁻¹ at low moose density and declining further to 319.5 tC km⁻² year⁻¹ at high moose density (Schmitz et al. 2014). Here we define low moose densities as 0.5 moose per km² and high moose densities as 1–1.5 moose per km² (Schmitz et al. 2014). We use a nonlinear moose-carbon relationship given moose's type-II functional response and the nonlinear effects of moose density on timber damages (Wam et al. 2005). Hence, NEP varies with moose density in an inverse sigmoidal manner (Table 1) where the marginal impact of increasing moose density is most significant between 0.3 and 1.25 moose per km². We generated an empirical sigmoid curve using a cubic spline regression fit through the above estimates of carbon uptake in relation to moose density (Main text Fig. 1).

This NEP-moose population relationship dictates the carbon dynamics for moose impacts on the forest ecosystem. We assume that varying moose impacts on carbon storage change only in direct proportion to standing tree biomass (as opposed to further altering carbon uptake by altering photosynthetic rates). This assumption is corroborated by a simulation of moose impacts on

standing biomass showing that the steady-state impacts of moose foraging at low and high population densities decrease standing biomass carbon by approximately 25% (De Jager et al. 2017), in line with our estimate above of carbon impact in relation to moose density calculated from the independent experimental data. Therefore, moose impacts on NEP are used as a measure of moose impacts on standing biomass, while carbon impacts from timber harvesting are governed by the mass and growth of standing biomass itself.

The second empirical relationship concerns the maximal range of natural moose densities to be considered in the moose hunting analysis and its feedback on NEP. Moose hunting yields can be calculated using the traditional sustainable yield (MSY) curve, obtained by taking the derivative of the moose logistic growth function with respect to population density (Eq. S2), but excluding moose harvest (H_M). This curve peaks at half of the carrying capacity, where carrying capacity is defined as $K_M = \frac{\varepsilon \mathcal{F}_M(T) - d_M}{\Lambda}$ (from Eq. S2, assuming no hunting) with a MSY of $\frac{K_M r_M}{4}$ (Getz 2012; Clark 2010). We assume a moose carrying capacity of 2.0 per km² based on a region of boreal forest absent from hunting or predation (Crête 1989). Intrinsic growth rates ($r_M = \varepsilon \mathcal{F}_M(T) - d_M$) in Eq. S2 of moose is estimated to be 0.4 (Solberg et al. 2003; Wam et al. 2005). Assuming that this intrinsic population growth rate value reflects saturated consumption rates of tree biomass by moose (i.e. $\mathcal{F}_M(T) = \max$), we apply this rate and carrying capacity to yield a maximum sustained hunting rate of 0.2 moose per km² per year (Table S1). Since moose harvest yields must be zero when moose are absent or at their carrying capacity, K_M (K_M implies no hunting pressure), these assumptions bound a sustained yield curve for different moose harvest levels, H_M .

Forest age can impact moose populations as well, with very young or old forests offering levels of forage quantity and quality that decreases moose carrying capacity. Fully mature forests offer less nutritious biomass, much of which is above the browsing height of moose. While young forests (such as those immediately post-timber harvest) exhibit highly nutritious forage opportunities, they lack the total biomass to support a high moose population. Only in boreal forests of intermediate ages do conifers such as spruce and pine offer ample and highly nutritional forage at browsing height (Hjeljord, et al. 1990; Randveer and Heikkilä 1996; Jiang et al. 2005) leading to carrying capacities higher than 2.0 moose per km². For the purposes of simplifying our analysis, meant to illustrate the process, we assume that a carrying capacity of 2.0 moose per km² applies across both non-harvested and harvested forests (Hjeljord et al. 1990).

Moose abundance, timber yield and forest carbon

We consider carbon dynamics and forest harvest yields across a range of moose densities. This analysis considers the steady-state carbon flows and harvest yields between the empirical boundary conditions: moose absence to moose carrying capacity (2 moose per km²). We translate the effect of a varying NEP-moose density relationship on timber biomass and growth by applying a timber and biomass loss factor derived from the moose-NEP relationship described above. Using the TIPSy forest biomass simulator and Chapman Richards functions employed by Asante et al. (2011) as a starting point (moose absence), we apply a percentage reduction to biomass and timber yield proportional to our documented moose-NEP reductions. This assumes that moose impact on standing biomass varies in proportion to their impact on NEP, which is supported by simulation analyses (De Jager et al. 2017). The parallel impact of moose browsing on NEP and on standing biomass and timber yields across the range of moose population densities is illustrated in Fig 1 (main text).

We illustrate the steps that are taken to arrive at a solution for the bioeconomic model, by applying representative values for the dynamical system presented above. We present solutions assuming that the dynamical system is at a steady state in our numerical analysis, thereby facilitating analyses of change in discrete increments of time and in ways that align our dynamical ecosystems model with forest harvest management modeling.

To do so, we integrate forest biomass, T , timber yield, H_{TY} , and the OM dynamics into the carbon-forestry model of Asante et al. (2011). We estimate T and H_{TY} for any forest age $t = 1, 2, \dots, n$, by estimating the standing timber biomass and standing timber yield, T_t and V_t respectively, adapted from the Chapman-Richards functions in Assante et al. (2011):

$$T_t = T = b_1(1 - e^{-b_2 t})^{b_3} \quad (S23)$$

$$V_t = \frac{v_1(1 - e^{-V_2 t})^{V_3}}{\lambda} \quad (S24)$$

$$H_T = \frac{T}{\tau r} = \frac{T_{t=r}}{r} \quad (S25)$$

$$H_{TY} = (1 - \pi)H_T = \frac{V_{t=r}}{r} \quad (S26)$$

Whereas H_{TY} and H_T represent the harvest rates per unit time, T_t and V_t are the total biomass and harvest yield for a certain forest area. These discrete-time estimates translate to harvest rates by

dividing the standing biomass level by the rotation period r , and τ which is the proportion of overall biomass held in the oldest stand age ($T_r V_r$). Therefore, τ translates the rotation period into a biomass fraction of the total forest area.

For standing timber yield (V_t), we convert the volumetric yield accounting of Asante et al. (2011) to mass of merchantable timber carbon, to make yield compatible with the biomass carbon dynamics represented in the ecological system. λ converts timber volume (m^3/km^2) into tons of merchantable timber carbon (tC/km^2). For the purposes of this analysis, we assign λ a constant value of 0.2 (tC/m^3) to reflect an estimated carbon content of 200 kg per m^3 of wood (Jessome 1977).

In these equations b_x and v_x are regression parameters that determine the slope and shape of the forest and merchantable timber growth curves. Based on the TIPSy forest biomass simulator modelled by Asante et al (2011), parameters b_1 , b_2 , and b_3 have been determined to be 19,860, 0.0253, and 2.64, respectively. Similarly, parameters v_1 , v_2 , and v_3 are determined to be 50,040, 0.027 and 4.003, respectively (Asante et al. 2011). These two growth equations replace the need to estimate the proportion of biomass that is merchantable, $(1 - \pi)$, estimated instead with the equation $H_{TOM} = T_t - V_t$. To vary Eqs. S23 and S24 for the impact of moose browsing, we apply the timber and biomass loss factors outlined above.

Organic matter inputs in a given time period OM_t represents the total OM in year t coming from natural litterfall and debris inputs from timber harvesting. OM inputs are examined in discrete time using equations that are annualized adaptations of the Forest Growth and Yield Model linked to the discretized dynamical ecosystems model where

$$OM_{nh\ t} = (1 - m_s)OM_{nh\ t-1} + \rho T_t \quad (\text{S27})$$

$$OM_{h\ t} = (1 - m_s)OM_{h\ t-1} + \rho T_t + H_{TOM}. \quad (\text{S28})$$

This set of equations accounts for OM in year t in relation to all OM from the previous year not lost to soil respiration, plus the addition of any litterfall, ρT_t , or harvest inputs H_{TOM} .

The forest carbon market considers the annual change in soil carbon, tree biomass, and merchantable timber volume. The annualized equations facilitate calculating the annual change in total ecosystem carbon to determine the annual carbon payment or liability. The average of all

OM_t from $t = 0$ to $t = r$ represents the average of all forest plots. In turn, this average results in the net annual OM accrual or loss from the system across the entire forest plot.

We assume that old growth forests have an average stand age of 100 years (McCarthy and Weetman 2006, McLaren and Peterson 1994). In line with common boreal forestry practices, our model assumes that managed forests are spruce and pine stands managed as even-aged stands. For boreal stands without a forest carbon market, ~ 80 years tends to be the ideal age to clear-cut a forest stand. In turn, a rotation of $1/80^{\text{th}}$ size plots harvested annually ensures consistent revenues (Asante et al. 2011). In the numerical analysis we assume that harvested forest stands revert to a stand age of 0, with all non-harvested biomass remaining in the system as dead organic matter as outlined above. Upon harvest, we assume all non-merchantable biomass, such as roots, bark and branches, enters the OM pool, and all harvested timber is removed from the ecosystem. Because the carbon market considers *changes* in ecosystem carbon, it treats harvested biomass as an emission (Asante et al. 2011; United Nations Environment Programme 2009). The OM pool increases due to litterfall and harvest additions and decreases due to the decomposition of biomass to CO_2 .

Values for decomposition rate, $m_S = 0.00841$, and litterfall rate, $\rho = 0.01357$, used in our analysis come from the same TIPSYS simulation designed for forest plantations (Asante et al. 2011). While litterfall rates likely remain the same, the dense forest cover and cool soil of mature forests inhibits decomposition in old growth forests. Because significant decomposition in old growth forests can occur under heavy browsing which may open up the forest canopy, we apply the decomposition rate, m_S , to the non-harvested forest scenario only when moose populations exceed 0.8 moose per km^2 , the threshold designated for high moose-carbon impacts. To smooth the transition between no decomposition and full decomposition, we assume an incremental increase in decomposition rate from $0.1m_S$ at 0.55 moose per km^2 to m_S for moose densities above 0.8 per km^2 (Bonan 1992; Kielland and Bryant 1998; Schmitz et al. 2003).

Numerical Analyses

Our bioeconomic analysis involves converting the economic and ecological program into empirical benefit functions. To this end, we have financially quantified the steady-state harvest yields and carbon flows in relation to moose abundances to consider trade-offs among competing

actors on the same landscape. Here, the numerical analysis estimates the optimal levels of moose and timber harvesting at various carbon prices by quantifying the net financial implications of the competing interests according to the maximands in Eqs. S18 through S21.

Moose Benefit

Moose harvest benefits equate to the number of moose harvested annually multiplied by the benefit of each successful moose harvest, as shown in Eq. S13. Both the level of harvesting and the benefit per harvest are a function of the moose population density. Our moose harvest assumptions reflect the trend depicted in Fig. 2 of the main text, based on a simplified solution to the steady-state dynamical system. As this only considers the benefits to moose hunters (Eq. S13), we use hunter's willingness to pay (WTP) per moose to quantify moose harvest benefits.

A recent survey of hunters in Sweden examined WTP under three different moose populations (Mattsson et al. 2014). These values represent WTP to participate in a year's hunt, excluding additional costs for equipment and travel. It therefore reflects the net benefit value for the moose hunt itself, a suitable proxy for hunters' benefits. Adjusting for historical local inflation and expressing WTP as 2021 US dollars values yields WTP values of \$692, \$844, and \$964 for equivalent densities of 0.5 1.0 and 2.0 moose per km², respectively (Lavsund, Nygrén, and Solberg 2003).

Following standard practice, we express the relationship between WTP and moose density as a logarithmic function. To produce a financial yield curve, we multiply WTP per moose by the sustainable harvest per year for a given moose density where moose density is determined by the level of forest harvesting. This annual hunting benefit represents the annual steady-state revenue curve for a forest with a maximum carrying capacity of 2.0 moose per km².

Forest Harvest Benefits

Harvest benefits are estimated using a simple estimation of timber harvest profits. To financially quantify Eq. S14, we construct a basic forestry cost and revenue function applicable to a range of standing biomass levels, representative of the range of moose densities. This leverages the harvest expenses and timber sale price estimates from the same carbon-forestry model that produced the Chapman Richard's functions (Asante et al. 2011). Converted to present US dollars, the model assumes that every ton of merchantable biomass processed costs \$199.9 to harvest and generates

\$375.9 of revenue. These expenses include hauling, milling, and overhead costs. Additionally, every square kilometer of forest costs \$525,625 for road construction and harvesting, and \$105,125 for replanting after harvest (Asante et al. 2011). Based on Eq. S25, each square kilometer of 80-year old forest contains just over 6,100 tons of merchantable biomass carbon (30,000 cubic meters), worth an estimated 2.3 million dollars in revenue and \$450,000 in profit, depending on timber prices. These cost and revenue assumptions serve as the starting point from which we differentiate moose impacts on forestry yields. Applying our moose and biomass loss factors to the estimated timber yield in Eq. S25, we create a moose population-specific forest profit function. In turn, we can estimate the change in timber harvest benefits across the range of moose densities, the harvest curve depicted in Fig. 1 in the main manuscript.

Carbon Payments

We numerically estimate carbon payments across the range of moose densities by applying the empirical assumptions to moose, forest, and timber dynamics into Eqs. S16 and S17. $\hat{T}(M)$ is estimated using the Chapman Richards function for biomass by stand age (Eq. S23) and the moose-carbon inverse sigmoidal loss factor.

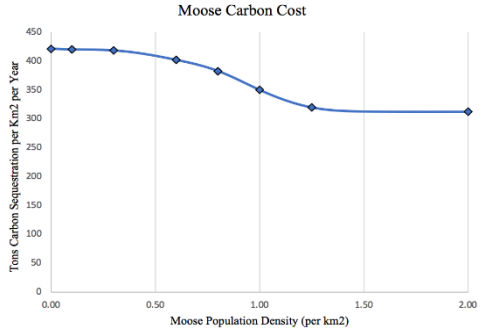
The change in soil carbon payments (Eq. S17) are estimated by applying the empirical assumptions to Eqs. S27 and S28. Although soil carbon storage varies spatially, we assume the 34,000 tC per km² average to be standard across the boreal (Watson et al. 2000). After harvest, forest stands approximately aged 0-25 years see net carbon loss due to the decomposition of the H_{TOM} outweighing forest regrowth. Between stand ages of 20 and 30 years, we assume that OM decomposition progressively diminishes to zero in year 30, unless moose over-browsing or further harvest occurs. This assumption is driven by the acceleration of biomass regrowth and forest canopy cover, and the system's return to its initial OM conditions. This culminates in an assumption of net carbon loss for stands age 0 to approximately 25 years, and net carbon accrual and therefore positive carbon payments begin thereafter. As described in Eq. S17, the net change in OM additions are estimated by taking the average of all r forest plots, here estimated as the average annual OM delta from Eqs. S27 and S28. We have chosen to exclude $d_M M$ as carbon inputs from moose mortality, as they are assumed to be negligible relative to the other carbon drivers assessed here.

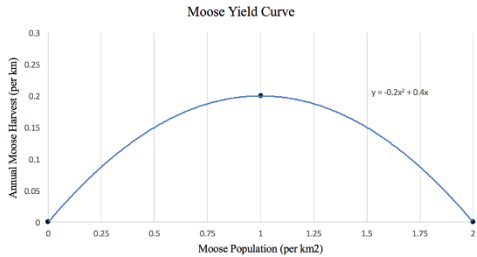
Equilibria

With each benefit function numerically estimated, the equilibria moose population at a given carbon price is the maximum of the combined total benefits across each benefit function. This solution is the maximum of Eqs. S20 and S21 according to the baseline moose populations before (Eq. S18) and after the introduction of timber harvesting (Eq. S19). Our baseline starting moose population has been estimated for both $M^* = 0.5$ and $M^* = 1.0$ in Eq. S18. The results of these maximand solutions are shown in Fig. 3 and Fig. 4, in the main text.

Table 1. Description of parameters used in the modeling, their values and the source for the estimates.

Parameter	Description	Numerical Model	Notes	Citation
T	Standing tree biomass	Estimated using Chapman Richards Function (Eq. S22) for biomass by forest stand age. From this, moose and harvest losses are subtracted accordingly	In the non-harvested forest case, T is estimated assuming average stand age of 100 years in (Eq. S22). In the harvested case, total T is the average of all rotation plots ages 0 to r	TIPSY forest biomass simulator; Asante et al (2011)
$\mathcal{F}_T(T)$	Net biomass growth rate of trees or net primary productivity (NPP = carbon uptake – carbon respiration) before other sources of biomass loss.	Estimated by comparing discrete-time annual intervals in Chapman Richards Function (Eq. S22)	Growth is numerically determined by taking $(T_t - T_{t-1})$, or can be solved by taking the derivative of T_t .	TIPSY forest biomass simulator; Asante et al (2011)
M	Moose Density	Choice variable, determined by H_M	Assessed in this report from zero to carrying capacity, K_M	
α	Fraction of Biomass that is carbon	Assumed as a constant fraction 0.5 of T and OM of biomass		(Houghton et al. 2009, Jain et al. 2010)
H_T	Timber harvest rate	Steady-state harvest rate is calculated based on the forest rotation time, r , where the annual harvest is the oldest $1/80^{\text{th}}$ of the forest plot, with biomass levels equal to forest age r (Eq. S24).	The impact of carbon pricing on the optimal rotation period has not been assessed in this analysis, though the addition of carbon and moose cost/benefits may motivate changes to this rotation depending on the economic program.	Asante et al (2011)
r	The timber rotation period	assumed at a fixed 80-year rotation $\frac{1}{r}$ is the areal proportion of standing biomass harvested each year		
τ	The proportion of overall biomass held in the oldest stand age of the forest rotation	Used to convert rotational period into biomass fraction to estimate H_T . Using the chapman Richards functions, timber yields can be		

		calculated using (Eq. S23), avoiding the need to explicitly estimate τ .																						
H_{TY}	Merchantable timber yield	Estimated using Chapman Richards Function (Eq. S23) for harvest yield by forest stand age.	Can be used to estimate either biomass or timber volume yield with coefficient λ	TIPSY forest biomass simulator; Asante et al (2011)																				
λ	Coefficient of timber volume (m ³) per tons of merchantable timber carbon	we assign λ a constant value of 0.2 to reflect an estimated carbon content of 200 kg per m ³ of wood		(Jessome 1977)																				
$\mathcal{F}_M(T)M$	Moose consumption of tree biomass	For moose-biomass losses, we converted the NEP-moose relationship into a 1:1 biomass-loss factor. We use a nonlinear moose-carbon relationship given moose’s type-II functional response and the nonlinear effects of moose density on timber damages.	<p>The graph below shows the inverse sigmoidal relationship between forest carbon/timber and moose density in our assumptions.</p>  <table><caption>Data points estimated from the 'Moose Carbon Cost' graph</caption><thead><tr><th>Moose Population Density (per km2)</th><th>Tons Carbon Sequestration per Km2 per Year</th></tr></thead><tbody><tr><td>0.00</td><td>420</td></tr><tr><td>0.25</td><td>415</td></tr><tr><td>0.50</td><td>410</td></tr><tr><td>0.75</td><td>395</td></tr><tr><td>1.00</td><td>350</td></tr><tr><td>1.25</td><td>320</td></tr><tr><td>1.50</td><td>315</td></tr><tr><td>1.75</td><td>310</td></tr><tr><td>2.00</td><td>310</td></tr></tbody></table>	Moose Population Density (per km2)	Tons Carbon Sequestration per Km2 per Year	0.00	420	0.25	415	0.50	410	0.75	395	1.00	350	1.25	320	1.50	315	1.75	310	2.00	310	(McInnes et al. 1992) (Schmitz et al. 2014) (Wam et al. 2005) (De Jager et al. 2017)
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2.00	310																							
$[\varepsilon\mathcal{F}_M(T) - d_M - \Lambda M]M$	<p>The moose growth function excluding hunting, specifically:</p> <p>ε is the efficiency by which moose-consumed plant biomass is assimilated and converted into per capita moose growth,</p>	The moose population growth curve is estimated using a logistic growth function with respect to population density	We assume a moose carrying capacity, K_M , of 2.0 per km ² based on a region of old growth boreal forest absent from hunting or predation. Intrinsic growth rates ($r_M = \varepsilon\mathcal{F}_M(T) - d_M$) of moose is estimated to be 0.4 from a study in Scandinavia.	(Crête 1989) (Solberg et al. 2003; Wam et al. 2005)																				

	d_M is the per capita natural mortality rate of moose, ΛM is a rate cost of density-dependent interactions among members of the moose population			
H_M	Sustained harvest rate of moose	Moose hunting yields for any are calculated using a traditional sustainable yield curve, the derivative of the logistic growth function above.	<p>Sustained hunting yields are increasing up to $\frac{1}{2}K_M$, here assumed to be 1 moose per km².</p> 	(Getz 2012; Clark 2010)
WTP_M	Hunters' willingness to pay for moose hunting (per moose) at a given moose population level	WTP is assumed at \$692, \$844, and \$964 per moose for equivalent densities of 0.5 1.0 and 2.0 moose per km ²	Moose benefit is evaluated using hunters' willingness to pay (WTP) as a proxy for economic benefit to hunters. This is multiplied by H_M to calculate total moose benefits (Eqs. S10 and S11).	(Lavsund, Nygrén, and Solberg 2003)
$d_M M$	debris inputs from the natural mortality rate of moose	Carbon from dead moose is considered negligible (for OM) so excluded from the model.	Mortality is naturally incorporated into the sustained yield curve for steady-state moose populations.	

πH_T	Debris inputs from timber harvesting, where π is the proportion of harvested biomass that is not sold	Non-merchantable biomass is estimated using Chapman Richards Function (Eqs. S23 and S24), where $\pi H_T = T_t - V_t$.	All non-merchantable biomass is assumed to be left in-situ in the OM pool.	TIPSY forest biomass simulator; Asante et al (2011)
ρT	The rate of natural detrital inputs from standing biomass	Litterfall rate is taken as a constant of standing biomass, where $\rho = 0.01357$		TIPSY forest biomass simulator; Asante et al (2011)
m_S	The soil respiration rate of OM	Similar to litterfall, decomposition rate is taken as a constant of OM biomass for managed timber rotations, where $m_S = 0.00841$. In mature forests with sufficient canopy cover for cool soils, decomposition may be near-zero. To account for this, no decomposition is included ($m_S = 0$) for forest plots over 30 years old, scaled down progressively starting in stand age 20.	Similarly, heavy moose browsing can open up the forest canopy, triggering decomposition non-harvested mature forests. We apply the decomposition rate, m_S , to the non-harvested forest scenario when moose populations exceed 0.8 moose per km ² , the threshold designated for high moose-carbon impacts. We assume an incremental increase in decomposition rate from 0.1 m_S at 0.55 moose per km ² to m_S for moose densities above 0.8 per km ²	(Bonan 1992; Kielland and Bryant 1998; Schmitz et al. 2003)
P_C	Carbon Price	Varied from \$0 to \$50 across the analysis		
δ	Mass conversion of carbon dioxide to carbon	To convert a carbon dioxide price into a biomass carbon price	A constant 3.67	

OM	Organic matter, where OM_0 represents the existing OM in the system before adjustments in moose management.	<p>OM_0 is assumed at 34,000 tC per km² for all cases.</p> <p>The model simplifies the dynamical OM system by using annual discrete-time equations (Eqs. S25 and S26) in line with the annual Chapman Richards forest equations.</p>	<p>Like T, the average annual dOM is calculated as the average of all r forest rotation plots to determine the steady-state level of OM accrual or decomposition.</p> <p>The steady state condition for $\frac{dOM}{dt}$ (Eq. S3) is assumed to be constant, though unlike $\frac{dT}{dt}$ (Eq. S1), $\frac{dOM}{dt} \neq 0$.</p>	(Asante et al. 2011; United Nations Environment Programme. 2009; Schmitz et al. 2003, Watson et al. 2000)
P_T	The timber unit sale price	Assumed to be \$375 per ton	Often described as a function of volume rather than mass. Multiplying by λ yields sale price \$75 per m ³ .	(Asante et al. 2011)
$C_H(H_T)$	The harvest cost as a function of harvest rate	\$200 per ton for hauling, milling, and overhead costs. Plus fixed costs per km ² of \$525,625 for road construction and harvesting, and \$105,125 for replanting after harvest	\$200 per ton equates to \$40 per m ³ using coefficient λ .	(Asante et al. 2011)

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