

Research article

Contents lists available at ScienceDirect

# Journal of Environmental Management



journal homepage: www.elsevier.com/locate/jenvman

# Controlling the stock or the habitat – The crisis of native invasive encroachment in the grazing land of Norwegian reindeer husbandry

Pham M. Nhat<sup>a,\*</sup>, Claire W. Armstrong<sup>a</sup>, Kari Anne Bråthen<sup>b</sup>, Maria Tuomi<sup>b</sup>

<sup>a</sup> Norwegian College of Fishery Science, UiT The Arctic University of Norway, 9019, Tromsø, Norway
<sup>b</sup> Department of Arctic and Marine Biology, UiT The Arctic University of Norway, 9019, Tromsø, Norway

ARTICLE INFO

Keywords: Bioeconomic modelling Native invasive species Reindeer husbandry Pasture depression Supplementary feeding

# ABSTRACT

Climate change negatively impacts reindeer grazing in Fennoscandia, with the encroachment of Empetrum nigrum (crowberry) being a significant, yet largely unrecognized problem. Crowberry encroachment affects the neighboring palatable vegetation negatively, homogenizing the pasture and decreasing ecosystem biodiversity. Current husbandry management aims are based on sustainable use of the pasture land, yet pasture quality is not considered a central indicator. To prevent overgrazing, reindeer numbers are limited, but as the animals avoid crowberry, this invasive species exacerbates the Norwegian reindeer husbandry's pasture crisis. Herders therefore intervene with two adaptive strategies, supplementary feeding and/or crowberry control. We develop a general three-species bioeconomic model with five variants to understand the economic impact of an invasive species on herbivore husbandry, and the net benefits of the two adaptive measures at the steady state. Our analytical results show that the native invasive encroachment causes a decrease in not only the nutrient-high grazing land but also the optimal herbivore herd and slaughter volume. Supplementary feeding is implemented to increase the herd size, yet the measure further depletes the grazing pasture, making this practice unsustainable. Instead, controlling crowberry protects both the grazing pasture and reindeer herd size. Applying this to the Norwegian reindeer husbandry case, we find crowberry control more cost-effective and less stressful for the pasture land than supplementary feeding. Government subsidies are shown to be essential for restoring herd sizes to the status quo.

# 1. Introduction

Tundra and boreal biomes are greatly impacted by climate change (Ims et al., 2013). Climate change also links to shifts in existing Arctic vegetation communities, such as the encroachment of the native *Empetrum nigrum* (crowberry) (Bråthen et al., 2007; González et al., 2019; Kaarlejärvi et al., 2012). Although *E. nigrum*'s berries are food sources for a number of wild animals (Pulliainen, 1972; Stenset et al., 2016), through allelopathy its leaves interfere chemically with other organisms to the extent that ecosystem process rates decline (Tybirk et al., 2000). Hence, crowberry encroachment reduces pasture quality (Bråthen et al., 2018; Tuomi et al., 2024). Besides, in the face of increasing land-use, Arctic grazing land has been decreasing (SSB, 2020). Reindeer (*Rangifer tarandus*), a dominant herbivore in Fennoscandia, an area covering the Scandinavian and Kola peninsulas, as well as mainland Finland and Karelia, is impacted by loss of grazing pasture (Vistnes and Nellemann, 2008). In this work we ask to what extent reindeer are impacted by the

encroachment of *Empetrum nigrum*, and what adaptations to the impacts can be implemented.

The Sami people commenced reindeer herding around the fifteen hundreds and over time it has become central to the identity of this ethnic minority (Riseth, 2007). Reindeer husbandry is special compared to other livestock husbandries in a Fennoscandian setting, as reindeers are only semi-herded. While most other livestock is raised in domestic settings of closed farmland, the Sami people let reindeer graze freely in the wild pasture. Reindeer husbandry in Norway operates under auspices of the Directorate of Agriculture and Food (*Landbruks-og matdepartementet*). The total reindeer stock size is regulated by the Norwegian government (Norwegian Government, 2021). To avoid tragedy of the commons, the husbandry is regulated with the goal of sustainable grazing pasture, in which the number of reindeer per land area is the target determined such that pasture collapse is prevented (Ministry of Local Government and Modernisation, 2023). However, only pasture quantity (km<sup>2</sup> area) is taken as the indicator for pasture sustainability,

\* Corresponding author. E-mail addresses: phamminhnhat0512@gmail.com, nhat.m.pham@uit.no (P.M. Nhat).

https://doi.org/10.1016/j.jenvman.2024.122457

Received 26 April 2024; Received in revised form 6 September 2024; Accepted 6 September 2024 Available online 10 September 2024

0301-4797/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

not pasture quality; the share of nutrient-rich versus nutrient-poor plants on the grazing pasture, which can critically affect the herd size (Tuomi et al., 2024). Currently, the husbandry faces many issues, such as declining pasture due to loss of land to wind turbines (Skarin et al., 2018), tourism, housing (Risvoll and Hovelsrud, 2016), and especially climate change. Climate change induced effects are occurring in the Arctic, both in winter and summer pastures (Horstkotte et al., 2020), but ongoing changes in the pastures themselves and the consequences to reindeer husbandry have received limited attention (Tuomi et al., 2024).

E. nigrum encroachment can have indirect effects on the husbandry through the decline in grazing pasture quality. For instance, E. nigrum leaves are nutrient poor, have low palatability, and contain allelopathic substances which inhibit the establishment of other primary producers, potentially reducing the abundance of other palatable species comprising the biodiverse grazing pasture (González et al., 2015; Nilsson et al., 2000; Pilsbacher et al., 2020). Hence, though a native species, E. nigrum possesses properties more familiar in invasive species, and can be considered a native invader (Carey et al., 2012; Valéry et al., 2009). Loss of grazing pasture for semi-domestic reindeer by crowberry may in the short-run place economic strain on reindeer herders, and could in the long-run alter local lifestyles, and even further threaten Sami identity (Tuomi et al., 2024). As the minority indigenous identity is actively protected in the Nordic countries, maintaining reindeer herders' way of life in the face of these challenges is therefore called for, making it vital to understand the impact of E. nigrum on grazing pasture of semi-domesticated reindeer.

When facing climate change consequences, two strategies are usually suggested - mitigation and adaptation (IPCC, 2014). The former refers to human behaviour that reduces climate change, while we focus on the latter which involves practices allowing adaptation to the changing situation. To adapt to the climate change induced pasture lock phenomenon, i.e. rain-on-snow events which freeze the snow, locking the underlying pasture from herbivores (Hansen et al., 2019), Norwegian and Swedish reindeer herders have started adopting supplementary feeding to sustain the reindeer herd size. This practice has been conducted in recent decades in Finland, as an adaptive behavioural response to limited grazing land there, but also due to climate change consequences in recent years (Horstkotte et al., 2020). The practice is not considered a sustainable solution for multiple reasons, from its impact in altering the natural migration behaviour of reindeer, to the socio-economic challenges of the practice (Horstkotte et al., 2020). For example, the herders are forced to handle challenging weather conditions to feed their herds, requiring more human effort, and greater financial burden (NORUT, 2018).

Another potential adaptive approach is to control crowberry via burning, plucking or plowing, methods which have also been used in relation to encroaching shrubs in sheep husbandry (Hare et al., 2020). Though cutting and/or burning practices for *Empetrum nigrum* (crowberry) are under testing (Tuomi et al., 2024), the same methods have been adopted for the heath of *Calluna vulgaris* (ling or heather), and have proved their effectiveness in removing this dwarf shrub to allow establishment of other more nutrient-rich plants (Calvo et al., 2020; Måren et al., 2010). Burning is also applied as one of several controls of the spread of Red Cedar in the Great Plains in North America (Jeffries et al., 2023; Ortmann et al., 1998).

The effect of crowberry on reindeer husbandry, though indirect, can to a large extent be captured by bioeconomic models. These models are the combination of biological and economic sub-models with the purpose of suggesting optimal management behaviour given economic and biological influences (Brown, 2000). The feedback loops between economic behaviour and biological interactions are embedded, thus

shedding light on the optimal strategies for the benefit of society as a whole (Din et al., 2021; Koen-Alonso, 2007). We develop a bioeconomic model following the classic prey-predator approach, with some extensions including plant-herbivore relationships, to assess the behaviour of herders facing imminent native invasive species encroachment. We choose to maximise the objective function in a static perspective mainly due to attainability of analytical solutions, and tractable comparisons between the models developed.

After shaping the general model, and assessing the analytical solutions, we tailor it to the case study of *E. nigrum* and reindeer husbandry in northern Norway. There exists empirical data from large scale ecosystem pasture surveys along with experiments that provide a number of relevant parameter values for our models (Bråthen et al., 2007; Bråthen and Lortie, 2015; Murguzur et al., 2019). The paper has four major contributions: 1) developing a three-species bioeconomic model of invasive and non-invasive plant-herbivore interactions modelling pasture loss due to native invasive species encroachment, 2) testing analytically the ecological and economic effects on the husbandry from management actions including feeding the herbivore and burning the native invader, 3) applying the model to the case of Norwegian reindeer herding, and 4) proposing a comprehensive approach to sustainable development of land use for the grazing pasture of Norwegian reindeer husbandry.

# 2. Bioeconomic model

# 2.1. Earlier models

Bioeconomic modelling of reindeer husbandry has expanded upon pure ecological models (see Gaare and Skogland (1980) referenced in Danell and Petersson (1994) for early biological reindeer models) in order to understand the interactions between the herd and its surrounding environment, and supply knowledge for better management and herder decision-making. An age-sex structured continuous-time bioeconomic model of lichen and reindeer was developed by Moxnes (1993), focusing on the role of lichen in winter grazing. Later works of Moxnes et al. (2001), Tahvonen et al. (2014), and Pekkarinen et al. (2015, 2017, 2021, 2022a, 2022b) scrutinize the bioeconomic impact of the pasture on reindeer herds, but focus on lichens and supplementary feeding, rather than the overall diet of reindeer which to a large extent, at least seasonally, involves vascular plants. Economic and ecological impacts of supplementary feeding on Finnish reindeer husbandry were for the first time studied in the works of Pekkarinen et al. (ibid). Their models depict in much detail the consumer-resource relationship between reindeer and its food sources, with emphasis on different optimized choices based on changes in discount rates, supplementary feeding cost, and governmental subsidies. Another herbivore-carnivore model for reindeer was constructed by Johannesen et al. (2019), in which they addressed food competition between individual reindeer together with other mortality reasons, such as predation and natural causes. Their model also incorporated age-sex structure as in previous models, but used total number of grazing animals as a proxy for food scarcity of reindeer.

Several gaps can be identified in the existing bioeconomic modelling literature of reindeer husbandry. First, though the existing literature does focus on reindeer diet, the importance of pasture quality and quantity has not been studied in detail. The works of Pekkarinen et al. (2015, 2017, 2021, 2022a, 2022b) scrutinize the bioeconomic impact of the pasture on reindeer herds, but focus on lichens and supplementary feeding, rather than the overall diet of reindeer which to a large extent involves vascular plants. Vascular plants are more protein-rich than

lichens and are also essential to reindeer (Storeheier et al., 2002). The existing literature mainly acknowledges reindeer feeding either by embedding their food source into the logistic growth function (Johannesen et al., 2019; Johannesen and Skonhoft, 2011) or by choosing lichen as a representative entity (Pekkarinen et al. (2015, 2017, 2021; 2022a; 2022b)), thereby neglecting the critical role of biodiversity in grazing pasture. Reindeers only consume lichen heavily in winter and graze on many other palatable plants for the rest of the year (Storeheier et al., 2002; Villrein, 2019). Besides, a diverse diet seems to be better choice for reindeer than a pure lichen diet (Aagnes et al., 1996; Olsen et al., 1997). Second, none of the existing models in the literature address environmentally induced shifts in Arctic vegetation communities, especially the case of invasive or native invasive species, and how this alteration will impact the grazing pasture of reindeer husbandry.

Though ecological and bioeconomic models of invasive alien species have been developed, the literature of invasive native species<sup>1</sup> has not been much studied. There exist a number of bioeconomic models investigating invasive species management (for example Carrasco et al., 2010; Finnoff et al., 2008; Kotani et al., 2011), but only two studies of optimal harvesting of invasive species following a prey-predator approach were found (Gupta et al., 2012; McDermott et al., 2013). Gupta et al. (2012) model the logistic growth of two competing species, though not via the feed from any other species in the habitat. While the work of Gupta et al. (2012) is theoretical, McDermott et al. (2013) is an applied study with a two-species model including interspecies competition and harvest of one of the invasive species. They model not only the population dynamics of both species but also introduction and eradication policies for the invasive one. Neither of these papers relate to the problem of a native invasive species, where there is no introduction phase to the local ecosystem. Furthermore, the modelled species do not have explicit food sources, ignoring species interactions.

Acknowledging the above-mentioned gaps, we build a three-species model in which reindeer is the herbivore that depends directly or indirectly on two plant types, one palatable vegetation and one unpalatable and native invasive species, namely crowberry. Ecological differential equations are coupled with human behaviour related to supplementary feeding and crowberry treatment. The effect of crowberry encroachment is modelled via its allelopathic impact, which diminishes intrinsic growth rates and carrying capacities of other palatable vegetation, hence indirectly influencing the reindeer stock. We first apply a basic static bioeconomic reindeer model consisting of two species, one representing grazing pasture and the other representing reindeer (Johannesen, 2014). From that, we develop three model variants to illustrate the differences between when there is no native invasive species encroachment (baseline model), and when an invasive species exists and impacts negatively on the grazing pasture (encroachment model). The last comprehensive model introduces two adaptative measures, one is the native invasive species treatment effort and the other is the reindeer feeding effort, to investigate the static optimal efforts to increase the reindeer herding profit.

Our model is simpler than most resource-based and consumerresource models, (Moxnes et al., 2001; Pekkarinen et al., 2015; van Opheusden et al., 2015), as well as viable control models (De Lara and Doyen, 2008), as in choosing the simple prey-predator approach allows attainment of analytical solutions, and general results. Furthermore, these more complex models require greater data availability than what is currently the case for crowberry. Therefore, the age-sex structure and several other factors typically included in the three aforementioned model types are omitted from this analysis.

# 2.2. A three-species bioeconomic reindeer model

# 2.2.1. Baseline model

We use the reindeer grazing/herding model of Johannesen (2014) in our baseline model, a model that is also relevant for other grazing herbivores, such as free-ranging sheep. Grazing land consists of biodiverse communities of palatable plants with variable nutritional value in summer and winter. However, for simplicity we treat these communities as a basket of species and thus assume that the pasture is homogenous year-round with only one representative palatable species, and reindeer graze on this pasture as their only natural food source. Let *V* and *R* denote the palatable aboveground high-quality vegetation biomass and herbivore population, respectively,  $M_V$  is the carrying capacity of palatable vegetation,  $\alpha_V$  is its intrinsic growth rate, and *g* is the herbivore grazing rate on vegetation. This gives the equation of change of palatable vegetation stock (subscripts referring to time are in the following ignored for ease of exposition):

$$\dot{V} = \alpha_V V \left( 1 - \frac{V}{M_V} \right) - g V R \tag{1}$$

The first part of the differential equation (1) refers to the vegetation biomass growth while the second part refers to the vegetation amount grazed by herbivores. Of the different Holling functional response types for herbivore grazing rate, we choose the Holling type 1 with linear functional grazing rate to simplify the model. The dynamics of the herbivore population through time can be described as:

$$\dot{R} = egVR - S \tag{2}$$

As the consumed vegetation biomass is transformed into herbivore numbers, we denote e as the biomass conversion rate. The first part of equation (2) refers to the growth of the herbivore population, and the second part to the slaughtered number of reindeer, *S*. Here we ignore explicit wildlife predation of reindeer and assume that the reindeer population is controlled only by slaughter.

The economic sub-model takes the form of a profit function, which includes costs and revenues from herding. As the food source of the herd is a commons, in order to maximise the social welfare function, a social planner is required. Assuming the unit price and cost factors are constant, the profit of herders, or the social welfare function, is:

$$\pi_B = pS - c_1 R \tag{3}$$

with subscript *B* denoting the baseline model, *p* being the firsthand price of one slaughtered herbivore and  $c_1$  the unit cost of maintaining one reindeer in the stock (including costs for transportation, equipment, administration, etc.).

In the following we study different reindeer management approaches and their impacts. We choose a static analysis, for several reasons, the first being mathematical convenience and the provision of comparable analytical results. Furthermore, the static equilibrium implies a discount rate equal to zero, which can be justified from an inter-generational indigenous people perspective, in this case the Sami, where arguments have been given for discount rates being closer to zero (Stoeckl et al., 2021; Tait, 2023; Trosper, 2002). Another reasoning for a static scrutiny is that crowberry can form long-lasting states in which the native invader dominates large parts of the ecosystem, causing a steady state of

<sup>&</sup>lt;sup>1</sup> In this study, we adopt a broad definition of invasive species that encompasses both native and non-native organisms exerting significant ecological impacts on local ecosystems. This aligns with recent shifts in the scientific community's understanding, as exemplified by the International Platform on Biodiversity and Ecosystem Services (IPBES) definition of invasive species in their latest report, moving away from the exclusive association to alien origins (IPBES et al., 2023). We emphasize that invasive species can originate from within the local ecosystem, encroaching upon and competing with other native species, often exacerbated by environmental changes such as climate shifts (Carey et al., 2012; Mooney and Cleland, 2001; Valéry et al., 2009).

# Empetrum-dominant heath (Tybirk et al., 2000).

**Proposition 1.** The reindeer stock at the maximum sustainable yield (MSY) level,  $R_{B,MSY}$ , increases with increasing vegetation intrinsic growth rate  $\alpha_V$  and decreases with increasing herbivore grazing rate g.

Proof: The static equilibrium is defined by setting equations (1) and (2) equal to zero, giving  $V = \frac{(\alpha_V - gR)M_V}{\alpha_V}$  and  $S = egM_VR - \frac{eg^2M_V}{\alpha_V}R^2$ . Maximising S for R, we obtain the herbivore MSY stock size:

$$R_{B,MSY} = \frac{\alpha_V}{2g}$$

satisfying Proposition 1. Intuitively, at MSY, increased vegetation intrinsic growth rate will increase  $R_{B,MSY}$  while increased grazing rate gives the opposite effect, due to the decrease in the equilibrium vegetation stock. Substituting  $R_{base,MSY}$  into the ecological equilibrium of

vegetation, we have  $V_{B,MSY} = \frac{\left(\alpha_V - g \frac{\alpha_V}{2g}\right)M_V}{\alpha_V} = \frac{M_V}{2}$ , which then gives the maximum sustainable slaughter volume  $S_{B,MSY} = egV_{B,MSY}R_{B,MSY} = \frac{eM_V\alpha_V}{4}$ .

**Proposition 2.** In the baseline scenario, the herbivore stock size and slaughter numbers at the maximum economic yield (MEY) level are smaller than for MSY, while the opposite is the case for vegetation stock.

Proof: Now focusing on the MEY of the husbandry, substituting the slaughter at equilibrium into the profit function, equation (3) becomes:

$$\pi_B = p \left( egM_V R - \frac{eg^2 M_V}{\alpha_V} R^2 \right) - c_1 R \tag{4}$$

Maximising equation (4) with regard to R, we obtain the equilibrium stocks:

$$\begin{cases} V_{B,MEY} = \frac{1}{2} \left( \frac{c_1}{peg} + M_V \right) \\ R_{B,MEY} = \frac{\alpha_V}{2g} \left( 1 - \frac{c_1}{pegM_V} \right) \\ S_{B,MEY} = \frac{eM_V \alpha_V}{4} \left( 1 - \frac{c_1^2}{p^2 e^2 g^2 M_V^2} \right) \end{cases}$$

For  $R_{B,MEY}$  and  $S_{B,MEY}$  to be ecologically feasible, we need

$$egM_V > \frac{c_1}{p} \tag{5}$$

which can be interpreted in such a way that the price-adjusted maintenance unit cost needs to be smaller than the marginal maximum growth of reindeer (as the marginal growth of reindeer is  $\frac{\partial eg VR}{\partial R} = eg V$  and  $V \leq M_V$ ).

Comparing maximum sustainable and maximum economic yields of the system,  $R_{B,MEY} < R_{B,MSY}$  and  $S_{B,MEY} < S_{B,MSY}$ , while  $V_{B,MEY} > V_{B,MSY}$ . Proposition 2 results as the manager gains revenue from slaughtering reindeer, but the maintenance cost of the stock decreases the economic optimal reindeer stock and slaughter volume relative to that of MSY, leading to larger optimal vegetation biomass. The commercially relevant reindeer stock at MEY being smaller than that at MSY ( $R_{B,MEY} < R_{B,MSY}$ ), is the opposite of the conclusion in the existing literature related to e.g. fisheries (Anderson et al., 2010; Clark, 2010; Narayanakumar, 2017). The reason being that we operate with a cost function that is linear in the stock itself, not relative to the harvest effort as in other studies. Nonetheless, the habitat stock at MEY level is larger than that at MSY ( $V_{B,MEY} > V_{B,MSY}$ ), implying that to achieve the optimal slaughter yield, the herbivore herd at the MEY level needs to be smaller than that at the MSY. This is compensated for by the habitat stock being larger than its maximum sustainable yield level.

# 2.2.2. Encroachment model

In this model we expand the growth function for the native invader as its encroachment can cause great pressure on the grazing land. Allelopathy has mainly been modelled in three ways in the literature, either as incorporated in the logistic growth function of other species (Li and Feng, 2010; McDermott et al., 2013), non-linearly included in the differential equations (Gupta et al., 2012; Solé et al., 2005) or inserted linearly as inter-specific competition (Gupta et al., 2012). We choose the simplest form of competition – linear interaction – for our model, to better understand the interactions of the species. The negative effect of this invasion is modelled as a decrease in growth of the palatable vegetation stock, transforming equation (1) into

$$\dot{V} = \alpha_V V \left( 1 - \frac{V}{M_V} \right) - g V R - \varphi V K \tag{6}$$

where *K* denotes the biomass of the native invasive species and  $\varphi$  is the positive allelopathy coefficient. The growth dynamics of *K* is described by

$$\dot{K} = \alpha_K K \left( 1 - \frac{K}{M_K} \right) \tag{7}$$

with  $\alpha_K$  being the intrinsic growth rate and  $M_K$  the carrying capacity of the population. *V* and *K* are measured in biomass, which is also the unit of the carrying capacities.<sup>2</sup>

**Proposition 3.** The allelopathic coefficient imposes a negative impact on the vegetation and reindeer stocks at MSY, and also reduces the maximum sustainable slaughter volume.

Proof: Setting equations (2), (6) and (7) equal to zero, we obtain the static equilibria  $K = M_K$ ,  $V = M_V \left(1 - \frac{g}{a_V}R - \frac{\varphi}{a_V}M_K\right)$ , and  $S = egM_V R \left(1 - \frac{g}{a_V}R - \frac{\varphi}{a_V}M_K\right)$ . K = 0 is also an equilibrium (corner) solution, but we are only

concerned with the equilibria where the native invasive species exists and impacts other stocks. Maximising the equilibrium slaughter, i.e. securing MSY, gives:

$$\begin{aligned} V_{EMSY} &= \frac{M_V}{2} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right) \\ R_{EMSY} &= \frac{\alpha_V - M_K \varphi}{2g} \\ K_{EMSY} &= \frac{M_K}{2} \\ S_{EMSY} &= \frac{eM_V \alpha_V}{4} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right)^2 \end{aligned}$$

with subscript E denoting the encroachment model and bold parts representing the difference between the MSY results of the encroachment model and that of the baseline scenario. Comparing to the baseline scenario, we have a decline in slaughter when

$$\left(1 - \frac{\varphi M_K}{\alpha_V}\right)^2 < 1 \leftrightarrow -1 < 1 - \frac{\varphi M_K}{\alpha_V} < 1 \leftrightarrow \varphi < \frac{2\alpha_V}{M_K}$$
(8)

<sup>3</sup>If condition (8) does not hold, then we have a reverse situation where the

<sup>&</sup>lt;sup>2</sup> Crowberry encroachment may compete with the palatable vegetation through allelopathic impact, but niche complementarity (Loreau et al., 2022) of crowberry and palatable vegetation species allows for non-overlapping utilization of different resources within each their niches, enabling potentially greater total mass of vegetation and crowberry per area than the carrying capacity of either (Begon and Townsend, 2021).

<sup>&</sup>lt;sup>3</sup> as all parameters are positive reals, hence  $\frac{\varphi M_K}{\alpha_V} > 0$ .

Journal of Environmental Management 370 (2024) 122457

native invader actually affects positively the MSY of the vegetation stock and slaughter volume. However, for this to be the case, we have

$$\varphi > \frac{2\alpha_V}{M_K} \leftrightarrow \varphi M_K > 2\alpha_V \leftrightarrow 2\alpha_V - \varphi M_K < 0$$

which leads to an ecologically unfeasible result as  $R_{E,MSY} < 0$  and  $V_{E,MSY} < 0$ . Thus, the inequality condition (8) holds, making  $V_{E,MSY} < 0$  $V_{B,MSY},\,R_{E,MSY}<\,R_{B,MSY}$  and  $S_{E,MSY}< S_{B,MSY}.$ 

The profit or social welfare function of the encroachment model becomes

$$\pi_E = p \left[ egM_V \left( 1 - \frac{g}{\alpha_V} R - \frac{\varphi}{\alpha_V} M_K \right) R \right] - c_1 R \tag{9}$$

Intuitively, the native invader's carrying capacity  $M_{\kappa}$  impacts negatively on the social welfare function, while the situation is the opposite regarding vegetation's carrying capacity. Besides, the allelopathic impact on the objective function is adjusted by the vegetation intrinsic growth rate  $\alpha_{v}$ , with higher  $\alpha_V$  dampening the allelopathic impact of crowberry on the pasture. This is also in line with literature on species competition (Gupta et al., 2012; Li and Feng, 2010; Solé et al., 2005). The optimal analytical solutions are

$$V_{E,MEY} = \frac{1}{2} \left( \frac{c_1}{peg} + M_V \left( 1 - \frac{\varphi M_K}{\alpha_V} \right) \right)$$
$$R_{E,MEY} = \frac{\alpha_V}{2g} \left( 1 - \frac{c_1}{pegM_V} - \frac{\varphi M_K}{\alpha_V} \right)$$
$$K_{E,MEY} = M_K$$
$$S_{E,MEY} = \frac{eM_V \alpha_V}{4} \left[ \left( 1 - \frac{\varphi M_K}{\alpha_V} \right)^2 - 1 + 1 - \left( \frac{c_1}{pegM_V} \right)^2 \right]$$

M. /

from the available grazing pasture and one artificial from the herders. This converts equation (2) into

$$\dot{R} = egVR + \beta FR - S \tag{10}$$

where F is the feeding effort the herder exerts to adapt to the native invasive encroachment, and  $\beta$  is the feeding coefficient.<sup>4</sup> Assuming that the manager will control the native invader by burning and/or cutting, equation (7) transforms into

$$\dot{K} = \alpha_K K \left( 1 - \frac{K}{M_K} \right) - \varepsilon T K \tag{11}$$

where the variable T is the treatment effort and  $\varepsilon$  is the coefficient. The reason for incorporating the treatment effort is due to the herders only being able to control their treatment effort, not the exact eradicated quantity of invasive species (Jardine and Sanchirico, 2018; Kotani et al., 2011). See appendix B and C for detailed analyses of the two feeding and controlling models, which take into account each individual adaptive measure, respectively. With subscript C denoting the comprehensive scenario, we have the following propositions:

Proposition 4. Both adaptive measures - feeding and treatment - will increase the herbivore stock at the MSY level,  $R_{C,MSY}$ , compared to the encroachment scenario. Changes in the vegetation, V<sub>C,MSY</sub>, and the slaughter volume, S<sub>C.MSY</sub>, at the MSY level, may be positive or negative, depending on the magnitude of the impacts of the two measures. The treatment measure decreases the crowberry stock at MSY, K<sub>C.MSY</sub>.

Proof: The MSY outputs of the comprehensive model take into account both adaptive measures, which thus read

$$\begin{split} V_{C,MSY} &= \frac{M_V}{2} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right) - \left[ \frac{\beta F}{2eg} \right] + \left\{ \frac{M_V M_K \varphi \varepsilon T}{2 \alpha_V \alpha_K} \right\} \\ R_{C,MSY} &= \frac{\alpha_V - M_K \varphi}{2g} + \left[ \frac{\alpha_V \beta F}{2eg^2 M_V} \right] + \left\{ \frac{M_K \varphi \varepsilon T}{2 \alpha_K g} \right\} \\ K_{C,MSY} &= \frac{M_K \{ (\alpha_K - \varepsilon T) \}}{2} \\ S_{C,MSY} &= \frac{e M_V \alpha_V}{4} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right)^2 - \left[ \frac{\alpha_V e}{M_V} \left( \frac{\beta F}{2eg} \right)^2 \right] + \left\{ \frac{e M_V M_K \varphi \varepsilon T [2 \alpha_V \alpha_K + M_K \varphi (\varepsilon T - 2 \alpha_K)]}{4 \alpha_V \alpha_K^2} \right] \end{split}$$

[ RE]

 $(M_{-}M_{-}acT)$ 

with the bold parts marking the differences between the baseline and encroachment models. Encroached by the native invader, the optimal vegetation and reindeer stocks will decrease by  $\frac{\varphi M_V M_K}{2a_V}$  and  $\frac{\varphi M_K}{2g}$  respectively. Regarding the optimal slaughter volume,  $S_{E,MEY} < S_{B,MEY}$  when the inequality condition (8) is satisfied. Relationships between the stocks at MSY and MEY levels are similar to the baseline model. See Appendix A for the comparative statics of the baseline and controlling models.

# 2.2.3. Comprehensive model

The comprehensive model depicts the situation where the herders exert two types of effort to sustain the herbivore herd and adapt to crowberry encroachment. One way to compensate for the lost grazing pasture is to provide supplementary feeding for the herbivores. The herbivore stock now grows via two different sources of food, one natural

The terms in square brackets are the impacts of supplementary feeding while those in curly brackets are the effects of controlling treatment on four variables at the MSY level. It is clear that the herbivore stock at MSY will increase due to the combination of both adaptive measures, while the changes in the vegetation at MSY and the maximum

<sup>&</sup>lt;sup>4</sup> Given a domestic setting, supplementary feeding can offset the nutritional intake from the pasture due to saturization of energy intake of the domesticated animals. However, the indigenous Sami in different Fennoscandian countries adopt this practice in various ways. While the husbandry in Finland now considers supplementary feeding a normal and common practice (Pekkarinen et al., 2022), Norwegian herders largely only feed the herd when facing harsh winter conditions, such as locked pasture because of rain-on-snow events (Helle and Jaakkola, 2008; Horstkotte et al., 2020; Turunen et al., 2016). Furthermore, Norwegian herders apply a greater degree of free-range grazing than Finnish herders. The animals have established their migration behaviour which is heavily dependent on heterogeneity and biodiversity of the summer and winter pastures. Therefore, we assume in this paper that the feeding only takes place under harsh winter conditions and thus does not affect reindeer's energy intake from the pasture.

slaughter yield will depend on the differences in magnitude of impact between the two measures.

**Proposition 5.** The larger the plant species' carrying capacities, reindeer grazing and biomass conversion rates, allelopathy and treatment coefficients, the less treatment is needed to increase the vegetation at MSY level compared to the encroachment scenario. Larger plant intrinsic growth rates and reindeer feeding coefficient works in the opposite direction.

*Proof:* In order for proposition 5 to hold, we need the inequality condition of

$$-\frac{\beta F}{2eg} + \frac{M_V M_K \varphi \varepsilon T}{2\alpha_V \alpha_K} > 0 \iff \frac{T}{F} > \frac{\beta \alpha_V \alpha_K}{eg M_V M_K \varphi \varepsilon}$$
(12)

Higher intrinsic growth rate of both plants,  $\alpha_V$  and  $\alpha_K$ , or feeding coefficient  $\beta$  will decrease the possibility of vegetation's MSY to increase in the comprehensive scenario. On the contrary, higher herbivore predation rate g and biomass conversion rate e, the carrying capacities of both plants,  $M_V$  and  $M_K$ , or the allelopathic coefficient  $\phi$  together with controlling coefficient  $\epsilon$  will support the inequality condition (12) . No simple conclusion can be derived similarly for the maximum slaughter,  $S_{C,MSY}$ .

The comprehensive social welfare function is  $\pi_C=pS-~c_1R-c_2F^2-~c_3T^2,$  which becomes

$$\pi_{C} = p \left[ eg M_{V} R \left( 1 - \frac{g}{\alpha_{V}} R - \frac{\varphi}{\alpha_{V}} M_{K} \left( 1 - \frac{\varepsilon}{\alpha_{K}} T \right) \right) + \beta F R \right] - c_{1} R - c_{2} F^{2} - c_{3} T^{2}$$

$$\tag{13}$$

where  $c_2$  and  $c_3$  are the effort unit costs of reindeer feeding and crowberry treatment respectively. We propose that the feeding cost function is quadratic, reflecting the increasing marginal costs associated with labor, which constitutes a significant portion of the feeding expenses (Horstkotte et al., 2020; NIBIO, 2020). Similarly, the labor-intensive tasks of managing invasive or pest species suggests that cost exhibits a convex relation to effort (Jardine and Sanchirico, 2018; Kotani et al., 2011). The social planner maximizes with regard to R, T, and F, and we obtain the optimal solutions (see appendix D). Since the analytical optimal solutions of the comprehensive scenario are rather complex, we apply the data from the case of Norwegian reindeer husbandry to scrutinize the best management option.

## 3. Data for the models

We study Norwegian reindeer husbandry under the impact of *E. nigrum* as an applied case for the 20 herding districts<sup>5</sup> in which crowberry treatment is currently being tested (Fig. 1). Data for model parameters are either sourced, estimated, or calibrated (Table 1). In his bioeconomic reindeer model, Moxnes (1993) set the vegetation intrinsic growth rate to 0.7; while in another bioeconomic model this parameter was set equal to 0.5 (Skonhoft et al., 2010), and we therefore choose our value as 0.6. We calculated the carrying capacity of vegetation and crowberry based on a study of vegetation biomass and species richness in northern Norway, using 1.2 kg biomass per square meter to determine the carrying capacity as this is the highest level of species richness (Bråthen and Lortie, 2015). The grazing land of the 20 herding districts is approximately 14,000 km<sup>2</sup>, making the carrying capacities of both plant species equal to 1,68 x 10<sup>10</sup> kilogram biomass.

We tuned the conversion rate *e* and grazing rate *g* to fit with the total reindeer population of the studied area of around 78,000 reindeers (Norwegian Government, 2021). Given the growth function of *V*, the marginal grazing coefficient of one reindeer is  $\frac{\partial g V R}{\partial R} = g V$ , which

demonstrates the amount of biomass (here in kilograms) grazed by one reindeer per year. A reindeer can consume from one tonne to maximum ten tonnes of biomass per year (Bakka et al., 2021; White and Trudell, 1980). We choose  $g = 9 \ge 10^{-7}$  such that, with magnitude of V being  $10^{10}$ , the marginal grazing rate of one reindeer gV can logically fit with the literature on reindeer diet and the current Norwegian reindeer herd size (Bakka et al., 2021; Norwegian Government, 2021; White and Trudell, 1980). Similarly, the biomass conversion rate  $e = 2.8x10^{-5}$  is chosen to fit with the growth of the herd and the magnitude of R. Moreover, our choice of these two parameters also results in an acceptable optimal slaughter volume which accounts for approximately 40% of the total reindeer herd in the baseline model. This mimics the slaughter rate of many other Norwegian herding districts, especially those in eastern Finnmark county where reindeer husbandry is the main industry (Norwegian Government, 2021). These two parameters are also in line with other numerical models of plant-herbivore dynamics (Feng and DeAngelis, 2018).

Growth rate and nutritional content of plants have been shown to be strongly correlated, implying that palatable plants, producing nutritionrich leaves that are advantageous for herbivores, grow faster than unpalatable ones which form nutrition-low leaves for energy conservation purposes (Freschet et al., 2010; Wright et al., 2004). As the difference in nutritional content between crowberry and the palatable vegetation is approximately a multiple of four (Murguzur et al., 2019), we set crowberry's intrinsic growth rate  $\alpha_K$  to 0.15. This parameter choice is also based on the fact that this species is proven to have a very slow growth (Hortipedia, 2022; Zverev et al., 2008). The allelopathic impact  $\varphi$  is given a lower value than that found in ecological research on allelopathy (Li et al., 2006) because this is the parameter for the allelopathic impact of one stock on another, not of one individual plant on others.

Value of maintenance  $\cot c_1$  per reindeer (including transportation, materials, administration  $\cot c_1$  is estimated from the national data on reindeer husbandry in 2020 (Norwegian Government, 2021), by dividing the total cost (excluding labour  $\cot c_2$ ) by the total number of reindeer in 2020. Unit price per reindeer *p* was calculated by dividing the total revenue by the total number of slaughtered reindeer. Economic compensation for reindeer lost due to predation and accidents (traffic, etc.) and governmental subsidies are not included.

Regarding the feeding cost, we assume, in the worst case the herder has to feed the reindeer for three months in the winter. Given an average reindeer consumes 0.65 kg of dry feed per day (NIBIO, 2020), it will require 4500 tonnes dry feed to feed the total 78,000 reindeers of 20 districts annually. The average price of dry feed is 6 NOK per kilogram (data gained through discourses with herders on fieldwork), which makes the feeding unit cost  $c_2$  equal to 6 million NOK per thousand tonnes. The price per kilogram dry feed used is similar to that found in a study of supplemental feeding in reindeer husbandry in Finland, where the price of dry feed was 0.4 Euro or about 4.2 NOK per kilogram in 2015 (Pekkarinen et al., 2015). There exists no reference to cost of effort for crowberry treatment  $c_3$  in Norway as the measure is still under testing (Tuomi et al., 2024). We choose the number of 2000 NOK for  $c_3$  as it reflects the labour cost for a 7-h fieldwork day.

The parameters  $\varepsilon$  and  $\beta$  reflect the efficiency of the effort in the controlling and feeding methods, or how vulnerable crowberry is to the treatment and how susceptible reindeer is to supplementary feeding. This is similar to how the catchability coefficient is interpreted in fishery economics (Arreguín-Sánchez, 1996). As the practice of crowberry treatment is currently at the trial stage, and feeding has only emerged in Norway in recent years, data is lacking related to these adaptations, and we therefore apply calibrated values. Since the annual quota for the reindeer population in Norway is managed by the government, our applied results are achieved by the maximization of profit from the perspective of the social planner. Likewise, the adaptive strategies are assumed to be secured by social planner policies. We set both  $\varepsilon$  and  $\beta$  to be equal to compare the effects of both the adaptive measures on the

<sup>&</sup>lt;sup>5</sup> Name of 20 districts: Orda, Fala, Nuorta-Sievju, Joahkonjarga, Seakkesnjarga, Aborassa, Favrrosorda, Lagesduottar, Marrenj-Skuohtanj, Lahtin-Vuorji-Njeaidan, Spalca, Gearretnjarga, Oarje-Sievju, Cuokcavuotna, Silvvetnjarga, Beahcegeailli, Cohkolat, Spierttanjarga, Spierttagaisa, Boalotnj-Jahkenj-Ravdol.



Fig. 1. Geographical map of the 20 chosen herding districts.

Table 1	
Ecological and economic parameter values.	

Parameters	Unit	Value	Source
$\alpha_V$		0.6	May 1975; Moxnes (1993); Skonhoft et al. (2010)
$\alpha_K$		0.15	Murguzur et al. (2019)
$M_V$	kg	1.68 x 10 <sup>10</sup>	Calculated from Bråthen and Lortie (2015)
$M_K$	kg	1.68 x 10 <sup>10</sup>	Calculated from Bråthen and Lortie (2015)
<i>c</i> <sub>1</sub>	NOK/ reindeer	1220	Calculated from Regjeringen (2021)
<i>c</i> <sub>2</sub>	NOK/1000 tonne dry feed	6,000,000	Provided by herders
<i>c</i> <sub>3</sub>	NOK/labour davs	2000	Calibrated
р	NOK/ reindeer	3760	Calculated from Regjeringen (2021)
е		$2.8 \ge 10^{-5}$	Calculated from Regjeringen (2021)
g		9 x 10 <sup>-7</sup>	Bakka et al., (2021); White and
φ		$5 \ge 10^{-12}$	Trudell (1980) Calculated from Bråthen and Lortie (2015); Bråthen & Ravolainen, 2015;
			González et al. (2015); Pilsbacher
$\varepsilon$ $\beta$		$2  ext{ x } 10^{-3}$ $2  ext{ x } 10^{-3}$	et al. (2020); Tuomi et al., 2022 Calibrated Calibrated

reindeer husbandry.

# 4. Results

The baseline model (Table 2) reflects the actual size of the reindeer stock, in the studied area in recent years, of roughly 78,000 reindeers, and the average slaughter rate of 40% of the herd size (Norwegian Government, 2021). Notice that the baseline model reflects and implies, to a large extent, the current management strategy of the husbandry, which focuses on pasture quantity, not quality. The total net benefit found here includes labour cost. These net benefits do not cover the total labour identified in the Norwegian reindeer industry, pointing to the need for substantial subsidies from the state (Norwegian Government, 2021). Numerical results indicate that *E. nigrum* (encroachment model) not only decreases the optimal vegetation stock around 10% but also drastically more than halves the optimal reindeer stock, while the optimal slaughter volume is reduced by 60%. The results show that the reindeer husbandry may lose 84% of profits due to the invasion of crowberry on grazing pasture, underlining the potential seriousness of the native invasive species and, explicitly, the important role of pasture quality in deciding the optimal herd size.

Additionally, we include two more models in this section – separate feeding and controlling models – to compare their impacts on the maximized herding profit separately (see Table 3). Mathematical details for each model can be found in appendix B and C, respectively. On the one hand, facing the loss of grazing pasture, the herders may optimally feed reindeer intensively, especially in the winter. This feeding effort assists the recovery of the optimal reindeer stock and slaughter volume

# Table 2

Applied results of five models.

	Baseline model	Encroachment model	Feeding model	Controlling model	Comprehensive model	Unit
<b>V</b> *	14.84	13.662	13.661	13.94	13.95	Million tonne biomass
$R^*$	77,863	31,196	31,227	42,157	42,213	Reindeer
<b>K</b> *		16.8	16.8	12.86	12.85	Million tonne biomass
<b>S</b> *	29,114	10,740	10,751	14,807	14,828	Reindeer
$F^*$			0.02		0.03	Thousand tonne dry feed
$T^*$				23.5	23.6	Labour days
Total effort cost			2298	1,103,310	1,110,460	NOK
Total net benefit	14.48	2.32	2.32	3.1	3.2	Million NOK

Table 3

Applying subsidies in the two adaptive models to bring the reindeer herd size back to status quo.

	Feeding model	Controlling model	Unit
<b>V</b> *	12.52	14.8	Million tonne biomass
<b>R</b> *	76,478	76,257	Reindeer
<b>K</b> *	16.8	0.58	Million tonne biomass
<b>S</b> *	28,529	28,436	Reindeer
$F^*$	28.8		Thousand tonne dry
			feed
$T^*$		96.6	Labour days
Unit effort cost	10,000	880	NOK
Total effort cost	8.3	8.2	Million NOK
Total net	5.7	5.7	Million NOK
benefit			

by 0.1%. However, due to the expansion of the reindeer stock and the uncontrolled situation of crowberry encroachment, the optimal vegetation stock shrinks slightly. Total supplementary feeding cost is only 2298 NOK, thus the net benefit increases only 2296 NOK, making this adaptive measure insufficient to support the husbandry under crowberry encroachment. On the other hand, optimally depressing E. nigrum encroachment with treatment (controlling model), without the feeding effort, helps to increase the vegetation stock by roughly 2%. This is, however, sufficient to increase the optimal reindeer stock by 35% and the optimal slaughter volume by almost 38%, via the 24% decrease in the E. nigrum stock. Hence the control assists a 35% increase in profit, leading to the result of 3.1 million NOK, despite the treatment costs requiring an additional 1.1 million NOK. Combining both adaptive behaviours, reindeer feeding and crowberry treatment, in the comprehensive model, comparing to the encroachment model, results in optimal vegetation stock growth of 2% while the reindeer stock increases 37%, leading to a nearly 40% recovery of the slaughter volume. E. nigrum thus is controlled, decreasing 25%. The total adaptation effort costs the herders 1.1 million NOK, and the solution provides a net benefit of 3.2 million NOK.

As reindeer husbandry is important for the cultural identity of the Sami people, the social planner may want to bring the optimal reindeer stock back to the status quo found in the baseline model. We therefore estimate what the cost of adaptive effort would have to be in order to attain this goal (Table 3). We decrease the unit costs of the two effort types in the feeding and the controlling models until the reindeer stock returns to the status quo level (approximately 78,000 reindeers). Regarding only supplementary feeding measures, the unit feeding cost c2 needs to shrink to 10,000 NOK/thousand tonne dry feed, which is an unrealistically low number. In total, bringing back the herd in the studied area will cost 8.3 million NOK for dry feed. The supplementary feeding strategy will, however, pull the optimal vegetation stock down an additional 8% compared to the encroachment model. Regarding the controlling model, the unit controlling cost c3 must decline to 880 NOK/ labour day. This will thus incentivize increased optimal effort to control E. nigrum by four-fold, which eventually will cost 8.2 million NOK. In both models, returning back to the status quo naturally results in higher net benefit compared to the non-status-quo results, due to the lower effort costs, but the required total effort cost exceeds the total benefit gained from herding. Nonetheless, we have not accounted for the subsidies in slaughtering, compensation for loss of reindeers by natural or other mortality, or additional subsidies related to climate change impacts.

Table 4 shows the sensitivity analysis with percentage changes in the optimal variables of the comprehensive model when the parameters increase by 10%. Studying the signs in the sensitivity analysis, all signs of the optimal variables in relation to a 10% increase in parameters are as expected. In general, optimal vegetation stock  $V_{MEY}$  is shown to be robust, while other optimal variables are more sensitive in relation to vegetation intrinsic growth rate  $\alpha_V$  and carrying capacity  $M_V$ , price p, maintenance cost  $c_1$ , biomass conversion coefficient e and grazing rate g. As  $\alpha_V$ ,  $M_V$ , p, and  $c_1$  are all obtained from actual data, the model is sensitive in relation to only two parameters, e and g.

# 5. Discussion

Via the results, the feedback loops between ecological factors and

#### Table 4

Sensitivity analysis of a 10% increase in parameter values on optimal variables in the comprehensive model (unit: %). (Sensitive results are in bold).

Parameters	Notations	Comprehensive model					
		$\Delta V_{MEY}$	$\Delta R_{MEY}$	$\Delta S_{MEY}$	$\Delta K_{MEY}$	$\Delta F_{MEY}$	$\Delta T_{MEY}$
Intrinsic growth rates	$\alpha_V$	0.8	21.1	22	-3.1	21.1	10
	$\alpha_K$	-0,4	-5.8	-6.2	6.8	-5.8	-14.3
Carrying capacity	$M_V$	7.5	18.8	19.4	-13.4	18.8	19.9
	$M_K$	-0.6	-8.2	-8.8	9.7	-8.2	1
Costs and price	$c_1$	3	-18.9	-18.3	25.2	-18.9	-18.9
	<i>c</i> <sub>2</sub>	0.0004	-0.01	-0.01	0.004	-9.1	-0.01
	<i>c</i> <sub>3</sub>	-0.2	-3.1	-3.3	3.7	-3.1	-12
	р	-2.2	18.8	16.8	-13.4	18.9	18.9
Biomass conversion coefficient	е	-2.2	18.8	14.4	-20.4	18.8	18.9
Grazing coefficient	g	-2.7	15.6	19.7	-22.9	18.6	14.4
Allelopathy coefficient	$\varphi$	-0.6	-8.2	-8.8	-0.3	-8.2	1
Treatment coefficient	ε	0.6	8	8.6	-9.4	8	18.8
Feeding coefficient	β	-0.001	0.03	0.03	-0.009	10	0.03

economic behaviour are identified. We first develop the baseline model comprising of only two species, reindeer and vegetation, and fit to the approximate actual herd size in recent years. The baseline model reflects, to a large extent, the current reindeer management strategy of the government, which only focuses in keeping the herd size based on pasture quantity, not pasture quality. E. nigrum is then introduced in the encroachment model with its allelopathic interaction with vegetation, curbing not only the availability of the optimal palatable vegetation but also of the optimal reindeer population and slaughter volume, thus leading to a substantial loss in net benefit. Our encroachment model now incorporates the issue of pasture quality in the ecosystem, supporting the argument that the lower quality of the pasture land, given the grazing area is unchanged, leads to a smaller optimal herd size. This indicates the critical importance of the inclusion of pasture quality in the government's sustainable development strategy for reindeer husbandry, which is currently largely ignored (Tuomi et al., 2024).

Facing environmental change induced consequences through crowberry encroachment, we study two adaptive strategy choices, either feeding reindeer in a supplementary fashion or controlling the native invasive species via treatment. While the feeding strategy increases the optimal reindeer stock, it simultaneously depresses further the palatable vegetation population, the latter result not occurring in the controlling model. Combining two effort types in the comprehensive model results in higher net benefit than in the two separate effort models. Interestingly, the required effort levels for both strategies in the comprehensive model are larger than the effort levels in either the feeding or the controlling model. One explanation is that as the feeding strategy increases the reindeer herd, there is a need to control more crowberry so that the pasture can be maintained in order to sustain this larger herd.

Our results point to necessary intervention to ensure high biodiversity and pasture quality for reindeer husbandry, which in this case involves controlling crowberry encroachment. This outcome is also in line with the current development strategy of the government for reindeer husbandry, emphasizing the importance of access to different types of pasture land under climate change consequences (Ministry of Local Government and Modernisation, 2023). Due to the large study area involved, effectively controlling crowberry in Norway requires a substantial and long-term initiative which would involve subsidies from the government. Furthermore, as has been underlined elsewhere, there may be challenges in ensuring broad stakeholder acceptance for burning, which may require more than purely monetary efforts (Jeffries et al., 2023).

Our analysis, additionally, provides the crowberry control effort required to sustain the status quo of reindeer husbandry. To bring the reindeer stock back up to the pre-encroachment, status quo level, governmental subsidies are essential for both adaptive strategies, potentially allowing the cost per unit effort to decline. This is the case since net benefit estimated here is net labour cost, and the results reflect the fact that reindeer herding is a subsidized industry in Norway, i.e. to cover labour costs and a normal return on investment requires subsidization. In 2020, the Norwegian government increased the annual subsidy to herders due to climate issues in reindeer husbandry by 20 million NOK, to cover solely increased feed cost, and not labour and other costs connected to feeding (County Governor, 2020). Given our calibrated treatment cost, the treatment not only costs slightly less in total to keep the status quo - with the same net benefit - but also provides a larger vegetation stock. Indeed, management decisions impact greatly on biodiversity of the pasture (Sabatier et al., 2015), and by controlling the native invader, unfavourable vegetation homogeneity can be avoided, embracing plant biodiversity which begets pasture function as biodiveristy underlies ecosystem stability (Tilman et al., 2011).

The model is generally robust. Optimal variables do not show great sensitivity to changes in the less well-known parameters, except for the grazing rate *g* and biomass conversion rate *e*. Moreover, our sensitivity analysis also shows that the model is less robust to only a few more trustworthily estimated parameters, mainly the vegetation carrying ca-

pacity, maintenance cost and price per reindeer. We suspect the high level of sensitivity to changes in vegetation carrying capacity is due to the pasture being modelled to be impacted by both reindeer and crowberry. The vegetation stock is the link between reindeer and E. nigrum, thus a slight increase in vegetation carrying capacity can cause large changes in the system. This further emphasizes how the pasture is vital to many species in the ecosystem as well as being vulnerable to crowberry encroachment in practice. Although there is no direct impact from E. nigrum on reindeer in our models, increasing unit price per reindeer or vegetation carrying capacity may indirectly help to decrease the crowberry population, through an increase in the optimal reindeer stock and slaughter volume. This is reflected in some experimental ecological studies where E. nigrum is believed to be vulnerable to heavy trampling by reindeer (Egelkraut et al., 2020; Hylgaard and Liddle, 1981); though the cause-effect relationship remains controversial, as some herders believe that reindeers usually leave the E. nigrum-dominant heath instead of trampling the species to find other food sources (Iversen et al., 2014).

Relating to the real-world situation, our models reflect the relationships between ecological variables and economic decisions as expected. It can be inferred from the optimal results, that if supplementary feeding is encouraged in coming years, reindeer grazing pasture can be further depressed. Since we do not know the exact shape of the controlling effort, the actual cost is highly uncertain. Therefore, experience and actual data of controlling effort cost and how this effort produces stock changes are needed to provide a clearer understanding of the second adaptive measure.

In our applied model we focus on the reindeer herding values, and exclude potential non-use values, though implicitly some cultural values are inherent in the current subsidization of reindeer herding (Norwegian Government, 2023). Other non-use values could potentially be E. nigrum providing a source of carbon sequestration (Ylanne et al., 2015), or alternative values from regulating and supporting ecosystem services of the pasture to other wild herbivores. Besides, there are several different options of treatment for E. nigrum, such as physical (plucking, plowing), ecological (burning) or even chemical (pesticides). Future studies could compare the efficiency of these different treatments with their corresponding costs to further assist the social planner in selecting and potentially promoting the best option. Another untouched aspect in our study includes cultural values related to social status and insurance of the herd size (Johannesen and Skonhoft, 2011). Furthermore, out-of-equilibrium trajectories, and stability of the system could be studied using optimal control theory, something we did not apply in this paper, given our focus on the analytical and comparable solutions, the pasture's steady state dominated by crowberry, and management decision-making. Applying optimal control theory could provide better insights into how to control the resources dynamically with discounted social welfare, leading to optimized outcomes following real-world ecological and economic variations.

Our paper provides four main contributions to the literature on bioeconomic reindeer modelling. First, we develop a simple bioeconomic application of the Norwegian grazing pasture and reindeer husbandry, which can be applied to other semi-domesticated husbandry cases, providing analytical solutions for the system's steady states. Second, we measure the ecological and economic impacts of two adaptive measures – reindeer feeding and invasive control – on reindeer, vegetation, and crowberry stocks. Third, we calculate the required effort of each measure and potential governmental subsidies to bring the stock back to the status-quo level, in the face of encroachment by the native invader. Fourth, we propose the critical importance of the grazing pasture quality, particularly plant heterogeneity, in sustainable development of Norwegian reindeer husbandry, which can be achieved by effectively managing crowberry.

In conclusion, *E. nigrum* encroachment with its allelopathic effect can be expected to have significant negative impact on the pastures of reindeer husbandry. Facing this environmental change, application of two adaptive strategies can be considered – either feeding reindeer or controlling crowberry, or both. One needs to bear in mind that not only reindeer graze the wild pasture but also other domestic herbivores such as sheep and wild herbivores such as moose, hares and small rodents, emphasizing the importance of high-quality pasture. Therefore, controlling *E. nigrum* could be considered one possible sustainable adaptive strategy for meeting the broader consequences of climate change in Fennoscandia.

# Funding

This work was supported by The Research Council of Norway (project number 302749).

# CRediT authorship contribution statement

Pham M. Nhat: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. Claire W. Armstrong: Writing – review & editing, Conceptualization. Kari Anne Bråthen: Validation, Project administration, Conceptualization.

# Maria Tuomi: Project administration, Conceptualization.

# Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pham Minh Nhat reports financial support was provided by Norges Forskiningsrad. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Data availability

The data sources are mentioned in the manuscript at the data section.

# Acknowledgement

We want to acknowledge the full support of Prof. Dr. Tove Aagnes Utsi, who is also a life-long reindeer herder who provided us with precious information and insights about the husbandry.

# Appendix

Appendix A. Comparative statics of the baseline and encroachment models

**Proposition A.1.:** Inequality conditions (5) and (8) have to hold so that the optimal MEY solutions in the encroachment scenario are feasible and smaller than those of the baseline scenario, illustrating the negative consequences of the native invader. These two conditions also decide the sign in changes of the optimal solutions with regards to changes in each parameter.

Proof: Analytical results for comparative statics of the optimal stocks of both baseline and encroaching models are reported in table A.1. Regarding the baseline model, given all parameters are positive real numbers, the signs of changes in stocks with regard to each parameter are apparent and reasonable, except inequality conditions required for identifying the signs of  $\frac{\partial R_{B,MEY}}{\partial \alpha_v}$ ,  $\frac{\partial R_{B,MEY}}{\partial \alpha_v}$ , As vegetation is assumed to be the only source of

growth for the herbivore in our model, we expect  $\frac{\partial R_{B,MEY}}{\partial a_V} = \frac{egM_V p - c_1}{2eg^2 M_V p} > 0$  and  $\frac{\partial S_{B,MEY}}{\partial a_V} = \frac{eM_V}{4} \left(1 - \frac{c_1^2}{p^2 e^2 g^2 M_V p^2}\right) > 0$ , which then requires  $pegM_V - c_1 > 0 \leftrightarrow \frac{c_1}{p} < c_1 = 0$ 

 $egM_V$ , which is exactly the inequality condition (5). The sign of the function  $\frac{\partial R_{B,MEY}}{\partial g} = \frac{\alpha_V \left(\frac{2c_1}{eM_V p} \cdot g\right)}{2g^3}$  depends on the term in the parenthesis. Similar to the herbivore maximum economic yield, we expect  $\frac{\partial R_{B,MEY}}{\partial g} < 0$ , which then requires

$$\frac{2c_1}{eM_V p} - g < 0 \leftrightarrow \frac{c_1}{p} < \frac{egM_V}{2}$$
(A.1)

Regarding the encroachment model, the functions' signs are mostly clear and similar to the baseline model. Inequality conditions are required to determine the signs of some functions, such as of  $\frac{\partial V_{EMEY}}{\partial M_V}$  and  $\frac{\partial R_{EMEY}}{\partial g}$ . We expect  $\frac{\partial V_{EMEY}}{\partial M_V} = \frac{a_V - M_K \varphi}{2a_V} > 0$ , which then requires that  $a_V - M_K \varphi > 0$  or  $\frac{M_K \varphi}{a_V} < 1$ , which is satisfied by the inequality condition (8). This provides negative signs for other functions, such as  $\frac{\partial S_{EMEY}}{\partial M_K} < 0$  and  $\frac{\partial S_{EMEY}}{\partial \varphi} < 0$ . Following the baseline model, we also expect that  $\frac{\partial R_{EMEY}}{\partial g} < 0$ , which then requires  $\frac{c_1}{p} < \frac{egM_V}{2} \frac{(a_V - M_K \varphi)}{a_V}$ , which is also satisfied when the inequality condition (8) holds. More conditions are required for the comparative statics of  $S_{E,MEY}$ , but as they are very complex, we assess their signs via the sensitivity analysis from our numerical application.

# Table A.1

Comparative statics of the optimal stocks of the baseline and encroaching models showing the change in equilibrium solutions for a unit change of each parameter (expressions in bold are differences between the two models)

Parameters	Baseline model			Encroachment model				
	V <sub>B,MEY</sub>	$R_{B,MEY}$	S <sub>B,MEY</sub>	$V_{E,MEY}$	$R_{E,MEY}$	S <sub>E,MEY</sub>	K <sub>E,MEY</sub>	
$\alpha_V$	0	$\frac{egM_Vp-c_1}{2eg^2M_Vp}$	$\frac{eM_V}{4}\left(1-\frac{c_1^2}{2\cdot 2\cdot 2}\right)$	$\frac{M_V M_K \varphi}{2 \alpha_V^2}$	$\frac{egM_Vp-c_1}{2eg^2M_Vp}$	$\frac{eM_V}{4}\left(1-\frac{{c_1}^2}{p^2e^2g^2{M_V}^2}-\left(\frac{M_K\varphi}{\alpha_V}\right)^2\right)$		
$M_V$	$\frac{1}{2}$	$\frac{\alpha_V c_1}{2eg^2 M_V{}^2 p}$	$\frac{p^2 e^2 g^2 M_V^2}{\frac{a_V \left(e^2 + \frac{c_1^2}{g^2 M_V^2 p^2}\right)}{4e}}$	$\frac{1}{2}\left(\frac{\pmb{\alpha_V}-\pmb{M_K}\pmb{\varphi}}{\pmb{\alpha_V}}\right)$	$\frac{\alpha_V c_1}{2eg^2 M_V{}^2 p}$	$\frac{\alpha_V\left(e^2+\frac{c_1^2}{g^2M_V^2p^2}\right)-2e^2M_K\varphi+\frac{e^2M_K^2\varphi^2}{\alpha_V}}{4e}$		
$M_K$				$-rac{M_V \varphi}{2 lpha_V}$	$-rac{arphi}{2g}$	$-\frac{eM_V\varphi(\alpha_V-M_K\varphi)}{2\alpha_V}$	1	
<i>c</i> <sub>1</sub>	$\frac{1}{2egp}$	$-rac{lpha_V}{2eg^2M_Vp}$	$-rac{lpha_V c_1}{2 e g^2 M_V p^2}$	$\frac{1}{2egp}$	$-rac{lpha_V}{2eg^2M_Vp}$	$-\frac{\alpha_V c_1}{2 e g^2 M_V p^2}$		

(continued on next page)

# Table A.1 (continued)

(B.1)

Parameters	Baseline model		Encroachment model				
	V <sub>B,MEY</sub>	$R_{B,MEY}$	S <sub>B,MEY</sub>	$V_{E,MEY}$	$R_{E,MEY}$	$S_{E,MEY}$	K <sub>E,MEY</sub>
р	$\frac{c_1}{2egp^2}$	$\frac{\alpha_V c_1}{2eg^2 M_V p^2}$	$\frac{\alpha_V c_1{}^2}{2eg^2M_Vp^3}$	$-rac{c_1}{2egp^2}$	$\frac{\alpha_V c_1}{2eg^2 M_V p^2}$	$\frac{\alpha_V c_1^2}{2eg^2 M_V p^3}$	
е	$\frac{c_1}{2e^2gp}$	$\frac{\alpha_V c_1}{2e^2 g^2 M_V p}$	$\frac{\alpha_V\left(M_V^2+\frac{c_1^2}{e^2g^2p^2}\right)}{4M_V}$	$-rac{c_1}{2e^2gp}$	$\frac{\alpha_V c_1}{2e^2 g^2 M_V p}$	$\frac{\alpha_V\left(M_V^2 + \frac{c_1^2}{e^2g^2p^2}\right) - 2M_V^2M_K\varphi + \frac{M_V^2M_K^2\varphi^2}{\alpha_V}}{4M_V}$	
g	$\frac{c_1}{2eg^2p}$	$\frac{\alpha_V \left(-g + \frac{2c_1}{eM_V p}\right)}{2g^3}$	$\frac{\alpha_V c_1^2}{2eg^3 M_V p^2}$	$-rac{c_1}{2eg^2p}$	$\frac{\alpha_V \left(-g + \frac{2c_1}{eM_V p}\right) + gM_K \varphi}{2g^3}$	$\frac{\alpha_V c_1^2}{2eg^3 M_V p^2}$	
φ		0		$-rac{M_VM_K}{2lpha_V}$	$-\frac{M_K}{2g}$	$-\frac{eM_VM_K(\alpha_V-M_K\varphi)}{2\alpha_V}$	

# Appendix B. Feeding model

The set of equations for static equilibrium are determined by setting equations (6), (7) and (12) equal to zero. The equilibrium results are similar to that of the encroachment model above except  $S = egM_VR - \frac{eg^2M_VR^2}{a_V} + \beta FR - \frac{egM_VM_RR\varphi}{a_V}$ . The native invader is unchanged compared to the encroachment model, while the *MSY* expressions of vegetation and herbivore stocks, as well as slaughter now read as

$$\begin{cases} V_{feed,MSY} = \frac{M_V}{2} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right) - \frac{\beta F}{2eg} \\ R_{feed,MSY} = \frac{\alpha_V - M_K \varphi}{2g} + \frac{\alpha_V \beta F}{2eg^2 M_V} \\ S_{feed,MSY} = \frac{eM_V \alpha_V}{4} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right)^2 - \frac{\alpha_V e}{M_V} \left( \frac{\beta F}{2eg} \right)^2 \end{cases}$$

with subscript *feed* denoting the feeding model and the bold parts describing the effects of the feeding. Feeding decreases the vegetation stock and slaughter at *MSY* level, but increases the herbivore stock. The decrease of vegetation stock due to supplementary feeding is an important finding as existing studies regarding supplementary feeding in reindeer husbandry emphasize the negative impact of this practice on reindeer health and the indigenous traditional lifestyle in the long-run (Horstkotte et al., 2020; Pekkarinen et al., 2017; Turunen et al., 2016), without acknowledging how this adaptive measure can impact negatively on the grazing pasture.

The herders take into account the cost of supplementary feeding, which alters the social welfare function (3) to:

$$\pi_{feed} = pS - c_1R - c_2F^2$$

where  $c_2$  is the cost parameter of feeding. We choose a quadratic form for the supplementary feeding cost function for mathematical convenience, but it can also be justified based on the feeding circumstances. Herders only choose to feed in harsh winter conditions, where increasing effort may be expected to meet increasing costs, especially in relation to labour, which constitutes the largest part of the feeding cost. In a static setting, equation (B.1) thus equals

$$\pi_{feed} = p \left[ egM_V R \left( 1 - \frac{g}{\alpha_V} R - \frac{\varphi}{\alpha_V} M_K \right) + \beta F R \right] - c_1 R - c_2 F^2$$
(B.2)

Again, assuming a social planner that maximizes the herders' profit with regard to *R* and *F*, we obtain the optimal results. Analytical optimal results are:

$$\begin{split} V_{feed,MEY} &= \frac{1}{2} \left( \frac{c_1}{peg} + M_V \left( 1 - \frac{\varphi M_K}{\alpha_V} \right) \right) - \frac{\alpha_V c_1 \beta^2 - \alpha_V eg M_V p \beta^2 + eg M_V M_K p \beta^2 \varphi}{2\alpha_V eg p \beta^2 - 8c_2 e^2 g^3 M_V} \\ R_{feed,MEY} &= \frac{\alpha_V}{2g} \left( 1 - \frac{c_1}{peg M_V} - \frac{\varphi M_K}{\alpha_V} \right) + \frac{\alpha_V \beta^2 (\alpha_V (eg M_V p - c_1) - eg M_V M_K p \varphi)}{2eg^2 M_V (4c_2 eg^2 M_V - \alpha_V p \beta^2)} \end{split}$$

$$K_{feed,MEY} = M_K$$

$$S_{feed,MEY} = \frac{eM_{V}\alpha_{V}}{4} \left[ \left( 1 - \frac{\varphi M_{K}}{\alpha_{V}} \right)^{2} - 1 + 1 - \left( \frac{c_{1}}{pegM_{V}} \right)^{2} \right] \\ + \frac{\beta^{2} (\alpha_{V}(c_{1} - egM_{V}p) + egM_{V}M_{K}p\varphi) (\alpha_{V}^{2}(c_{1} + egM_{V}p)\beta^{2} + 8c_{2}e^{2}g^{3}M_{V}^{2}M_{K}\varphi - \alpha_{V}egM_{V} (8c_{2}eg^{2}M_{V} + M_{K}p\beta^{2}\varphi))}{4eM_{V} (-4c_{2}eg^{3}M_{V} + \alpha_{V}gp\beta^{2})^{2}}$$

 $F_{feed,MEY} = \frac{\beta(\alpha_V(c_1 - egM_Vp) + egM_VM_Kp\varphi)}{-4c_2eg^2M_V + \alpha_Vp\beta^2}$ 

# Appendix C. Controlling model

If herders choose to avoid supplementary feeding effort and instead adopt controlling treatment, then the static equilibrium is calculated by setting equations (2), (6) and (11) equal to zero. Solving this set of equations gives the equilibrium  $K = \frac{(\alpha_K - \varepsilon T)M_K}{\alpha_K}$ ,  $V = \frac{M_V}{\alpha_V} \left( \alpha_V - gR - \varphi M_K + \frac{\varphi \varepsilon}{\alpha_K} TM_K \right)$ , and  $S = \left( egM_V - \frac{eg\varphi M_V M_K}{\alpha_V} \right) R + \frac{eg\varphi \varepsilon M_V M_K}{\alpha_V \alpha_K} TR - \frac{eg^2 M_V}{\alpha_V} R^2$ . The new stocks at the *MSY* level read

$$\begin{cases} V_{ctrl,MSY} = \frac{M_V}{2} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right) + \frac{M_V M_K \varphi \varepsilon T}{2 \alpha_V \alpha_K} \\ R_{ctrl,MSY} = \frac{\alpha_V - M_K \varphi}{2g} + \frac{M_K \varphi \varepsilon T}{2 \alpha_K g} \\ K_{ctrl,MSY} = \frac{M_K (\alpha_K - \varepsilon T)}{2} \\ S_{ctrl,MSY} = \frac{e M_V \alpha_V}{4} \left( 1 - \frac{M_K \varphi}{\alpha_V} \right)^2 + \frac{e M_V M_K \varphi \varepsilon T [2 \alpha_V \alpha_K + M_K \varphi (\varepsilon T - 2 \alpha_K)]}{4 \alpha_V \alpha_K^2} \end{cases}$$

with subscript *ctrl* denoting the controlling scenario and the bold parts being the effects of the controlling effort on the variables at the *MSY* level compared to the encroachment model. Given all parameters are positive reals, the vegetation and reindeer stocks at *MSY* will increase due to the controlling of the native invader.

The cost of treatment can be captured in the social welfare function as

$$\pi_{ctrl} = pS - c_1 R - c_3 T^2 \tag{C.1}$$

where  $c_3$  is the cost parameter of treatment. We also formulate a quadratic function for treatment cost because in practice increasing treatment requires access to more and more geographically distant places, thereby increasing costs (Epanchin-Niell, 2017; Kotani et al., 2011). Equation (C.1) then becomes

$$\pi_{ctrl} = p \left[ egM_V R \left( 1 - \frac{g}{\alpha_V} R - \frac{\varphi}{\alpha_V} M_K \left( 1 - \frac{\varepsilon}{\alpha_K} T \right) \right) \right] - c_1 R - c_3 T^2$$
(C2)

Introducing crowberry treatment provides a positive impact on the profit function by a magnitude of  $pegM_VR\frac{\varphi}{\alpha_V}M_K\frac{\varepsilon}{\alpha_K}T$  but also increases the total cost for the herders. Increasing both the controlling coefficient  $\varepsilon$  and effort T intuitively diminishes the negative impact of the native invader. Since equation (C.2) contains two control variables R and T, we maximise with regard to both variables. Optimal analytical results of the controlling model are:

$$\begin{aligned} V_{ctrl,MEY} &= \frac{1}{2} \left( \frac{c_1}{peg} + M_V \left( 1 - \frac{\varphi M_K}{\alpha_V} \right) \right) + \frac{M_V M_K^2 \varepsilon^2 \varphi^2 (\alpha_V (c_1 - eg M_V p) + eg M_V M_K p \varphi)}{2\alpha_V g (e M_V M_K^2 p \varepsilon^2 \varphi^2 - 4\alpha_V \alpha_K^2 c_3)} \\ R_{ctrl,MEY} &= \frac{\alpha_V}{2g} \left( 1 - \frac{c_1}{peg M_V} - \frac{\varphi M_K}{\alpha_V} \right) + \frac{M_K^2 \varepsilon^2 \varphi^2 (\alpha_V (c_1 - eg M_V p) + eg M_V M_K p \varphi)}{2\sigma^2 (e M_V M_K^2 p \varepsilon^2 \varphi^2 - 4\alpha_V \alpha_K^2 c_3)} \end{aligned}$$

$$K_{ctrl,MEY} = M_{K} - \frac{M_{K}^{2} \varepsilon^{2} \varphi(\alpha_{V}(egM_{V}p - c_{1}) - egM_{V}M_{K}p\varphi)}{g(4\alpha_{V}\alpha_{K}^{2}c_{3} - eM_{V}M_{K}^{2}p\varepsilon^{2}\varphi^{2})}$$

$$S_{ctrl,MEY} = \frac{eM_V \alpha_V}{4} \left[ \left( 1 - \frac{\varphi M_K}{\alpha_V} \right)^2 - 1 + 1 - \left( \frac{c_1}{pegM_V} \right)^2 \right]$$

$$+\frac{eM_{V}M_{K}^{2}\varepsilon^{2}\varphi^{2}(\alpha_{V}(c_{1}-egM_{V}p)+egM_{V}M_{K}p\varphi)\left(8\alpha_{V}^{2}\alpha_{K}^{2}c_{3}g+egM_{V}M_{K}^{3}p\varepsilon^{2}\varphi^{3}-\alpha_{V}M_{K}\varphi(8\alpha_{K}^{2}c_{3}g+M_{K}(c_{1}+egM_{V}p)\varepsilon^{2}\varphi)\right)}{\left(-4\alpha_{V}g^{2}\left(4\alpha_{V}\alpha_{K}^{2}c_{3}-eM_{V}M_{K}^{2}p\varepsilon^{2}\varphi^{2}\right)^{2}\right)}$$

 $T_{ctrl,MEY} = \frac{\alpha_{K} M_{K} \varepsilon \varphi(\alpha_{V}(c_{1} - egM_{V}p) + egM_{V}M_{K}p\varphi)}{g(-4\alpha_{V}\alpha_{K}^{2}c_{3} + eM_{V}M_{K}^{2}p\varepsilon^{2}\varphi^{2})}$ 

# Appendix D. Optimal analytical results of the comprehensive model:

The optimal solutions for the comprehensive model at are:

$$V_{C,MEY} = \frac{M_V \left( \alpha_V^2 \alpha_K^2 c_3 p^2 \beta^2 + c_2 eg M_V M_K p \varphi (2 \alpha_K^2 c_3 g + c_1 M_K e^2 \varphi) - \alpha_V \alpha_K^2 c_3 \left( 2 c_1 c_2 g + p \left( 2 c_2 e g^2 M_V + M_K p \beta^2 \varphi \right) \right) \right)}{p \left( -4 \alpha_V a 2^2 c_3 c_2 eg^2 M_V + \alpha_V^2 \alpha_K^2 c_3 p \beta^2 + c_2 e^2 g^2 M_V^2 M_K^2 p e^2 \varphi^2 \right)}$$

 $R_{C,MEY} = \frac{2\alpha_V \alpha_K^2 c_3 c_2 (\alpha_V (c_1 - egM_V p) + egM_V M_K p \varphi)}{p \left( -4\alpha_V \alpha_K^2 c_3 c_2 eg^2 M_V + \alpha_V^2 \alpha_K^2 c_3 p \beta^2 + c_2 e^2 g^2 M_V^2 M_K^2 p \varepsilon^2 \varphi^2 \right)}$ 

$$K_{C,MEY} = M_K - \frac{c_2 e g M_V M_K^2 \varepsilon^2 \varphi(\alpha_V(c_1 - e g M_V p) + e g M_V M_K p \varphi)}{-4 \alpha_V \alpha_K^2 c_3 c_2 e g^2 M_V + \alpha_V^2 \alpha_K^2 c_3 p \beta^2 + c_2 e^2 g^2 M_V^2 M_K^2 p \varepsilon^2 \varphi^2}$$

$$S_{C,MEY} = \frac{2\alpha_{V}\alpha_{K}^{2}c_{3}c_{2}(\alpha_{V}(c_{1} - egM_{V}p) + egM_{V}M_{K}p\varphi)(-2\alpha_{V}\alpha_{K}^{2}c_{3}c_{2}eg^{2}M_{V}(c_{1} + egM_{V}p) + \alpha_{V}^{2}\alpha_{K}^{2}c_{1}c_{3}p\beta^{2} + c_{2}e^{2}g^{2}M_{V}^{2}M_{K}p\phi(2\alpha_{K}^{2}c_{3}g + c_{1}M_{K}\varepsilon^{2}\varphi))}{2\alpha_{K}^{2}c_{3}c_{2}eg^{2}M_{V}(c_{1} + egM_{V}p) + \alpha_{V}^{2}\alpha_{K}^{2}c_{1}c_{3}p\beta^{2} + c_{2}e^{2}g^{2}M_{V}^{2}M_{K}p\phi(2\alpha_{K}^{2}c_{3}g + c_{1}M_{K}\varepsilon^{2}\varphi))}$$

$$p^{2}(-4\alpha_{V}\alpha_{K}^{2}c_{3}c_{2}eg^{2}M_{V}+\alpha_{V}^{2}\alpha_{K}^{2}c_{3}p\beta^{2}+c_{2}e^{2}g^{2}M_{V}^{2}M_{K}^{2}p\varepsilon^{2}\varphi^{2})^{2}$$

$$F_{C,MEY} = \frac{\alpha_V \alpha_K^2 c_3 \beta(\alpha_V(c_1 - egM_V p) + egM_V M_K p \varphi)}{-4\alpha_V \alpha_K^2 c_3 c_2 eg^2 M_V + \alpha_V^2 \alpha_K^2 c_3 p \beta^2 + c_2 e^2 g^2 M_V^2 M_K^2 p \varepsilon^2 \varphi^2}$$

$$T_{C,MEY} = \frac{\alpha_{K}c_{2}egM_{V}M_{K}\varepsilon\varphi(\alpha_{V}(egM_{V}p - c_{1}) - egM_{V}M_{K}p\varphi)}{4\alpha_{V}\alpha_{K}^{2}c_{3}c_{2}eg^{2}M_{V} - \alpha_{V}^{2}\alpha_{K}^{2}c_{3}p\beta^{2} - c_{2}e^{2}g^{2}M_{V}^{2}M_{K}^{2}p\varepsilon^{2}\varphi^{2}}$$

#### References

- Aagnes, T.H., Blix, A.S., Mathiesen, S.D., 1996. Food intake, digestibility and rumen fermentation in reindeer fed baled timothy silage in summer and winter. J. Agric. Sci. 127 (4), 517–523. https://doi.org/10.1017/S0021859600078746.
- Anderson, L.G., Seijo, J.C., Juan, C., 2010. Bioeconomics of Fisheries Management. Wiley-Blackwell.
- Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. Rev. Fish Biol. Fish. 6 (2), 221–242. https://doi.org/10.1007/bf00182344.
- Bakka, S.V., Kiseleva, N.Y., Shestakova, A.A., Shukov, P.M., Surov, S.G., Zykov, J.V., 2021. An attempt to estimate the habitat capacity of reintroduction sites for the forest reindeer in the Nizhny Novgorod region. IOP Conf. Ser. Earth Environ. Sci. 723 (2) https://doi.org/10.1088/1755-1315/723/2/022095.
- Begon, M., Townsend, C.R., 2021. Ecology: from Individuals to Ecosystems, fifth ed. 5th ed.). https://www.wiley.com/en-us/Ecology%3A+From+Individuals+to+Ecosyst ems%2C+5th+Edition-p-9781119279358.
- Bråthen, K.A., Gonzalez, V.T., Yoccoz, N.G., 2018. Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient. Perspect. Plant Ecol. Evol. Systemat. 30, 71–81. https://doi. org/10.1016/j.ppees.2017.06.005.
- Bråthen, K.A., Ims, R.A., Yoccoz, N.G., Fauchald, P., Tveraa, T., Hausner, V.H., 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10 (5), 773–789. https://doi.org/10.1007/s10021-007-9058-3.
- Bråthen, K.A., Lortie, C., 2015. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Funct. Ecol. 30 (1) https:// doi.org/10.1111/1365-2435.12458.
- Brown, D.R., 2000. A review of bio-economic models. In: The Cornell African Food Security And Natural Resource Management (CAFSNRM) Program. September.
- Calvo, L., Tarrega, R., Luis, E., 2020. Regeneration patterns in a Calluna vulgaris heathland in the Cantabrian mountains (NW Spain): effects of burning, cutting and ploughing. Forests 23 (2), 81–90. https://doi.org/10.1016/S1146-609X(02)01137-2.
- Carey, M.P., Sanderson, B.L., Barnas, K.A., Olden, J.D., 2012. Native invaders challenges for science, management, policy, and society. Front. Ecol. Environ. 10 (7), 373–381. https://doi.org/10.1890/110060.
- Carrasco, L.R., Mumford, J.D., MacLeod, A., Knight, J.D., Baker, R.H.A., 2010. Comprehensive bioeconomic modelling of multiple harmful non-indigenous species. Ecol. Econ. 69 (6), 1303–1312. https://doi.org/10.1016/j.ecolecon.2010.02.001.
- Clark, C.W., 2010. Mathematical Bioeconomics: the Mathematics of Conservation, third ed. John Wiley & Sons, Ltd.
- County Governor, 2020. 20 millioner mer til kriserammet reindrift | Statsforvalteren i Troms og Finnmark. https://www.statsforvalteren.no/troms-finnmark/landbruk/re indrift/20mill-beitekrise/.
- Danell, Ö., Petersson, C.J., 1994. A comprehensive transition matrix model for projecting production and resource consumption in reindeer herds. Rangifer 14 (3), 99. https:// doi.org/10.7557/2.14.3.1142.
- De Lara, M., Doyen, L., 2008. Sustainable Management of Natural Resources -Mathematical Models and Methods. Springer Berlin Heidelberg.
- Din, Q., Yousef, A.M., A A, E., 2021. Stability and bifurcation analysis of discrete dynamical systems. Discrete Dynam Nat. Soc. 2021 https://doi.org/10.1155/2021/ 9821615.
- Egelkraut, D., Barthelemy, H., Olofsson, J., 2020. Reindeer trampling promotes vegetation changes in tundra heathlands: results from a simulation experiment. J. Veg. Sci. 476, 476–486. https://doi.org/10.1111/jvs.12871.
- Epanchin-Niell, R.S., 2017. Economics of invasive species policy and management. Biol. Invasions 19 (11), 3333–3354. https://doi.org/10.1007/s10530-017-1406-4.
   Feng, Z., DeAngelis, D., 2018. Mathematical Models of Plant-Herbivore Interactions.
- Taylor & Francis Group.
  Finnoff, D., Strong, A., Tschirhart, J., 2008. A bioeconomic model of cattle stocking on rangeland threatened by invasive plants and nitrogen deposition. Am. J. Agric. Econ. 90 (4), 1074–1090. https://doi.org/10.1111/j.1467-8276.2008.01166.x.
- Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P., Aerts, R., 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. J. Ecol. 98 (2), 362–373. https://doi. org/10.1111/J.1365-2745.2009.01615.X.

- Gaare, E., Skogland, T., 1980. Lichen-reindeer interaction studied in a simple case model. The Second International Reindeer/Caribou Symposium 17.-21. September 1979, Roros, Norway 47–56. https://www.cabdirect.org/cabdirect/abstract/19 820731051.
- González, V.T., Junttila, O., Lindgård, B., Reiersen, R., Trost, K., Bråthen, K.A., Gonzalez, V.T., Junttila, O., Lindgard, B., Reiersen, R., Trost, K., Brathen, K.A., 2015. Batatasin-III and the allelopathic capacity of Empetrum nigrum. Nord. J. Bot. 33 (2), 225–231. https://doi.org/10.1111/njb.00559.
- González, V.T., Moriana-Armendariz, M., Hagen, S.B., Lindgård, B., Reiersen, R., Bråthen, K.A., 2019. High resistance to climatic variability in a dominant tundra shrub species. PeerJ 7 (6), e6967. https://doi.org/10.7717/peerj.6967.
- Gupta, R.P., Banerjee, M., Chandra, P., 2012. The dynamics of two-species allelopathic competition with optimal harvesting. J. Biol. Dynam. 6 (2), 674–694. https://doi. org/10.1080/17513758.2012.677484.
- Hansen, B.B., Pedersen, Å.Ø., Peeters, B., Le Moullec, M., Albon, S.D., Herfindal, I., Sæther, B.E., Grøtan, V., Aanes, R., 2019. Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. Global Change Biol. 25 (11), 3656. https://doi.org/10.1111/GCB.14761.
- Hare, M.L., Xu, X., Wang, Y., Gedda, A.I., 2020. The effects of bush control methods on encroaching woody plants in terms of die-off and survival in Borana rangelands, southern Ethiopia. Pastoralism 10 (1), 1–14. https://doi.org/10.1186/S13570-020-00171-4/FIGURES/5.
- Helle, T.P., Jaakkola, L.M., 2008. Transitions in Herd Management of Semi-domesticated Reindeer in Northern Finland. https://doi.org/10.5735/086.045.0201, 10.5735/ 086.045.0201.
- Horstkotte, T., Lépy, É., Risvoll, C., 2020. Supplementary Feeding in Reindeer Husbandry - Results from a Workshop with Reindeer Herders and Researchers from Norway, Sweden and Finland. Umeå University. https://doi.org/10.13140/ RG.2.2.12202.13762 (Issue December 2020).
- Hortipedia, 2022. Hortipedia Empetrum nigrum. https://en.hortipedia.com/Empetr um nigrum.
- Hylgaard, T., Liddle, M.J., 1981. The effect of human trampling on a sand dune ecosystem dominated by Empetrum nigrum. J. Appl. Ecol. 18 (2), 559–569. https:// doi.org/10.2307/2402417.
- Ims, R.A., Ehrich, D., Forbes, B.C., Huntley, B., Walker, D.A., Wookey, P.A., Berteaux, D., Bhatt, U.S., Bråthen, K.A., Edwards, M.E., Epstein, H.E., Forchhammer, M.C., Fuglei, E., Gauthier, G., Gilbert, S., Leung, M., Menyushina, I.E., Ovsyanikov, N.G., Post, E., et al., 2013. Terrestrial ecosystems. In: Arctic Biodiversity Assessment. Status And Trends in Arctic Biodiversity (Meltofte H. Conservation of Arctic Flora and Fauna Akureyri, pp. 385–440.
- IPBES, 2023. In: Roy, H.E., Pauchard, A., Stoett, P., Renard Truong, T. (Eds.), Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://doi.org/10.5281/ZENODO.10127795.
- IPCC, 2014. Climate change 2014: synthesis report. https://ar5-syr.ipcc.ch/topic\_adaptat ion.php.
- Iversen, M., Fauchald, P., Langeland, K., Ims, R.A., Yoccoz, N.G., Bråthen, K.A., 2014. Phenology and cover of plant growth forms predict herbivore habitat selection in a high latitude ecosystem. PLoS One 9 (6), e100780. https://doi.org/10.1371/ JOURNAL.PONE.0100780.
- Jardine, S.L., Sanchirico, J.N., 2018. Estimating the cost of invasive species control. J. Environ. Econ. Manag. 87, 242–257. https://doi.org/10.1016/j. jeem.2017.07.004.
- Jeffries, K., Mishra, B., Russell, A., Joshi, O., 2023. Exploring opinions for using prescribed fire to control eastern redcedar (juniperus virginiana) encroachment in the southern great Plains, United States. Rangel. Ecol. Manag. 86, 73–79. https:// doi.org/10.1016/J.RAMA.2022.10.002.
- Johannesen, A.B., 2014. Samisk reindrift, 2014. In: Flåten, O., Skonhoft, A. (Eds.), Naturressursenes Økonomi. Gyldendal akademisk, pp. 272–303.
- Johannesen, A.B., Olaussen, J.O., Skonhoft, A., 2019. Livestock and carnivores: economic and ecological interactions. Environ. Resour. Econ. 74 (1), 295–317. https://doi.org/10.1007/s10640-019-00318-x.
- Johannesen, A.B., Skonhoft, A., 2011. Livestock as insurance and social status: evidence from reindeer herding in Norway. Environ. Resour. Econ. 48, 679–694. https://doi. org/10.1007/s10640-010-9421-2.

Kaarlejärvi, E., Baxter, R., Hofgaard, A., Hytteborn, H., Khitun, O., Molau, U., Sjögersten, S., Wookey, P., Olofsson, J., 2012. Effects of warming on shrub abundance and chemistry drive ecosystem-level changes in a forest—tundra ecotone. Ecosystems 15 (8), 1219–1233. http://www.jstor.org/stable/23325679.

Koen-Alonso, M., 2007. A process-oriented approach to the multispecies functional response. In: Rooney, N., Mccann, K.S., Noakes, D.L.G. (Eds.), From Energetics To Ecosystems: the Dynamics And Structure Of Ecological Systems (Issue January 2007. Springer, pp. 1–36. https://doi.org/10.1007/978-1-4020-5337-5.

Kotani, K., Kakinaka, M., Matsuda, H., 2011. Optimal invasive species management under multiple uncertainties. Math. Biosci. 233 (1), 32–46. https://doi.org/ 10.1016/j.mbs.2011.06.002.

Li, Y., Feng, Z., 2010. Dynamics of a plant-herbivore model with toxin-induced functional response. Math. Biosci. Eng. 7 (1), 149–169. https://doi.org/10.3934/ mbe.2010.7.149.

Li, Y., Feng, Z., Swihart, R., Bryant, J., Huntly, N., 2006. Modeling the impact of plant toxicity on plant-herbivore dynamics. J. Dynam. Differ. Equ. 18 (4), 1021–1042. https://doi.org/10.1007/s10884-006-9029-y.

Loreau, M., Hector, A., Isbell, F., 2022. The Ecological and Societal Consequences of Biodiversity Loss. John Wiley & Sons, Ltd. https://doi.org/10.1002/ 9781119902911.

Måren, I.E., Janovský, Z., Spindelböck, J.P., Daws, M.I., Kaland, P.E., Vandvik, V., 2010. Prescribed burning of northern heathlands: Calluna vulgaris germination cues and seed-bank dynamics. Plant Ecol. 207 (2), 245–256. https://doi.org/10.1007/ s11258-009-9669-1.

McDermott, S.M., Irwin, R.E., Taylor, B.W., 2013. Using economic instruments to develop effective management of invasive species: insights from a bioeconomic model. Ecol. Appl. 23 (5), 1086–1100. https://doi.org/10.1890/12-0649.1.

Ministry of Local Government and Modernisation, 2023. Nasjonale forventninger til regional og kommunal planlegging 2023-2027 Kommunal-og distriktsdepartementet. https://www.regjeringen.no/no/dokumenter/nasjonale-for

ventninger-til-regional-og-kommunal-planlegging-20232027/id2985764/?ch=1. Mooney, H.A., Cleland, E.E., 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. USA 98 (10), 5446–5451. https://doi.org/10.1073/ PNAS.091093398

Moxnes, E., 1993. Reindrift og beitegrunnlag : en modellanalyse. https://www.nb.no/ite ms/URN:NBN:no-nb digibok 2015090808166?page=7.

Moxnes, E., Danell, Ö., Gaare, E., Kumpula, J., 2001. Optimal strategies for the use of reindeer rangelands. Ecol. Model. 145 (2–3), 225–241. https://doi.org/10.1016/ S0304-3800(01)00393-3.

Murguzur, F.J.A., Bison, M., Smis, A., Böhner, H., Struyf, E., Meire, P., Bråthen, K.A., 2019. Towards a global arctic-alpine model for Near-infrared reflectance spectroscopy (NIRS) predictions of foliar nitrogen, phosphorus and carbon content. Scientific Reports 2019 9:1 9 (1), 1–10. https://doi.org/10.1038/s41598-019-44558-9.

Narayanakumar, R., 2017. Maximum Economic Yield and its Importance in Fisheries Management. CMFRI, Kochi.

NIBIO, 2020. Tilleggsforing av reinsdyr.

Nilsson, M.C., Zackrisson, O., Sterner, O., Wallstedt, A., 2000. Characterisation of the differential interference effects of two boreal dwarf shrub species. Oecologia 123 (1), 122–128. http://www.jstor.org/stable/4222599.

NORUT, 2018. Inngrepskartlegging for Reindrifta I Troms Fylke.

Norwegian Government, 2021. Totalregnskapet for reindriften 2020 - regjeringen.no. https://www.regjeringen.no/no/aktuelt/totalregnskapet-for-reindriften-2020/i d2891755/.

Norwegian Government, 2023. Reindeer husbandry. regjeringen.no. March 14). https:// www.regjeringen.no/en/topics/food-fisheries-and-agriculture/reindeer-husbandry/ reindeer-husbandry/id2339774/.

Olsen, M.A., Aagnes, T.H., Mathiesen, S.D., 1997. The effect of timothy silage on the bacterial population in rumen fluid of reindeer (Rangifer tarandus tarandus) from natural summer and winter pasture. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 24 (2), 127–136. https://doi.org/10.1111/J.1574-6941.1997.TB00429.X.

Ortmann, J., Stubbendieck, J., Masters, R.A., Pfeiffer, G., Bragg, T., 1998. Efficacy and costs of controlling eastern redcedar. J. Range Manag. 51 (2). https://digitalcommo ns.unl.edu/usdaarsfacpub/1072.

Pekkarinen, A.J., Kumpula, J., Holand, Ø., Åhman, B., Tahvonen, O., 2022a. Bioeconomics of reindeer husbandry in Fennoscandia. In: Horstkotte, T., Holand, Ø., Kumpula, J., Moen, J. (Eds.), Reindeer Husbandry and Global Environmental Change: Pastoralism in Fennoscandia. Routledge, pp. 211–231. https://doi.org/ 10.4324/9781003118565.

Pekkarinen, A.J., Kumpula, J., Tahvonen, O., 2015. Reindeer management and winter pastures in the presence of supplementary feeding and government subsidies. Ecol. Model. 312, 256–271. https://doi.org/10.1016/j.ecolmodel.2015.05.030.

Pekkarinen, A.J., Kumpula, J., Tahvonen, O., 2017. Parameterization and validation of an ungulate-pasture model. Ecol. Evol. 7 (20), 8282–8302. https://doi.org/10.1002/ ece3.3358.

Pekkarinen, A.J., Kumpula, J., Tahvonen, O., 2021. What drives the number of semidomesticated reindeer? Pasture dynamics and economic incentives in fennoscandian reindeer husbandry. In: Nord, D.C. (Ed.), Nordic Perspective on the Responsible Development of the Arctic: Pathways to Action. Springer, Polar S, pp. 249–270. Pekkarinen, A.J., Rasmus, S., Kumpula, J., Tahvonen, O., 2022b. Winter condition variability decreases the economic sustainability of reindeer husbandry. Ecol. Appl. 33 (1), 1–19. https://doi.org/10.1002/eap.2719.

Pilsbacher, A.K., Lindgard, B., Reiersen, R., Gonzalez, V.T., Brathen, K.A., 2020. Interfering with neighbouring communities: allelopathy astray in the tundra delays seedling development. Funct. Ecol. 35 (1), 266–276. https://doi.org/10.1111/1365-2435.13694.

Pulliainen, E., 1972. Nutrition of the arctic hare (Lepus timidus) in northeastern Lapland. Ann. Zool. Fenn. 9 (1), 17–22. http://www.jstor.org/stable/23731649.

Riseth, J.Å., 2007. An indigenous perspective on national parks and Sámi reindeer management in Norway. Geogr. Res. 45 (2), 177–185. https://doi.org/10.1111/ j.1745-5871.2007.00449.x.

Risvoll, C., Hovelsrud, G.K., 2016. Pasture access and adaptive capacity in reindeer herding districts in Nordland, Northern Norway. The Polar Journal 6 (1), 87–111. https://doi.org/10.1080/2154896X.2016.1173796.

Sabatier, R., Durant, D., Hazard, L., Lauvie, A., Lecrivain, E., Magda, D., Martel, G., Roche, B., Sainte Marie, C. de, Teillard, F., Tichit, M., 2015. Towards biodiversitybased livestock systems: review of evidence and options for improvement. CABI Reviews 10 (20), 1–13. https://doi.org/10.1079/PAVSNNR201510020.

Skarin, A., Sandström, | Per, Alam, Moudud, 2018. Out of sight of wind turbines-Reindeer response to wind farms in operation. https://doi.org/10.1002/ece3.4476.

Skonhoft, A., Austrheim, G., Mysterud, A., 2010. A Bioeconomic sheep-vegetation tradeoff model: an analysis of the nordic sheep farming system. Nat. Resour. Model. 23 (3), 354–380. https://doi.org/10.1111/j.1939-7445.2010.00067.x.

Solé, J., García-Ladona, E., Ruardij, P., Estrada, M., 2005. Modelling allelopathy among marine algae. Ecol. Model. 183 (4), 373–384. https://doi.org/10.1016/j. ecolmodel.2004.08.021.

SSB, 2020. Utbygging får konsekvenser for reinbeiteområder - SSB. https://www.ssb. no/natur-og-miljo/artikler-og-publikasjoner/utbygging-far-konsekvenser-for-reinbei teomrader.

Stenset, N.E., Lutnaes, P.N., Bjarnadottir, V., Dahle, B., Fossum, K.H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O., Ronning, O., Steyaert, S.M.J.G., Zedrosser, A., Brunberg, S., Swenson, J.E., 2016. Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. Wildl. Biol. 22 (3), 107–116. https://doi.org/10.2981/wlb.00194.

Stoeckl, N., Jarvis, D., Larson, S., Larson, A., Grainger, D., Corporation, Ewamian Aboriginal, 2021. Australian Indigenous insights into ecosystem services: beyond services towards connectedness – people, place and time. Ecosyst. Serv. 50, 101341 https://doi.org/10.1016/J.ECOSER.2021.101341.

Storeheier, P.V., Mathiesen, S.D., Tyler, N.J.C., Schjelderup, I., Olsen, M.A., 2002. Utilization of nitrogen- and mineral-rich vascular forage plants by reindeer in winter. J. Agric. Sci. 139 (2), 151–160. https://doi.org/10.1017/S0021859602002344.

Tahvonen, O., Kumpula, J., Pekkarinen, A.J., 2014. Optimal harvesting of an agestructured, two-sex herbivore-plant system. Ecol. Model. 272, 348–361. https://doi. org/10.1016/j.ecolmodel.2013.09.029.

Tait, P., 2023. Social discount rates in cost benefit analysis of regional pest management plans: guidance and recommendations for the uninitiated. https://bioheritage.nz /outputs/social-discount-rates-in-cost-benefit-analysis-of-regional-pest-manageme nt-plans-guidance-and-recommendations-for-the-uninitiated/.

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Sciences of the United States of America 108 (50), 20260–20264. https://doi.org/10.1073/ PNAS.1116437108/SUPPL FILE/PNAS.201116437SLPDF.

Trosper, R.L., 2002. Northwest coast indigenous institutions that supported resilience and sustainability. Ecol. Econ. 41 (2), 329–344. https://doi.org/10.1016/S0921-8009(02)00041-1.

Tuomi, M.W., Utsi, T.A., Yoccoz, N., Armstrong, C.W., Gonzalez, V., Hagen, S.B., Jónsdóttir, I.S., Pugnaire, F.I., Shea, K., Wardle, D.A., Zielosko, S., Bråthen, K.A., 2024. The increase of an allelopathic and unpalatable plant undermines reindeer pasture quality and current management in the Norwegian tundra. Communications Earth & Environment 5 (1). https://doi.org/10.1038/s43247-024-01451-2.

Turunen, M.T., Rasmus, S., Bavay, M., Ruosteenoja, K., Heiskanen, J., 2016. Coping with difficult weather and snow conditions: reindeer herders' views on climate change impacts and coping strategies. Climate Risk Management 11, 15–36. https://doi.org/ 10.1016/J.CRM.2016.01.002.

Tybirk, K., Nilsson, M.C., Michelsen, A., Kristensen, H.L., Sheytsova, A., Strandberg, M. T., Johansson, M., Nielsen, K.E., Riis-Nielsen, T., Strandberg, B., Johnsen, I., Shevtsova, A., Strandberg, M.T., Johansson, M., Nielsen, K.E., Riis-Nielsen, T., Strandberg, B., Johnsen, I., Sheytsova, A., et al., 2000. Nordic Empetrum dominated ecosystems: function and susceptibility to environmental changes. Ambio 29 (2), 90–97. https://doi.org/10.1579/0044-7447-29.2.90.

Valéry, L., Fritz, H., Lefeuvre, J.C., Simberloff, D., 2009. Invasive species can also be native. Trends Ecol. Evol. 24 (11), 585. https://doi.org/10.1016/j.tree.2009.07.003.

van Opheusden, J.H.J., Hemerik, L., van Opheusden, M., van der Werf, W., 2015. Competition for resources: complicated dynamics in the simple Tilman model. SpringerPlus 4 (1). https://doi.org/10.1186/s40064-015-1246-6.

Villrein, 2019. Hva spiser reinen? — Villrein.no - alt om villrein. https://www.villrein. no/aktuelt/hva-spiser-reinen.

- Vistnes, I.I., Nellemann, C., 2008. Reindeer winter grazing in alpine tundra: impacts on ridge community composition in Norway. Arctic Antarct. Alpine Res. 40 (1), 215-224. http://www.jstor.org/stable/20181781. White, R.G., Trudell, A., 1980. Habitat preference and forage consumption by reindeer
- and caribou near atkasook, Alaska. Arct. Alp. Res. 12 (4), 511-529.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., 2004. The worldwide leaf economics spectrum. Nature 428 (6985), 821-827. https://doi.org/10.1038/ nature02403 al et.
- Ylanne, H., Stark, S., Tolvanen, A., 2015. Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19years of warming and simulated herbivory in the subarctic tundra. Global Change Biol. 21 (10), 3696–3711. https://doi.org/10.1111/gcb.12964. Zverev, V.E., Zvereva, E.L., Kozlov, M.V., 2008. Slow growth of Empetrum nigrum in
- industrial barrens: combined effect of pollution and age of extant plants. ENVIRONMENTAL POLLUTION 156 (2), 454-460. https://doi.org/10.1016/j. envpol.2008.01.025.