UiT The Arctic University of Norway

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Bioeconomic analysis of Norwegian reindeer husbandry in the face of crowberry encroachment

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1 Acknowledgements

The start of this doctorate journey was like stepping into an uncharted wilderness – challenging, unpredictable, but remarkably inspiring. Much like the tundra landscape of northern Norway, it was a journey that first seemed vast and immense. Yet, with the guidance of the shepherds, the journey started to show itself by continuous discoveries, numerous failures, and persevered breakthroughs that shaped the path forward. Through every obstacle, I found myself drawn deeper into the intertwined connections between nature and human decision-making, guided by the harmony and complexity that lie at the heart of both ecosystems and mathematical models. What inspires me through this PhD journey is the beauty of Norwegian nature and mathematics.

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2 Abbreviations

EDS – Ecosystem Disservices

ES – Ecosystem Services

NCP – Nature’s Contribution to People

SLR – Systematic Literature Review

3 List of papers and Declarations of contributions

1. How disservices illuminate divergence between “nature’s contribution to people” and “ecosystem services” – an assessment of *Empetrum nigrum*
   Condition: Submitted

2. Controlling the stock or the habitat – The crisis of native invasive encroachment in the grazing land of Norwegian reindeer husbandry
   Condition: published in *Journal of Environmental Management*

3. When climate change turns good plant bad – A dynamic multispecies model of reindeer herding in a changing Arctic
   Condition: Submitted

4. Dr. Jekyll and Mr. Hyde – How different ecosystem (dis)services perspectives alter management decisions of a native invasive encroachment
   Condition: Submitted

Table of author contributions

Contributions	Paper 1	Paper 2	Paper 3	Paper 4
Conceptualization	PN, CA	PN, CA	PN, CA, CS	PN, CA, SL
Study design & Methods	PN, CA, KB, MT	PN, CA	PN, CA, CS	PN, SL
Data gathering	PN	PN, CA, KB, MT	PN	PN
Data analysis	PN, CA, KB, MT	PN, CA	PN, CA, CS	PN, CA, SL
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MT – Maria Tuomi; CS – Charles B. Sims; SZ – Suzanne Lenhart.

With my signature I consent that the above listed articles where I am a co-author can be a part of the PhD thesis of the PhD candidate

Co-author's name	**Signature**
Prof. Claire W. Armstrong	C. Armstrong
Prof. Kari Anne Bråthen	Kari Anne Bråthen
Dr. Maria Tuomi	Maria Tuomi
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Prof. Suzanne Lenhart	Suzanne Lenhart

4 Abstract

Allelopathic encroachment of *Empetrum nigrum* (crowberry) is impacting the Norwegian reindeer husbandry. This thesis first explores both the negative and positive impacts of crowberry, and then analyses the effect of its encroachment on the husbandry under climate change. The thesis consists of four papers, one qualitative study conducting systematic literature review of *Empetrum nigrum*, and three quantitative studies applying the method of bioeconomic modeling. The first paper categorizes the benefits and detriments of crowberry using three different nature assessment concepts, and finds mixed impacts on the local socioecological system, particularly eight benefits and three detriments. Focusing on the detrimental impacts of crowberry, the three quantitative papers develop various versions of the reindeer bioeconomic model, including three stocks – vegetation, crowberry, and reindeer – along with two primary adaptive measures: reindeer feeding and crowberry control. The second paper applies static optimization and concludes that controlling crowberry alongside reindeer feeding can mitigate the negative impacts of encroachment. The third paper extends the analysis to dynamic optimization, confirming the importance of controlling crowberry to maintain high quality grazing pasture and reindeer population over time. Using optimal control theory, the fourth paper explores a specific yet neglected benefit of crowberry – carbon sequestration – and demonstrates that with this beneficial value, the optimal efforts to control crowberry should be less than in scenarios without.

The thesis hence underscores several policy implications. Firstly, adoption of the Nature's Contribution to People (NCP) concept may be embraced to provide a comprehensive perspective. Secondly, the socio-ecological system of the husbandry is impacted negatively by crowberry encroachment through deteriorating grazing pastures. Thirdly, while supplementary

feeding can increase reindeer numbers, it does not address the ecological issues of pasture degradation, thus should be considered only as a short-term solution. Fourthly, given governmental support, crowberry control can be considered a sustainable solution to improve pasture quality and increase reindeer population. Lastly, to effectively balance the benefits and detriments of this plant, crowberry control efforts must be carefully managed in the long-run (beyond a 10-year perspective) to achieve desired outcomes.

5 Sammendrag

Miljøendringer medfører allelopatisk gjengroing av *Empetrum nigrum* (krekling) som påvirker den norske reindriftsnæringen. Denne avhandlingen studerer både negative og positive effekter av gjengroing av krekling på reindriften. Avhandlingen består av fire artikler, én kvalitativ studie som gjennomfører en systematisk litteraturgjennomgang av *Empetrum nigrum*, og tre kvantitative studier som anvender bioøkonomisk modellering. Den første artikkelen kategoriserer kreklings fordeler og ulemper ved hjelp av tre forskjellige naturvurderingskonsepter og finner blandede effekter på det lokale sosioøkologiske systemet, spesifikt åtte fordeler og tre ulemper. Med fokus på de negative effektene av krekling, utvikler de tre kvantitative artiklene forskjellige versjoner av den bioøkonomiske modellen, inkludert tre bestander – vegetasjon, krekling og rein – sammen med to primære tilpasningstiltak: tilleggsfôring og kontroll av krekling. Den andre artikkelen anvender statisk optimering og konkluderer med at kontroll av krekling sammen med tilleggsfôring kan mildne de negative effektene av gjengroing. Den tredje artikkelen utvider analysen til dynamisk optimering og bekrefter viktigheten av å kontrollere krekling for å opprettholde høykvalitets beiteområder for reindriften over tid. Ved bruk av optimal kontrollteori utforsker den fjerde artikkelen en spesifikk, men neglisjert, fordel forbundet med krekling – karbonsekvestrasjon – og demonstrerer at med denne fordelaktige verdien, bør de optimale tiltakene for å kontrollere krekling være mindre enn i scenarier uten.

Avhandlingen understreker dermed flere forvaltningsmessige implikasjoner. For det første kan anvendelse av NCP-rammeverket omfavnes for å gi et bredere perspektiv på naturvurdering. For det andre påvirkes det sosioøkologiske systemet i reindriftsnæringen negativt av gjengroing av krekling gjennom forverring av beiteområder. For det tredje, selv om tilleggsfôring kan øke antall rein, adresserer det ikke de økologiske problemene på beiteområdet, og bør derfor kun vurderes som en kortsiktig løsning. For det fjerde, med statlig støtte, kan kontroll av krekling vurderes som en bærekraftig løsning for å forbedre beitekvaliteten og øke reinflokken. Til slutt, for å effektivt balansere fordelene og ulempene forbundet med krekling, må innsatsen for å kontrollere denne arten håndteres nøye på lang sikt (utover et 10-års perspektiv) for å oppnå ønskede resultater.

6 Introduction

The reindeer husbandry of the indigenous Sami people is suffering from a pasture crisis caused by climate and environmental changes (Ims et al., 2013; Rees et al., 2008; Skarin & Åhman, 2014; Tyler et al., 2021). A number of ecological effects of this crisis have been much studied (Albon et al., 2017; Hansen et al., 2019; Korosuo et al., 2014; Myers-Smith et al., 2020) but the economic effects are less well known. Among the identified climate change impacts in the Arctic (Ims et al., 2013), the emerging problem of *Empetrum nigrum* (crowberry)[1] encroachment has received some attention (see Tuomi et al. (2024)). Despite being a native plant, *E. nigrum* has similar traits as an invasive species, for instance strong competitiveness, and high endurance and resilience to climate and environmental change. Crowberry encroachment has been alarmed to have detrimental effects on the biodiverse grazing pasture, especially due to its allelopathic substances that inhibit growth of other neighboring plant species (Bråthen et al., 2018; González et al., 2015; Pilsbacher et al., 2020). Nonetheless, economic analysis for this impact has not been investigated. This thesis, thus, aims to study the intertwined ecological and economic impacts of *E. nigrum* on the Sami reindeer husbandry in Norway, to first, understand the entangled ecological dynamics of crowberry, the grazing pasture, and reindeer; and second, to determine whether and how crowberry should optimally be managed. The thesis analyses qualitatively and quantitatively how *E. nigrum* can affect the sustainable development of the husbandry, and to what extent this native invader should optimally be controlled. The key methodological approach of this thesis is bioeconomic

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[1] Throughout this manuscript, the terms "*Empetrum nigrum*", "*E. nigrum*", and "crowberry" are used interchangeably.

modeling, which is applied to investigate the static and dynamic impacts of crowberry on the pasture and the reindeer herd.

Before building bioeconomic models, a systematic literature review was conducted to have a comprehensive picture of *E. nigrum*'s benefits and detriments. To define and categorize the direct and indirect benefits and detriments of crowberry towards human beings, three concepts of ecosystem services (ES), ecosystem disservices (EDS), and nature's contribution to people (NCP) were applied (Braat & de Groot, 2012; Guo et al., 2022; Millennium Ecosystem Assessment, 2005; Ruckelshaus et al., 2020). The results indicate that while *Empetrum nigrum* provides several direct ecosystem services to humans (Hakkinen et al., 1999; Hellström et al., 2013; Ho et al., 2017; Kallio & Yang, 2014; Laaksonen et al., 2011; Lyanguzova, 2021; Moskaug et al., 2008; Ylanne et al., 2015), the plant also provides a number of indirect ecosystem disservices, such as inhibiting growth of neighboring plants, deteriorating other species' habitat, and decreasing the local ecosystem biodiversity (Bråthen & Ravolainen, 2015; Gallet et al., 1999; González et al., 2015; Hypponen et al., 2013; Pilsbacher et al., 2020).

After the qualitative study, analyses of the ecological and economic impacts of crowberry on reindeer were focused on for two reasons. First, although crowberry provides several direct benefits to humans and animals, the plant competes ferociously with other native vegetative species, which can have critically negative consequences for the stability of the local ecosystems and the Sami's reindeer husbandry (Bråthen et al., 2007; Gonzalez et al., 2021; Tuomi et al., 2024). Second, in the context of climate change, crowberry demonstrates a higher carbon sequestration capacity compared to many other vegetative species (Silvola et al., 1979; Silvola & Hanski, 1979; Ylanne et al., 2015). Nevertheless, crowberry's economic contribution in this regard remains insufficiently studied. Due to these two reasons, a quantitative study of crowberry's bioeconomic impacts on reindeer husbandry and the grazing pasture can contribute new insights and results to the literature of climate change in the Arctic and management of an Arctic native invasive species.

Following this perspective, a basic three-species bioeconomic model of vegetation (representing the biodiverse pasture), crowberry, and reindeer is developed to provide analytical static steady-state results of the impact of crowberry encroachment on reindeer husbandry and grazing pasture. Besides reindeer slaughter as a control in the model, two climate change adaptive measures were included – supplementary feeding for reindeer and burning crowberry. Static results display that crowberry encroachment causes a decrease in not only the grazing pasture but also the reindeer herd and slaughter volume. Applying only supplementary feeding will increase the optimal reindeer population yet decrease the optimal vegetation stock and further enhance growth of *E. nigrum*. Applying the alternative measure, burning, on the contrary, not only decreases crowberry population but also enhances growth of both vegetation and reindeer. The model is then developed further to better mimic realistic ecological conditions and to calculate the dynamic equilibria, including the fact that reindeer does graze on the unpalatable crowberry but in very short period of time annually. The results indicate that without human impact, the three-species ecosystem converges to a stable state where crowberry takes over the pasture and thus decreases the reindeer herd. Controlling crowberry by burning is, again, found to increase the optimal vegetation and reindeer stocks. Furthermore, a positive correlation between the optimal burning effort and the optimal slaughter volume was found.

Although crowberry is shown to affect negatively the reindeer herd size and burning it will enhance the sustainable biodiverse pasture for generational development of the husbandry, several studies did bring up the notable regulating ecosystem service of *Empetrum nigrum* – carbon sequestration (Silvola et al., 1979; Silvola & Hanski, 1979; Silvola & Heikkinen, 1979; Ylanne et al., 2015). This evergreen dwarf-shrub concentrates more carbon than other vascular plants in the tundra ecosystem, which then sparks another research question about the possible trade-offs in controlling *Empetrum nigrum*. Acknowledging crowberry's carbon sequestration properties, the question emerges whether the optimal controlling effort will be adjusted, and how. Optimal control theory is used to calculate the optimal trajectories of the controlling effort between two scenarios – including or excluding carbon capture. The carbon capture property is modelled for both plant species – the palatable vegetation and crowberry – and the results indicate a significant decrease in optimal management effort when carbon sequestration is accounted for.

6.1 Background

6.1.1 Literature overview and research motivation

Reindeer husbandry is one of the oldest economic activities in Fennoscandia (which includes Norway, Sweden, Finland, and a north-western area of Russia). The Sami people started this husbandry around the fifteen hundreds and after many centuries it has become a central part of the identity of this ethnic minority (Agriculture Directorate, 2022; Ministry of Agriculture and Food, 2017). Reindeer husbandry is special compared to other livestock husbandries, as reindeers are raised in a semi-domestic setting. While cows, sheep, and even goats are usually raised in domestic settings of closed farmland, the Sami people let reindeers graze freely in the wild pasture. The reindeer husbandry in Norway, under the auspices of the Directorate of Agriculture (Landbruksdirektoratet), Reindeer Section, takes place mostly in the northern part of the nation. Total reindeer stock size has been stable in recent years around 220,000 animals (Norwegian Government, 2021), though down 30% compared to the size in 2005. The Norwegian government manages the system via regulating the total reindeer population through quotas to ensure sustainable development of the husbandry and sustainable maintenance of the grazing pasture (Ministry of Agriculture and Food, 2017).

To acknowledge and emphasize the importance of nature, the ecosystem service (ES) concept was coined (Millennium Ecosystem Assessment, 2005). Ecosystem services are the outputs, conditions, or processes of natural systems that benefit humans and enhance quality of life (Braat & de Groot, 2012; Costanza et al., 2017; Fisher et al., 2008; Tallis et al., 2008). They can benefit people in many ways, either directly or as inputs into the production of other goods and services. The reindeer husbandry provides a unique set of ecosystem services for the

Fennoscandian nations. Critical provisioning services have been provided by the husbandry for centuries, as reindeer meat is still considered a highly prized food in Fennoscandia, with richer taste and higher nutritional value than other types of meat (Mielnik et al., 2011; Semenova et al., 2019; Wiklund et al., 2018). While the byproducts of the industry, such as reindeer skin for clothes, blankets, and carpets, contribute partly to the income of the local herders (Norwegian Government, 2021), cultural services from the husbandry are indispensable (Helander-Renvall, 2010; Johannesen & Skonhoft, 2011). Reindeer husbandry has been central to the cultural identity of the Sami people for centuries, in which, for instance, the herd size acts as an indicator for social status, economic insurance, and cultural images of the families in the community (ibid). This cultural image is actively advertised with tour packages for interacting experiences with reindeers and the Sami people's daily life (Axelsson-Linkowski et al., 2020; Reinert et al., 2009). Regarding regulating and supporting services, the husbandry in some specific cases contributes to the expansion of birch trees, which supports carbon sequestration of the boreal forests (Tømmervik et al., 2009). In-turn, the tundra and boreal ecosystems also provide ecosystem services and disservices towards the husbandry, closing the feedback socio-ecological loops of the husbandry and its habitat (Hallberg-Sramek et al., 2023; Holm, 2015; Korosuo et al., 2014).

The husbandry is currently affected by climate change and land-use development. Many conflicts remain among the herders and also between the herders and the management decision-makers (Axelsson-Linkowski et al., 2020; Johnsen et al., 2022; Pekkarinen, Kumpula, et al., 2022; Tyler et al., 2021). These conflicts relate to a variety of issues, such as lost pasture due to, for instance, encroachment of wind turbines (Skarin et al., 2018), tourism, and housing (Risvoll & Hovelsrud, 2016). Additionally, negative climate change consequences are threatening the husbandry's existence (Albon et al., 2017; Loe et al., 2021; Pekkarinen, Rasmus, et al., 2022; Reinert et al., 2009).

Winter is a critical season for reindeer survival, reproduction, and population growth (Albon et al., 2017; Tveraa et al., 2007). Milder and more fluctuating winter weather conditions increase the risk of rain-on-snow events, freeze-thaw cycles and deeper snow, all of which reduce access to ground lichens (Weladji & Holand, 2003), the main natural winter forage of reindeer (Skogland, 1984; Webber et al., 2022). Loss of access to winter food and increased energetic costs of foraging lead to higher body mass loss and risk of starvation (Albon et al., 2017; Tveraa et al., 2007). Owing to competing land-uses, resilience towards harsh winters may be already low in many districts, as alternative natural forage or access to better pastures – such as arboreal lichen forests or unaffected pastures – may not exist (Horstkotte et al., 2020). During harsh winters, supplementary feeding is used to reduce reindeer body mass loss, reproductive loss and mortality (Ballesteros et al., 2013).

Good summer pastures and forage conditions during the snow-free period act as key buffers against harsh winter conditions (Tveraa et al., 2013). Especially for juveniles, higher body mass during late autumn correlates with higher survival and body mass during late winter (Correia et al., 2022; Loe et al., 2021). Extended growing season following warmer autumns and earlier springs allow for prolonged easy access to high-quality forage, which may increase late autumn and late winter body mass, reproduction and individual survival through positive bottom-up effects (Albon et al., 2017; Loe et al., 2021; Tveraa et al., 2013). However, warming and an extended growing season have been linked with qualitative changes in pasture vegetation, whereby poor-quality forage plants proliferate in pastures, which acts as a negative bottom-up forcing on reindeer (Fauchald et al., 2017; Kaarlejärvi et al., 2012; Tuomi et al., 2024). In summary, supplementary feeding and warming-induced increase in availability of good-quality summer forage may both protect herds against worsening winters. In contrast, loss of high-quality summer pastures to warming-induced allelopathic encroachment – and reduced body mass accumulation – represent critical loss of resilience towards harsh winters.

Stimulated by climate and environmental changes, crowberry interferes chemically with other neighboring plants, to the extent that vegetation communities within the Arctic ecosystem are impacted severely (Bråthen et al., 2007; Tuomi et al., 2024; Wilson & Nilsson, 2009). Generally, crowberry possesses four ecological features that constitute its strong competitiveness against other vegetative organisms: (1) production of allelopathic substances which decrease growth rate and seedling development of neighboring plants, (2) horizontal spread, thus hindering photosynthesis of adjacent vegetation, (3) release of phenolic-rich litter which reduces soil nitrogen, and (4) unpalatability due to low nitrogen concentration in its leaves (Nilsson et al., 1993; Tybirk et al., 2000). These features systematically affect the vegetation communities (Bråthen et al., 2018), especially deteriorating the grazing pasture's quality and quantity for the Sami reindeer husbandry. Nonetheless, crowberry provides many benefits to other species, including human beings (Lorion & Small, 2021). Though the leaves are unpalatable, its berries are rich in antioxidants (Hyun et al., 2016) and thus are a food source for indigenous people and many herbivores (Lorion & Small, 2021). Furthermore, *E. nigrum* endophytes have been tested for their anti-inflammatory substances in the treatment of urinary catheter-associated infections (Monteiro et al., 2019). Additionally, polyphenolic compounds from the leaves contain orosensory properties, which potentially makes the species fit for industrial food production (Laaksonen et al., 2011, 2013; Viljakainen et al., 2002).

The above-mentioned benefits of *E. nigrum* can be categorized into different types of ES. However, to categorize crowberry's negative impacts in this particular case we need another concept as the ES concept does not provide a suitable framework. To identify and quantify detriments of nature in general, the concept of ecosystem disservices (EDS) was coined (Guo et al., 2022; Lyytimäki, 2014, 2015; Lyytimäki et al., 2008; Schaubroeck, 2017; Shackleton et al., 2016). Definitions and categorizations of EDS still vary between studies (Escobedo et al., 2011; Lyytimäki et al., 2008; Shackleton et al., 2016; Vaz et al., 2017; Von Döhren & Haase, 2015), posing challenges for adaptation of the concept. Besides, another more recent concept; nature's contribution to people (NCP), aims to provide a more pluralistic philosophy within nature-human relationships (IPBES, 2016). One goal of the NCP concept is to be an alternative to both the ES and EDS concepts, by addressing both nature's benefits and detriments (IPBES, 2019).

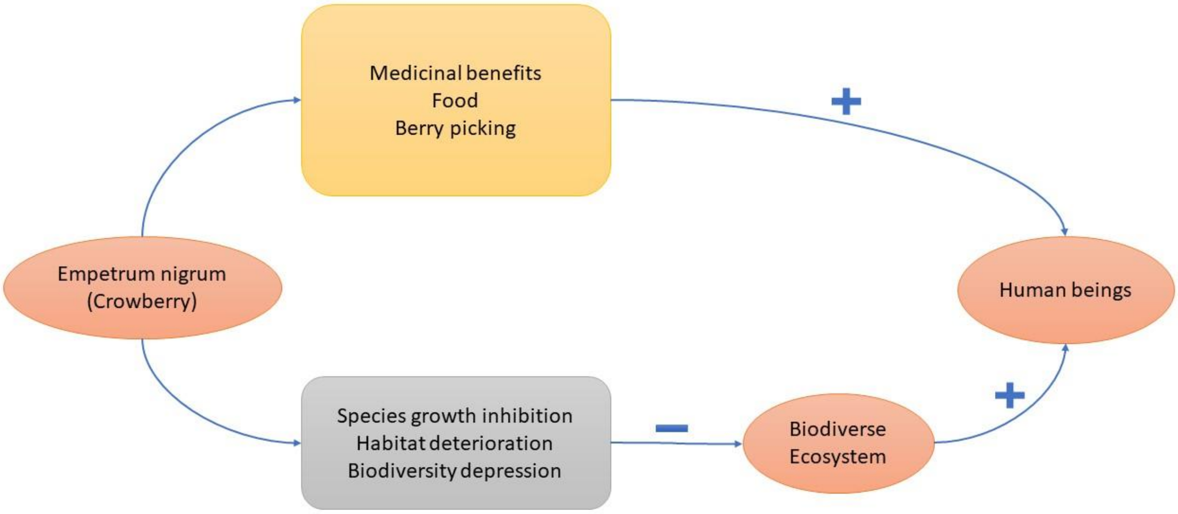

Figure 1: Examples of Empetrum nigrum's direct and indirect benefits and detriments

With the pasture crisis caused by several circumstances, for instance rain-on-snow events, shrubification, crowberry encroachment, land-use conflicts etc., the reindeer herders must enact adaptive measures to sustain their legacy. Habitat restoration is a common human intervention in species conservation (Ando & Langpap, 2018; Bulte & Horan, 2003; Mainka &

Howard, 2010; Salau & Fenichel, 2015), and controlling the native invader – crowberry – either by burning, plowing, or plucking, are some potential adaptative measures. Although the effect of fire to control *Empetrum* on *Empetrum*-dominated understorey vegetation has been briefly discussed (Bråthen et al., 2010; Penney et al., 2008; Wardle & Jonsson, 2014), long-term effects on crowberry removal by humans remain unclear.

Instead of restoring the habitat, many herders have been adapting to the new environmental situation by providing supplementary feeding. This practice has been adopted from the latter half of the last century in Finland, with other Fennoscandian nations following recently (Helle & Jaakkola, 2008; Horstkotte et al., 2020; Pekkarinen et al., 2015). The feeding choice can be considered a form of adaptation when the available grazing pasture declines, though it can facilitate disease spreading in the herd (Horstkotte et al., 2020). Supplementary feeding is evaluated as an unfavorable intervention which in the long-run can alter the herding customs of the Sami people (ibid). Despite ongoing supplementary feeding, there exist no economic studies of this intervention in the Norwegian reindeer husbandry setting. Supplementary feeding in the Finnish reindeer setting was modeled extensively in the studies of Pekkarinen et al., where the practice is widely adopted (Pekkarinen et al., 2015, 2017, 2021; Tahvonen et al., 2014).

6.1.2 Bioeconomic modelling and the Norwegian reindeer husbandry

Species interactions, both at individual and population levels, form the structure of ecosystems. Human beings have always interacted with, and thus altered the dynamics of natural ecosystems, intentionally or accidentally (Balmford & Bond, 2005; Chapin et al., 2000; DeGroot et al., 2010; Fisher et al., 2008; Friess, 2016; Haines-Young & Potschin, 2010;

Millennium Ecosystem Assessment, 2005; Power, 2010; TEEB, 2010). Interactions of multiple species can be modelled by using a set of differential equations, which take into account of both temporal and spatial dynamics (Castro et al., 2018; Din et al., 2021; Getz, 1991; Koen-Alonso, 2007; Ludwig et al., 1978; Pimm & Rice, 1987). Bioeconomic models were introduced to study how human beings interact with species dynamics (Armstrong, 2019; Bulte & Van Kooten, 1999; Clark, 2010; Schlüter et al., 2012) and how natural ecosystems are impacted by human behaviour (Albers et al., 2021; Georgescu-Roegen, 1977; Sanchirico & Springborn, 2011; Skonhoft & Kourantidou, 2021). Using this approach, given suitable parameters, the resource manager or the social planner can adjust their impacts according to the management goals (Arreguín-Sánchez, 1996; Clark, 2010).

The recognition of many natural species as profitable renewable common resources, which require management, was raised by Gordon (Gordon, 1954). Acknowledging the fluctuation in population density of fish species and fishing seasons, Gordon developed a simple static model, adapted from Schaefer, showing the relationship of fish stock and catch per unit effort, and how over-exploitation diminishes populations, thus emphasizing the importance of optimal resource management (Gordon, 1954; Munro & Sumaila, 2015). Two decades later, the importance of natural capital in economic theories was re-emphasized by Georgescu-Roegen, from whom the term “bioeconomic model” was used to underline the importance of sustainable resource management in economic studies (Georgescu-Roegen, 1977). Though Gordon did mention the importance of the law of diminishing returns in managing natural resources several times in his work (Gordon, 1954), it was not until Clark’s book: *“Mathematical Bioeconomics: The Mathematics of Conservation”* (now third edition (Clark, 2010)) that the dynamic bioeconomic models were introduced (Munro & Sumaila, 2015). The classical single species model has a general functional form of:

$$\dot{X} = G(X) - H(X)$$

where $G(X)$ is the growth function of the modelled stock X, and $H(X)$ is the harvest function. Different functional forms for the growth function $G(X)$, can be selectively modelled based on existing literature, data availability, computing capacity, and personal preference (Eide, 2021). The harvest function $H(X)$ usually takes the form of $H(X) = qEX$ in which q is the catchability coefficient (Arreguín-Sánchez, 1996) and E is the harvest effort, yet other functions can be chosen (Clark, 2010; Eide, 2021; Kvamsdal et al., 2016). The functional form commonly used for fishery management sets $G(X) = rX\left(1 - \frac{X}{K}\right)$ with r and K being the intrinsic growth rate and carrying capacity, respectively (Clark, 2010; Eide, 2021; Feng & DeAngelis, 2018). Using optimal control theory to find the best management strategy, not only could it be argued that a resource can be harvested sustainably, given a positive discount rate, but the fundamental equation of renewable resource exploitation, the golden rule, can also be derived, showing what governs the decisions of the resource manager and social planner (Clark, 2010; Munro & Sumaila, 2015).

The literature of bioeconomic modelling has developed rapidly, especially in studying the effect of multispecies interactions on different management objectives (Hoshino et al., 2018; May et al., 1979; Pimm & Rice, 1987) and emphasizing the importance of species habitat for sustainable harvest (Armstrong et al., 2014, 2017; Armstrong & Skonhoft, 2006; Conrad, 1999; Foley et al., 2012; Sanchirico & Springborn, 2011). Extensions of the one-stock bioeconomic model to multi-stock models have shown that multispecies interactions affect optimal harvest of the stocks, depending on economic importance of the modelled species interactions, such as symbiosis and competition. For $i = \{1,2,\dots,n\}$ as species number indicator, these multispecies models often take the general functional form of

$$\begin{cases} \dot{X}_1 = G_1(X_1, X_2, \dots, X_n) + \alpha_1 I_1(X_1, X_2, \dots, X_n) - \beta_1 H_1(X_1) \\ \dot{X}_2 = G_2(X_1, X_2, \dots, X_n) + \alpha_2 I_2(X_1, X_2, \dots, X_n) - \beta_2 H_2(X_2) \\ \qquad\qquad\qquad\qquad\qquad\qquad \vdots \\ \dot{X}_n = G_n(X_1, X_2, \dots, X_n) + \alpha_n I_n(X_1, X_2, \dots, X_n) - \beta_n H_n(X_n) \end{cases}$$

which model not only the interdependence in species' growth $G_i(X_1, X_2, \dots, X_i)$ but also species interactions $\alpha_i I_i(X_1, X_2, \dots, X_i)$. The coefficients α_i and β_i may be zero in cases where there is no interspecies interaction or if harvesting is unprofitable. For instance, in the case of baleen whales (predator) and krill (prey) fisheries, May et al. (1979) showed that within a two-species model, harvesting the prey while the predator's population is heavily exploited can easily lead to the collapse of the ecosystem. Heavy harvest of the profitable prey will impact negatively on all the dependent predators (May et al., 1979). Similarly, in a three-species bioeconomic model of krill, squid, and sperm whale, harvesting the top-predator (sperm whale) creates a cascading effect across trophic levels. This leads to a decrease in the optimal harvest of krill due to increased predation by a growing squid population. On the contrary, the highest krill yield can be obtained when sperm whale is not harvested, due to its importance in keeping the squid's population in balance (May et al., 1979). Thus, selective harvesting at different trophic levels within a multispecies ecosystem can provide better insights into feedback dynamics, emphasizing the need for careful management to maintain ecological balance and sustainable yields (Hoshino et al., 2018).

Modelling multispecies interactions has emphasized the importance of habitat of the harvested biological resources. Preys, particularly plant species, can represent the habitat for predators in many ecosystems (Feng & DeAngelis, 2018; Koen-Alonso, 2007). Researchers often use prey-predator models to scrutinize the importance of habitat for the harvesting of the predators, not only in marine but also in terrestrial ecosystems (De Lara & Doyen, 2008; Feng

& DeAngelis, 2018; Foley et al., 2012; Koen-Alonso, 2007). Studies applying multispecies modelling have shown that prey can have use values when harvested (May et al., 1979; Pal & Mahapatra, 2014; Pimm & Rice, 1987; Raymond et al., 2019), but also non-use values if not being harvested (Armstrong et al., 2017; Vondolia et al., 2020). One example of non-use value of prey as a predator's habitat is the contributions of kelp in supporting the profitable coastal cod's population and in storing carbon (Armstrong et al., 2017; Foley et al., 2012; Vondolia et al., 2020). Incorporation of carbon storage in the objective functional increases the required rate of return of the habitat, thus increasing the optimal stock levels of cod and kelp (ibid). In the case of a non-renewable or extremely slowly renewable habitat, it is shown that the social planner will prefer harvesting methods that avoid habitat destruction, though the optimal profit could be lower than with more habitat destructive harvesting methods (Armstrong et al., 2014; Kahui et al., 2016). Furthermore, in many bioeconomic models of terrestrial species, prey are often modeled as the harvested resources' habitats, especially when they are plant species (Feng & DeAngelis, 2018). For instance, in forage woodlands where domestic livestock and wildlife herbivores share the same habitat, accounting for the revenues from game, farming, wood harvesting, and non-market value of forests, it can be optimal to prioritize game and wood harvesting activities rather than livestock farming (Cornelis Van Kooten et al., 2001; Standiford & Howitt, 1992). Similarly, accounting for use and non-use values of habitat can also provide sustainable optimal land-use management decisions, which in some cases require the decrease of agricultural land-use area to preserve habitat for endangered species or even conserving and restoring the biodiverse resilient habitat as a better grazing land for livestock (Cunha-e-Sá, Maria & Mota, 2013; Skonhoft et al., 2010; Soltani et al., 2015; Tahvonen et al., 2014). In the complex reindeer models of Moxnes et al. (1993; 2001) and Pekkarinen et al. (2015, 2017, 2021; 2022; 2022), the dynamics of reindeer habitat and diet, especially lichen and supplementary feeding, can impact the systems' stability and optimal profits. Therefore, species' habitat plays a critical role in sustainable resource management (Bulte & Horan, 2003; Salau & Fenichel, 2015; Sanchirico & Springborn, 2011). Nonetheless, this does not mean that modelling without habitat is of little value, as many bioeconomic models of single terrestrial species have been successfully studied (Cooper, 1993; Keith & Lyon, 1985; Mensah et al., 2015; Rashford et al., 2008; Skonhoft et al., 2013). Yet including species habitat in bioeconomic models may change the optimal results significantly.

The earliest reindeer-lichen ecological model was developed by Gaare and Skogland (1980). In this model, lichen is considered the sole food source for reindeer, while reindeer's trampling effect on lichen is also captured. Danell and Petersson (1994) created a meta-population discrete-time and sex-age structured ecological model, which includes many ecological details of reindeer herding. The authors acknowledged that the model might be unnecessarily complicated, especially with variables for ages and seasons. This complexity generates some noise and increases the difficulty of analyzing several major factors, such as reindeer herd dynamics (ibid). Bioeconomic models of reindeer husbandry have been developed later on to understand the interactions between herders and the grazing pasture for better management and herder decision-making. Moxnes and colleagues (1993) developed an age-sex structured continuous-time bioeconomic reindeer-lichen model, focusing on the importance of lichen in winter grazing. Later works by Moxnes et al. (2001), Tahvonen et al. (2014), and Pekkarinen et al. (2015, 2017, 2021, 2022a, 2022b) include reindeer age-sex structured discrete-time models with various types of diets, particularly ground and arboreal lichens. Furthermore, Pekkarinen et al. (ibid) studied the economic and ecological impacts of supplementary feeding on Finnish reindeer husbandry for the first time after this practice was introduced in the 1960s. Their consumer-resource models depict in much detail the ecological 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. Johannesen et al. (2019) constructed a wolf-reindeer model, in which they addressed intraspecific competition and predation. The authors also incorporated age-sex structure as in previous models, but used total number of grazing animals as a proxy for food scarcity of reindeer. Although this proxy could capture the partial effect of reindeer on pasture, this perspective simplified food competition which could include exogenous ecological factors constraining reindeer populations such as shifts in vegetation community composition of the grazing pasture (Krebs 2002).

Although the ecological problem of invasive species has been addressed in many prey-predator models (Korobeinikov & Wake, 1999; Soia et al., 2017; Tonnang et al., 2009; W. G. Wilson et al., 2003), the modelling literature on reindeer husbandry has not studied non-native or native invasives. Invasive species are defined as alien species that compete intensively with native ones for resources and habitat, which can disrupt ecosystem stability (Mooney & Cleland, 2001). While interspecific competition often exists between native and invasive species, there may be situations where native species cannot compete against the invasive (Korobeinikov & Wake, 1999). Although prey-predator ecological models including invasive species are widely developed (for example Cao et al., 2019; Ebey, 2020; Wilson et al., 2003), bioeconomic models of a similar kind have not been extensively investigated. Several bioeconomic models have been developed to investigate invasive species management, but they are largely based on other types of models (Carrasco et al., 2010; Finnoff et al., 2008; Kotani et al., 2011). Yet, some studies on optimal harvesting of invasive species following a prey-predator approach exist (Falk-Petersen & Armstrong, 2013; Gupta et al., 2012; McDermott et al., 2013; Skonhoft & Kourantidou, 2021). Gupta et al. (2012) modeled the logistic growth of two competing species without considering feed from any other species in the habitat. While

Gupta et al.’s (ibid) work is theoretical, McDermott et al. (2013) is an applied study with a two-species model that includes interspecies competition and harvest of one of the invasive species. They modeled not only the population dynamics of both species but also introduction and eradication policies for the invasive one.

Despite the extensive bioeconomic research within the specific topic of reindeer modelling, several notable gaps persist in the literature. Firstly, existing bioeconomic models of reindeer husbandry have not adequately incorporated the induced impacts of environmental changes, especially of crowberry encroachment, in reindeer grazing pasture. Whether crowberry is a beneficial species or a pest, and if the latter then whether this native plant should be controlled, still remains unaddressed in both academia and the Norwegian management agency. Secondly, there is a scarcity of economic studies on supplementary feeding as an adaptive measure in the Norwegian reindeer husbandry setting, though this topic has been studied for Finnish husbandry. Although supplementary feeding is increasingly practiced due to climate change and pasture degradation, its long-term economic and ecological implications remain underexplored. The thesis addresses these gaps by developing several bioeconomic models to enhance sustainable management of the Norwegian reindeer husbandry under climate change.

6.2 Research objectives

Paper 1: Categorization of Empetrum nigrum's benefits and detriments and its' potential impact on the reindeer husbandry

To have a comprehensive assessment of *Empetrum nigrum*'s impacts on humans, a systematic literature review (SLR) was conducted. Three concepts for nature assessment were chosen – ecosystem services (ES), ecosystem disservices (EDS), and nature's contribution to people (NCP) – for categorizing *E. nigrum*'s benefits and detriments. Validity and quality of the review was ensured as we follow the AMSTAR guideline for a specific and transparent SLR. Three chosen scientific databases are ScienceDirect, Jstor, and Web of Science, from which two main keywords – "Empetrum nigrum" and "crowberry" – were used to extract the targeted articles. After inspection for duplication and screening, we focused on those articles that are geographically relevant to the Fennoscandia region (116 publications).

Systematically, *E. nigrum* provides eight benefits and three detriments: medicinal benefits, food, bioindicators, berry picking, phytoremediation, carbon sequestration, species growth facilitation, animal food, species growth inhibition, habitat deterioration and biodiversity depression. Under the ES-EDS conceptual framework, *Empetrum nigrum* provides eight ES, including two provisioning, two cultural, two regulating/supporting, two solely supporting, and three EDS. Under the NCP conceptual framework, *E. nigrum* provides two material NCP, two non-material NCP, and seven regulating NCP, consisting of four positive and three negative NCP. Nevertheless, these three indirect detriments of species growth inhibition, habitat deterioration and biodiversity depression can have negative impacts on the reindeer grazing pasture, causing further resource constraints for the Norwegian reindeer husbandry.

From the categorization practice, the NCP concept is more flexible and effective than the ES-EDS concept for several reasons. Firstly, the NCP concept resolves ambiguity in relation to regulating and supporting ES, as a regulating NCP can impact both directly and indirectly to human beings. Secondly, it provides clearer guidance in identifying indirect species impacts, which highlights the inclusion of eco-centric perspectives. Thirdly, the EDS classification based on types of impact is discordant with the ES classification. Lastly, the EDS classification based on types of disservices contains a semantic problem in the valuation phase. Although the NCP concept is shown to have some ambiguity in its classification, we recommend adopting it for clearer and more comprehensive assessments of species impacts on nature and humans.

Paper 2: Static optimization of Norwegian reindeer husbandry under climate change

Since crowberry negatively impacts the limited resources, i.e. the grazing pasture, of the reindeer husbandry, controlling this species is an essential adaptive measure to its allelopathic encroachment. To study this negative impact, the thesis starts by developing a simple three-species bioeconomic model of vegetation (representing the biodiverse grazing pasture), reindeer, and crowberry. Reindeer slaughter, as the first control variable, is incorporated for profit maximization, while crowberry treatment (by burning or plucking) is included as the second control variable to test its economic efficiency. Moreover, with pasture crisis in both summer (crowberry encroachment) and winter (crowberry encroachment and rain-on-snow event) pastures, we include supplementary feeding to study the effect of this new practice on the grazing pasture generally and on crowberry encroachment particularly. It is assumed that the Norwegian government is the social planner that has full control of the reindeer stock and comprehensive knowledge of the ecological interactions between vegetation and crowberry.

The simple three-species bioeconomic model developed has five variants: 1) basic model where crowberry encroachment is excluded, 2) encroachment model where allelopathic impact of crowberry is incorporated, 3) feeding model where supplementary feeding for reindeer is taken into account, 4) controlling model where crowberry treatment (burning) is conducted, and 5) comprehensive model which includes both supplementary feeding and crowberry treatment. Reindeer are modeled to feed only on either the palatable vegetation or on supplementary feeding. While the slaughter cost function is assumed to be linear for simplicity, the quadratic cost functions of the two adaptative measures are assumed to reflect the labour-intensiveness of both measures, and also ensure mathematical convenience. Solving the model variants in a static setting, the obtained results from the basic and encroachment models show that crowberry encroachment will suppress the optimal vegetation stock, thus decreasing the optimal reindeer herd size and slaughter volume. It was further shown analytically that the spread of this native invader will reduce the optimized profit of the resource manager.

Through numerical application, implementing supplementary feeding will increase the herd size, yet this measure dampens further the grazing pasture. Assuming similar cost per unit effort, the optimal grazing pasture and reindeer herd size are increased by crowberry treatment, even with a larger herd size than in the feeding model. When combining the two measures, an increase in the reindeer and vegetation stocks is supported, though higher levels of both efforts are required. This can be interpreted as the more feed the herders give their reindeers, the more crowberry controlling effort is required. We further calculated how much it costs to bring back the reindeer herd to the initial level applying each adaptive measure. Our results indicate that higher total effort cost from supplementary feeding than crowberry control is needed to achieve this goal, while also causing more stress to the pasture.

Paper 3: Dynamic optimization of Norwegian reindeer husbandry under climate change

Although analytical solutions can be achieved with static optimization, the non-zero discount rate is not accounted for. Therefore, we adjusted the simple model in order to study dynamic ecological interactions, and determine the system's stability and the dynamically optimized equilibria. In this paper we model the two plant species sharing the common pool of pasture's carrying capacity, that the increase of one species' population will lead to the decrease of the other. Moreover, we assume now that reindeer does graze on crowberry though much less than on the palatable vegetation.

The following system of differential equations captures the intertwined dynamics of vegetation biomass V, crowberry biomass K, and reindeer numbers R. The model reads

$$\begin{cases} \dot{V} = \alpha_V V\left(1 - \dfrac{V + \varphi K}{M}\right) - g_V VR \\ \dot{K} = \alpha_K K\left(1 - \dfrac{K}{M - V}\right) - g_K KR - \varepsilon TK \\ \dot{R} = \alpha_R R\left(1 - \dfrac{R}{d_V V + d_K K}\right) + \beta FR - S \end{cases}$$

in which S, F, and T are three control efforts – reindeer slaughter, supplementary feeding, and crowberry control, respectively. See the manuscript for detailed explanations of the parameters, including intrinsic growth rates (α_V, α_K, α_R), carrying capacity effects (M, φ), grazing coefficients (g_V, g_K), and conversion efficiencies (d_V, d_K).

Without human impact, i.e. no *S*, *F* or *T*, the three-species ecological model converges into a stable state where crowberry occupies a large part of the pasture, leading to a small reindeer population. Incorporating three controls – slaughtering and feeding reindeer, and burning crowberry – both the adaptative measures have similar impacts on the optimal vegetation and reindeer stocks as in the second paper. The law of diminishing returns is reflected in the dynamic optimized shadow prices of three species, which points out that crowberry encroachment will change the sign of the native invader’s shadow price, from positive to negative, signaling that *Empetrum nigrum* is unfavourable for the objective functional of the resource manager. Furthermore, we also found a complementary effect between the control variables, as increasing optimal supplementary feeding days optimally increases crowberry burning days and slaughter volume, and vice versa.

Paper 4: Optimal control of the Norwegian reindeer husbandry and native invasive encroachment under different ecosystem (dis)services perspectives

Although crowberry's benefits to humans can be replaced by other alternatives, several studies have emphasized its outstanding carbon sequestration property, which is higher than other plants in the understory level of the tundra ecosystem. Thus, incorporating one ecosystem service of crowberry besides its disservice, which was studied in the two bioeconomic modelling papers above, might shift the optimal crowberry treatment effort level. With the hypothesis that accounting for carbon sequestration of the pasture, especially of crowberry, will decrease the optimal burning effort, we apply optimal control theory to study numerically the temporal dynamics of three control variables in a bioeconomic model.

In this paper, we decrease the number of model variants into three scenarios: 1) baseline scenario where supplementary feeding is a critical control given the pasture crisis in winter pastures, 2) the burning scenario in which crowberry burning is incorporated, and 3) the carbon scenario with the additional non-use value from carbon sequestration of both plant species. To avoid the singular control case in the third paper, we find the temporal data of total variable costs of the husbandry and fit it with the quadratic cost function for the slaughter control. We also take into account the so-called salvage, scrap or terminal value of the reindeer herd, as the practice is expected to be continued by future generations, and of the palatable vegetation stock, as the pasture plays an important role in sustainability development of the husbandry.

Solving numerically for the optimal controls in finite time, our results indicate that the burning process only becomes profitable after the 12th year. If the resource manager or social planner does not acknowledge the vegetation's salvage term value then nearly at the end of finite time, burning effort will decrease to zero and crowberry will grow again. Incorporating non-use value for carbon sequestration of both plants switches the sign of the shadow price of crowberry from negative to positive, showing that with the carbon capture property, the native invader contributes positively to the objective functional of the social planner. Interestingly, higher carbon prices signal a decrease in the optimal reindeer stock and feeding effort. Since reindeer still grazes vegetation and crowberry, it is optimal to have fewer reindeer, or not let the herbivore graze all the available pasture, as the non-use value from carbon sequestration is significant.

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7 Paper 1 : How disservices illuminate divergence between “nature’s contribution to people” and “ecosystem services” – an assessment of *Empetrum nigrum*

How disservices illuminate divergence between “nature’s contribution to people” and “ecosystem services” – an assessment of *Empetrum nigrum*

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Abstract

Encroachment of a native invasive species – *Empetrum nigrum* (crowberry) – has impacted Arctic ecosystems and the indigenous Sami people. To understand comprehensively the impacts of this native invader, we adopted three concepts, ecosystem services (ES), ecosystem disservices (EDS), and nature's contributions to people (NCP), to identify and classify systematically crowberry's benefits and detriments. Through a systematic literature review of 116 articles, we show that among 11 positive and negative impacts of *E. nigrum*, the species only provide detriments to humans *indirectly*. However, these indirect detriments are altering other ecosystem functions and processes, which later can affect critically on the locals' way of life. We identify one additional benefit of crowberry – carbon fixation – which was not included in previous reviews. The analysis shows NCP to be a more suitable and flexible concept because (1) the regulating NCP resolves the ambiguity in relation to regulating and supporting ES, (2) the NCP concept provides clearer guidance in identifying indirect species impacts, which highlights the inclusion of eco-centric perspectives, (3) the EDS classification based on types of impact are in discord with the ES classification, and (4) the EDS classification based on types of disservices contains a semantic problem in the valuation phase. Although the NCP concept has some ambiguity in its own classification, we recommend the adoption of the this concept for clearer and more comprehensive assessments of species impacts on nature and humans. Besides, we emphasize the importance of how dynamics in species abundance can affect ES-EDS/ NCP categorizations.

Key policy highlights:

- Ecosystem disservices (EDS) contribute critically in ecosystems-people assessments, though there are challenges in integrating the concept with the Ecosystem services (ES) concept
- The Nature's contribution to people (NCP) concept proves to be more flexible and comprehensive than ES-EDS integration
- Under different contexts and perspectives, crowberry can provide either benefits or detriments, or both. Yet, crowberry only provides indirect negative impacts to humans.
- Indirect detriments of an invasive species may not only decrease other indirect benefits, but also direct benefits provided by other ecosystem functions and processes.

Keywords: ecosystem services, ecosystem disservices, nature's contributions to people, *Empetrum nigrum*, systematic literature review.

1. Introduction

The Arctic is being impacted significantly by climate change, and many ecosystems in this part of the planet are being destabilized (Bokhorst et al., 2018; Olofsson et al., 2011; Warwick, 2019). Arctic terrestrial ecosystems, particularly the tundra and the boreal landscapes, are experiencing several abrupt changes in species distribution, leading to shifts in flora and fauna communities (Svensson et al., 2018; Wardle et al., 2012; Ylanne et al., 2015). Since Arctic terrestrial ecosystems provide social, cultural, and economic benefits to many northern European countries, including Norway, Sweden, Finland, and a north-western part of Russia (this area is often called Fennoscandia), several aspects of Arctic people's lifestyles are directly and indirectly affected (Malinauskaite et al., 2019; Weladji & Holand, 2003). In particular, tundra and boreal landscapes act as common grazing pasture for the iconic reindeer husbandry of the indigeneous Sami people in Fennoscandia (Riseth, 2007). Due to extreme weather volatility, unfavourable conditions for the husbandry are happening more frequently, such as rain-on-snow events, expansion of the birch treelines (arctic greening), moth outbreaks (arctic browning), and invasive species introduction (Fauchald et al., 2017; Jepsen et al., 2013; Jones et al., 2015; Karlsen et al., 2013; Mainka & Howard, 2010; Maliniemi et al., 2018; Myers-Smith et al., 2020). These events decrease the quantity and quality of reindeer grazing pasture, causing disruption in reindeer natural habits and habitats (Bråthen et al., 2007; Risvoll & Hovelsrud, 2016; Tuomi et al., 2024; Turunen et al., 2016). The Sami reindeer herders, hence, are facing great difficulties in maintaining their traditional way of life.

Among the above-mentioned climate change consequences in the Arctic, invasive species have been destabilizing native ecosystems and causing severe damage to local people (Mainka & Howard, 2010; Milanović et al., 2020; Mooney & Cleland, 2001; Ziska et al., 2011). Invasive species in northern Europe, for example the Japanese knotweed and the giant hogweed, have caused serious socio-economic impacts on local residents, including the loss of harvest and production of key natural resources, the health cost caused by invasion of these alien species, and the removal/ control costs to return the ecosystems to their previous states (Keller et al., 2011; Milanović et al., 2020). Furthermore, alterations of ecosystem functions and processes, caused by climate change, can turn a native species into a native invader (Carey et al., 2012; Hellmann et al., 2008; Valéry et al., 2009). Research about identification, classification, and dynamic valuation of native invasive species are nevertheless few, and the term is not even mentioned in recent global climate and environmental reports (Invasive Species Centre, 2021; Convention on Biological Diversity, n.d.; IPCC, 2022). In these reports, invasive species are still considered only as non-native, or alien, invasive species; yet a native species can also become invasive due to habitat condition alterations (Carey et al., 2012). To contribute more to the study of non-alien invasive species, we focus our study on an encroaching native plant invader in the Arctic terrestrial ecosystem. An aim of this work is to understand comprehensively and systematically the impacts of a native invader, crowberry, on Fennoscandian nature and people.

Empetrum nigrum (crowberry), the evergreen dwarf shrub, has due to climate and environmental changes in recent decades abundantly encroached tundra ecosystems in Fennoscandia (Bråthen et al., 2007; Wilson & Nilsson, 2009). *E. nigrum* is an allelopathic species, producing leaf chemicals harmful to other organisms (Nilsson et al., 1993). In addition to allelopathy, *E. nigrum*'s three distinctive characteristics can explain its competitive success; (1) its horizontal creeping growth form which impedes access to light and hence growth of other subordinate species (2) its phenolic-rich litter which causes lowered nitrogen-availability in soil, and (3) its low nitrogen content in leaves inducing low palatability (Tybirk et al., 2000). Via these characteristics, *E. nigrum* can impact and shift the vegetation communities (Bråthen et al., 2018), which may provide indirect effects on the reindeer husbandry of the indigenous

Sami people, as crowberry can deteriorate the quality and quantity of the grazing pasture. Therefore, from an ecological perspective, this species is a profound example of how nature and human-wellbeing are affected by climate change consequences. On the other hand, *E. nigrum* provides berries, which are rich in anti-oxidant substances (Hyun et al., 2016), making them an important food source not only for indigenous people but also for many herbivores (Lorion & Small, 2021). Furthermore, *E. nigrum* endophytes have been tested for their anti-inflammatory substances in the treatment of urinary catheter-associated infections (Monteiro et al., 2019). Besides, polyphenolic compounds from the leaves contain orosensory properties, potentially making the species fit for industrial food production (Laaksonen et al., 2011). Conclusively, *E. nigrum* has both benefits and detriments, depending on which perspective we employ to evaluate this species. It is therefore of interest to have a comprehensive study of *E. nigrum* benefits and detriments on the native ecosystems and the local people.

Species benefits to human well-being are usually identified and classified by the ecosystem services (ES) framework of the Millennium Ecosystem Assessment (MA) (Millennium Ecosystem Assessment, 2004). Application of ES for assessment of species impacts has proven fruitful both academically and practically (Braat & de Groot, 2012a; Costanza et al., 2017; Fisher et al., 2008; Tallis et al., 2008). Yet, the ES concept only covers the species' benefits, leaving out the detriments that species cause. This led to the creation of an adverse concept – ecosystem disservices (EDS) – to address species' detriments, either real or perceived, that affect human well-being (Guo et al., 2022; Lyytimäki et al., 2008; Lyytimäki, 2014, 2015; Schaubroeck, 2017; Shackleton et al., 2016). Literature on EDS is more scarce than for ES, not only because the concept was developed later (Guo et al., 2022; Lyytimäki, 2015; Schaubroeck, 2017; Shackleton et al., 2016), but also because species' detriments have presumably always tacitly been acknowledged and accounted for (Shapiro & Báldi, 2014). A systematic literature review showed that EDS articles stand for 0.4% of the total ES literature, with 87% of EDS studies being published after 2012 (Kadykalo et al., 2019).

Although there exist challenges in relation to EDS definition and classification (Guo et al., 2022), integration of ES and EDS still creates more comprehensive species assessments in which the benefits and detriments are included holistically, resulting in better decisions (Campagne et al., 2018; Vaz et al., 2017; Wu et al., 2021). In practice, decision makers tend to act faster when both species' detriments and benefits are known rather than when only the positive impact is recognized (Blanco et al., 2019; Herd-Hoare & Shackleton, 2020; Schaubroeck, 2017). Many have used ES-EDS integration for comprehensive assessments of various ecological concepts, such as urban trees (Davoren & Shackleton, 2021; Delshammar et al., 2015; Escobedo et al., 2018; Lyytimäki, 2014, 2017; Lyytimäki et al., 2008; Teixeira et al., 2019), agricultural ecosystems (Herd-Hoare & Shackleton, 2020; Mouchet et al., 2017; Zhang et al., 2007), or rangeland ecosystems (Swain et al., 2013). Both ES and EDS are also included to identify benefits and detriments of many invasive species, such as mussels and weeds in freshwater ecosystems (Limburg et al., 2010; Sheergojri et al., 2022), different types of trees and plants in rangeland ecosystems (Milanović et al., 2020; Shackleton & Shackleton, 2018), and ants in agroecosystems (Wielgoss et al., 2013). However, ES-EDS of Arctic invasive species, either alien or native, have so far not been addressed or assessed.

The ES concept in itself has been criticized due to multifaceted values of nature not being reflected comprehensively (Díaz et al., 2018), suggesting that the MA framework has solely an anthropocentric perspective excluding ecocentric aspects (Wallace, 2007). Hence, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) constructed the more recent concept of nature's contribution to people (NCP) providing a more pluralistic philosophy within nature-human relationships (IPBES, 2016). One attempt of IPBES to promote the NCP concept as an alternative to the ES concept is to acknowledge that NCP consists of both species' positive and negative impacts towards human wellbeing. IPBES combined supporting and regulating ES-EDS to form a new group of regulating NCP, in addition to the so-called material and non-material NCP (IPBES, 2019)[2].

Comparisons of ES and NCP regarding how these concepts identify and classify species' benefits and detriments have been conducted, with some concluding that NCP is better and more inclusive as it addresses diversity of values under multiple perspectives (Ellis et al., 2019; Kadykalo et al., 2019); while others refute the novel contributions of NCP suggesting it is merely another name for ES (Muradian & Gómez-Baggethun, 2021). Moreover, while comparisons of both concepts' definitions and classifications were investigated, case studies to compare the two concepts' applicability are largely lacking. Here we contribute to the literature of ES, EDS, and NCP, and of native invaders, especially in the Arctic, by adopting these three concepts in the case study of an Arctic native invader – *Empetrum nigrum* (crowberry). We hence apply ES-EDS and NCP concepts to assess *E. nigrum*'s benefits and detriments. From our assessment, we first systematically determine crowberry's direct and indirect benefits and detriments, and second compare the applicability of ES-EDS and NCP in identifying and classifying crowberry's impacts. Our study, therefore, contributes to expand upon assessments of climate change impacts on the Arctic nature and people by studying the impacts of *E. nigrum* in the Fennoscandian socio-ecological system.

We assess *E. nigrum*'s benefits and detriments by applying a systematic literature review (SLR) and identify its impacts on human well-being following both ES-EDS and NCP concepts. The main research questions are:

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[2] Regarding the topic of invasive species, IPBES addresses invasive species as a significant topic for assessment, but the comprehensive thematic report on the topic is yet to be finalized.

1. What are the benefits and detriments of *E. nigrum* towards the native ecosystem and the local people?
2. Which concept, ES-EDS or NCP, is more suited for analyzing benefits and detriments of the native invader in particular, and of a species in general?

We give an overview of EDS and NCP concepts in the second section, while the methodological approach is detailed in the third section. This is followed by the results from the systematic literature review, with the final part discussing the findings and comparing the applicability of the two frameworks.

2. Introductions of EDS and NCP

2.1. EDS concepts

One big challenge of the EDS concept is its definition (Guo et al., 2022). EDS was first defined as ecosystem functions with negative impacts on human well-being (Lyytimäki et al., 2008), which then is dependent on personal perceptions. For instance, urban forests provide EDS to some but not to others (Conway & Yip, 2016; Lyytimäki, 2015, 2017). Others view EDS as biodiversity loss (Chapin et al., 2000) or decrease in ES caused by some ecosystem functions and processes (Shapiro & Báldi, 2014), which can be induced by humans (Balmford & Bond, 2005). While some agreed with the definition of Lyytimäki et al (2008) (Power, 2010; Zhang et al., 2007), Shackleton et al. (2016) redefined the concept particularly as nature's detriments which affect not ecosystem services but rather human well-being. Their definition has received support in several studies (Escobedo et al., 2011; Vaz et al., 2017; Von Döhren & Haase, 2015), although the wording used in these studies might vary (Guo et al., 2022). Overall, integration of ES-EDS in nature and species assessment has been encouraged (Blanco et al., 2019; Davoren & Shackleton, 2021; Delshammar et al., 2015; Escobedo et al., 2018; Guo et al., 2022; Mouchet et al., 2017; Schaubroeck, 2017; Swain et al., 2013; Vaz et al., 2017).

There are two ways to categorize EDS within the literature, dependent on whether one focuses on impacts or disservices. Regarding the first classification, different papers apply a variety of impact formulations (Table 1). EDS is divided into three impact groups by Shackleton et al. (2016), three other groups by Escobedo et al. (2011), six groups by Lyytimäki (2008), five groups by Von Döhren and Hasse (2015), and five other groups by Vaz et al. (2017). Among these classifications, several impact groups are mentioned repeatedly, such as health, security, economy, and leisure; while others give different names but can be understood to be largely the same EDS (such as economic and financial cost, or health and psychological impacts). Indirect EDS (ecological impacts group) are not usually the focus of this approach (only one paper identifies ecological EDS (table 1)). The reason might be that as EDS are categorized by their impacts on human-wellbeing, direct impacts can be easily thought of and thus receive much more focus than indirect ones. Overlap of EDS categories challenges not only the integration of EDS into the ES concept but also the validation of the concept itself.

Table 1: Differences of EDS categorizations

	Paper	Shackleton et al. (2016)	Lyytimäki (2008)	Escobedo et al. (2011)	Von Döhren & Hasse (2015)	Vaz et al. (2017)
Categorizations	Economic	X	X		X	
	Financial cost			X		
	Health	X	X		X	X
	Psychological				X	
	Safety	X	X			X
	Security		X			X
	Aesthetics		X			X
	Cultural	X				X
	Social nuisances			X		
	Environmental pollution			X		
	Ecological				X	
	Material					X
	Leisure and creation					X
	Mobility		X			
	General impacts on human wellbeing				X	

The second classification is to classify EDS according their disservices: provisioning, regulating, cultural, and supporting, which is similar to how ES are classified (Friess, 2016; Mouchet et al., 2017; Springer et al., 2018; Wu et al., 2021) (Figure 1). Differing from the first classification mentioned above, here indirect EDS (supporting disservices) are usually emphasized to an equal degree compared to other EDS groups. With the importance of identifying and classifying indirect species' detriments, this type of classification was used in many assessments of invasive species where the mention of both direct and indirect EDS in the ES-EDS assessment of these species are indispensable (Milanović et al., 2020; Shackleton & Shackleton, 2018; Vaz et al., 2017; Wielgoss et al., 2013). Various ES-EDS assessments show that invasive species, both native and non-native (or alien), can harm neighboring species, either by competing with the natives, reducing natural habitats (Shackleton et al., 2019; Sheergojri et al., 2022; Springer et al., 2018; Tebboth et al., 2020), disturbing stability of native ecosystems (Limburg et al., 2010; Tebboth et al., 2020), or by decreasing biodiversity (Milanović et al., 2020; Wielgoss et al., 2013). This classification approach hence allows easier integration of EDS into the MA framework, creating a better foundation for adoption of both ES and EDS. Moreover, it emphasizes the importance of species' indirect detriments for clearer and more comprehensive decision-making processes.

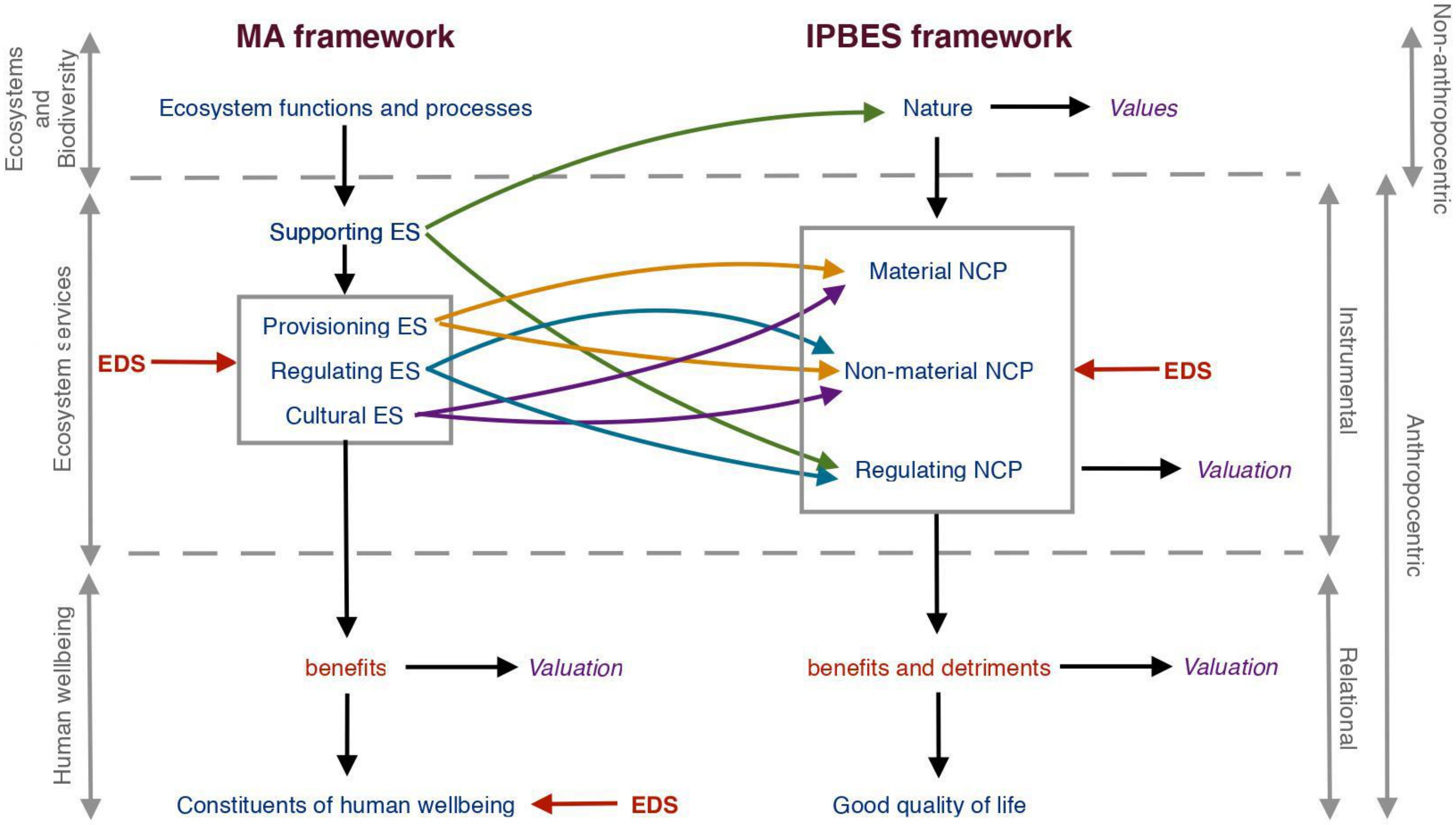

Figure 1: Differences in MA and IPBES frameworks. Schematic illustration of the relationship between ES and NCP, the various ways economic valuation enters and the different entrance points of EDS into the frameworks.

2.2. NCP concept

Critique of ES spans from anthropocentrism (Wallace, 2007) and over-optimism (Lyytimäki et al., 2008) to insufficient recognitions of biodiversity (Faith, 2018), intrinsic values of nature (IPBES, 2016), Indigenous and Local Knowledge, and the relational value of nature (Díaz et al., 2018). Based on these suggested limitations, the IPBES framework with the NCP concept was formed. IPBES reframes "services" as "contributions", since "services" were seen as an anthropocentric concept where humans are above nature, while "contribution" underlines the nature-human gifting relationship with a lesser lord-and-servant impression (Díaz et al., 2018). Moreover, nature's or species' contributions are recognized as potentially being both beneficial and detrimental depending on different contexts and perspectives. To emphasize not only anthropocentrism but also ecocentrism, the IPBES framework surrounds the NCP concept with two other entities: (1) nature – which includes the impact of the natural entity in question on other organisms, biodiversity, biophysical assemblages, and biophysical processes; and (2) good quality of life – which indicates how human wellbeing is impacted by nature (Figure 1). Including NCP, these three "foci of values" constitute the IPBES framework.

Significantly, the four different types of ES – supporting, provisioning, regulating, and cultural – were redefined in IPBES as regulating, material, and non-material NCP[3] (Díaz et al., 2018) (Figure 1). Provisioning ES became material NCP, consisting of materials, physical objects, and substances that humans extract from nature. Second, non-material NCP emanates from both provisioning and regulating ES, including human intellectual experiences with nature, such as in religion, education, recreation, etc. The reason non-material NCP covers both provisioning and regulating ES is because to obtain experiences and inspiration, both tangible

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[3] The term «NCP» and «contributions» are used interchangeably in the NCP literature.

and intangible contributions are necessary. Third, regulating and supporting ES combine into regulating NCP including ecosystem functions and processes which can provide both direct and indirect contributions to humans. Regulating NCP sustain natural environments and are the foundation for material and non-material NCP (IPBES, 2017). Furthermore, all three types of NCP include both nature's benefits and detriments.

Values are assessed differently under the IPBES and MA frameworks. Supporting ES were disregarded in the valuation phase to avoid double counting, since supporting ES influence indirectly human wellbeing via the direct services (Figure 1). IPBES adopted another perspective regarding valuation where all three compartments of the framework – nature, NCP, and good quality of life – are valued concurrently (Figure 1), using different methodologies. Furthermore, IPBES acknowledged that valuation of these three compartments can overlap, thus the mode of valuation should be based on the purpose of the assessment (IPBES, 2016). We distinctly separate "valuation" from NCP and Good quality of life with "values" from nature (Figure 1) since the latter compartment can provide pluralistic types of values in which some cannot be estimated economically.

Critiques of IPBES' works quickly emerged, especially with Kenter (2018) discussing challenges within the NCP terminology in relation to the viewpoints of Diaz et al. (2018) regarding the ES concept. Both ES and NCP are shown have their own semantic problems, suggesting that NCP is only a rephrasing of ES, though the latter concentrates solely on a unidimensional flow of values from nature to people, disregarding the reciprocal anthropogenic impact within the nature-human complex system. Kenter (op cit) stated that the term NCP puts much focus on the instrumental value of nature, which does not sufficiently encapsulate the pluralist philosophy of the overall framework. Thus, the author suggested keeping the ES concept within a pluralistic setting, including NCP. The NCP concept was further criticized (Braat, 2018; Maes et al., 2018), especially in response to Diaz et al.'s (2018) claim that the

MA framework lacks the weight of social science participation, especially anthropology. Maes et al. (2018) have pointed out that over the evolution of the ES concept, more recent studies included the participation of social scientists in policy-making, even with the involvement of local and ethnic practitioners. Therefore, they called for an integration of ES within the IPBES framework to compliment and revise it for improved environmental assessment. Additionally, Braat (2018) claimed that the article "Assessing nature's contribution to people" by Diaz et al. (2018) was narrow-sighted and contained false claims about the evolution and knowledge accumulation in relation to the ES concept, alerting readers to the problems of embracing the NCP concept too soon with insufficient time for practical application and peer-review. It seems fair to claim that the debate whether to adopt NCP or ES has not yet reached its conclusion.

3. Methodology

As discussed earlier, ES-EDS and NCP concepts possess their own advantages and disadvantages. While ES-EDS are more widely accepted and applied, NCP helps to clarify nature's positive and negative impacts on human well-being, especially with clear classifications and explanations regarding the indirect benefits and detriments. To compare their differences in detail, we applied the case of the allelopathic species *E. nigrum* in the context of the Fennoscandian tundra and boreal ecosystems as a case study. From a systematic literature review, we identified, classified, and analysed the direct and indirect benefits and detriments that can be associated with *E. nigrum* based on the guidelines of ES-EDS and NCP concept.

3.1. Systematic literature review

The Systematic literature review (SLR) method not only captures the big picture of research achievements and limitations in specific fields but also reduces the risks of bias within individual and selected studies, or across filtered studies, also providing reliable reference sources (Liberati et al., 2009). So far, three review studies of *E. nigrum* have been published (Lorion & Small, 2021; Nilsson & Wardle, 2005; Tybirk, Nilsson, Michelsen, Kristensen, Sheytsova, Strandberg, Johansson, Nielsen, Riis-Nielsen, Strandberg, & Johnsen, 2000). While Tybirk et al. (2000) and Nilsson and Wardle (2005) concentrated in the allelopathic impact of *E. nigrum* on ecosystems, Lorion and Small (2021) stress its role in relation to birds, mammals, and humans. None of the reviews were conducted systematically, or assessed broadly positive and negative contributions of *E. nigrum*.

3.2. Data collection

This SLR was conducted following the criteria of the AMSTAR framework (Welsh et al., 2015). The AMSTAR guideline was created to evaluate the quality of systematic literature reviews, thus enhancing validity of the SLR (Shea et al., 2017). The AMSTAR guideline requires the SLR research to be specific and transparent by meeting several conditions, ranging from the requirement of multiple databases to data inclusion, duplication, and exclusion control, statistical method in meta-analysis and details with respect to chosen studies.

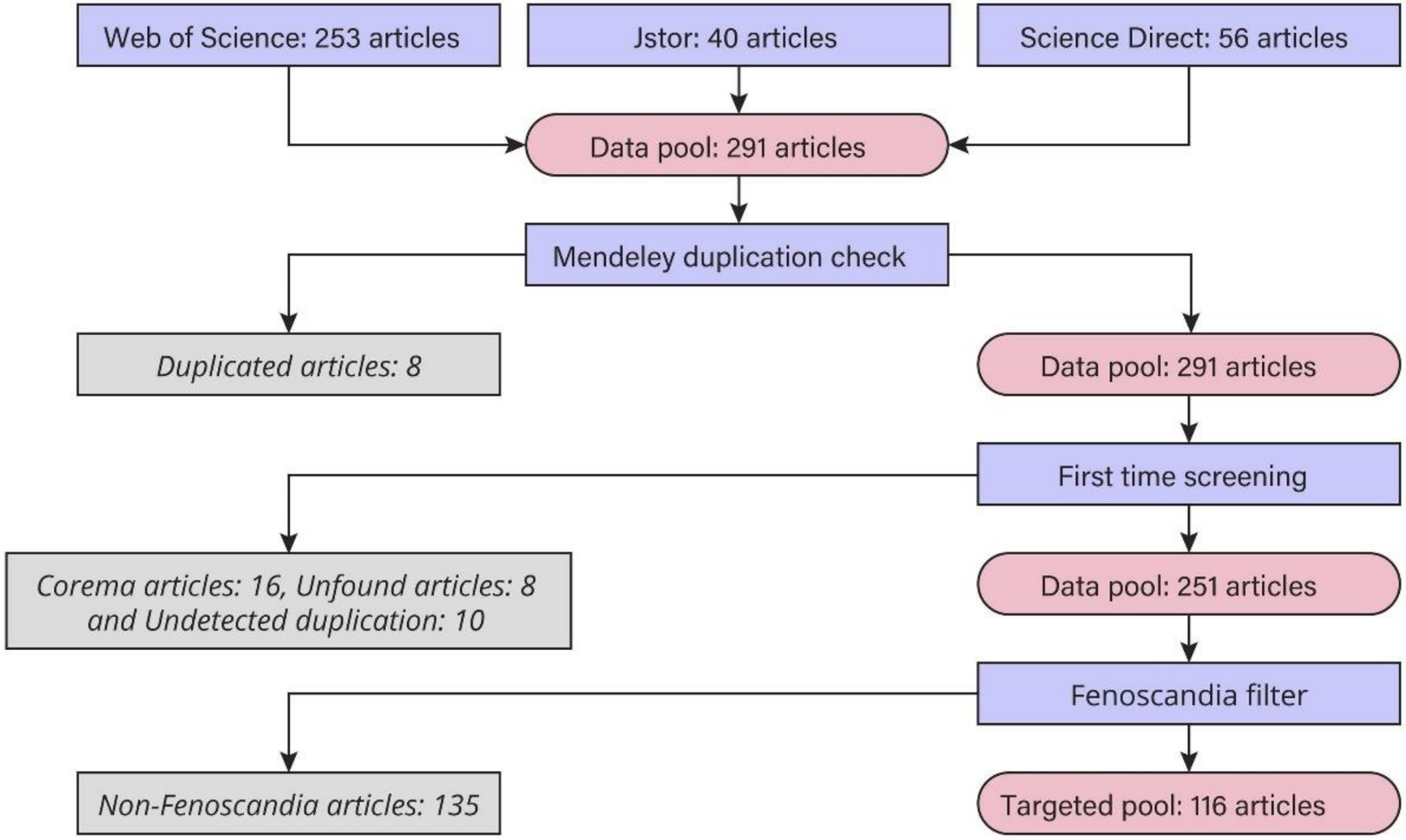

Figure 2: Data filtration and selection.

Amongst scientific databases, ScienceDirect, Jstor, and Web of Science (WoS) were chosen since they are central databases for peer- and non-peer-reviewed publications about *E. nigrum*. *Empetrum* includes several species, but we concentrated on *E. nigrum* and its common English name – crowberry. Two main keywords were chosen under a connected boolean: "Empetrum nigrum" OR "crowberry". From each database, only those mentioning the search query in titles, abstracts, or specified keywords were selected (Figure 2). Duplication among and between databases was eliminated first by the built-in checking tool in Mendeley, followed by a re-examination of title, abstract, and list of authors. Among the remaining 275 papers, 16 were eliminated due to either *E. nigrum* being mentioned only one time, or that it was not a central subject or object of the research, or the paper was about another type of crowberry – white crowberry (*Corema album*) – which falls outside the scope of this study. Among the remaining pool, eight publications were so old that their sources could not be found, leading to the final total number of chosen publications for inspection of 251 (see Figure 2).

Following the AMSTAR guideline, the chosen publications were double-checked, first by conducting another procedure to create the data pool, and then by inspection of two co-authors. The second procedure was operated by not merging three datasets into a pool within Mendeley as before but choosing the one with the most publications as a base source – in this case the WoS. Then comparison between ScienceDirect and Jstor datasets in relation to the WoS pool was handled manually to include those publications that were not listed in WoS. This second pool, then, was compared with the first to see whether any publication was excluded between pools. Following this, two co-authors were asked to go through the eliminated publications for re-confirmation. Duplicated papers which were not detected by Mendeley were handled within this double check procedure. This procedure fulfills the AMSTAR requirement for study selection and data inclusion, exclusion, and duplication management.

With the pool of 251 chosen publications, preliminary analysis was implemented. Different context variables were extracted, including geography – where the study was conducted, timeline – when the experiment took place, field of science – whether the study belongs to natural science or social science, and research areas – fields and sub-fields of the publications. Since Fennoscandia possesses the earliest and largest part of the publications, and also since *E. nigrum* is considered a key species within this region (Tybirk, Nilsson, Michelsen, Kristensen, Sheytsova, Strandberg, Johansson, Nielsen, Riis-Nielsen, Strandberg, & Johnsen, 2000), papers which are geographically relevant to the Fennoscandia region were filtered as a subset for quantitative analysis. This led to 116 publications being chosen for the final pool.

3.3. Data coding

Regarding ecological aspects, *E. nigrum* impacts on four different categories – on other organisms and species, on biodiversity, on biological assemblages and structure, and biophysical processes and functions. Organismal impact covers the responses of other species to *E. nigrum*'s pressure, while impacts on biological assemblages and structure indicate changes of ecological communities and habitats. Biodiversity impact involves alteration of taxonomic, functional, or genetic diversity of the community, while impact on biophysical functions and processes is concerned with changes in element dynamics through changed biotic and abiotic interactions, e.g. food web dynamics and nutrient cycling. Information related to anthropogenic aspects was extracted based on the researched and referenced benefits and detriments that *E. nigrum* provides.

We define as direct the benefits and detriments of crowberry that feed directly from dis-/services or contributions into well-being, not having come via more indirect contributions or supporting dis-/services.

Direct benefits and detriments were recognized and recorded through the title, abstract, discussion, and conclusion of each publication. Indirect benefits and detriments may often be unaccounted for, since they are regularly embedded within ecological publications and refer to supporting services, disservices, or regulating NCPs. Therefore, to include these aspects, impacts of the species on other species, towards whole communities or the dynamic of local ecosystems, can be seen as the supporting ecosystem services and disservices, or regulating contributions that *E. nigrum* provides. A piece of information within a study is grouped as explicit when that study explicitly researched *E. nigrum*'s benefits and detriments, and as implicit when the benefits and detriments were only mentioned via reference to other studies. Impacts of *E. nigrum* were then categorized based on NCP and ES concepts. Regarding negative impacts, we grouped the detriments following the functions of the disservices (provisioning, regulating, cultural, and supporting) or negative contributions (all three NCP groups). Data variables and their categories are summarized in table 2.

Cross-check reading was conducted by three co-authors to assess the reliability and validity of the analysis. Each co-author randomly chose 15% of the articles in the pool for reassessment.

Table 2: List of data variables and categories for paper analysis

Data variables	Categories
Geography	Finland; Norway; Sweden; Russia; Fennoscandia
Timeline	1971; 1972; ...; 2019
Field of science	Natural science; Social science; Both
E. nigrum impact on organisms	Negative or Positive; Implicit or Explicit,
E. nigrum impact on biodiversity	Negative or Positive; Implicit or Explicit
E. nigrum impact on biological assemblages and structure	Negative or Positive; Implicit or Explicit
E. nigrum impact on biophysical functions and processes	Negative or Positive; Implicit or Explicit
Ecological role	Inhibit growth of *Pinus sylvestris*; Diet for *Entephria polata*; Lower species richness and abundance of herbaceous vascular plants; ...
Direct Ecosystem services	Food; Medicinal effects; Bioindicators;...
Supporting Ecosystem services	Animal feed; Facilitate growth of some species;...
Direct Ecosystem disservices	N/A
Supporting Ecosystem disservices	Unpalatability; Inhibit growth of other species; Decrease biodiversity; ...
Direct Nature’s contribution to people (material, non-material)	Food; Medicinal effects; Bioindicators;...
Indirect Nature’s contribution to people (regulating)	Animal feed; Unpalatability; Facilitate growth of some species; Inhibit growth of other species; Decrease biodiversity; ...

4. Results

E. nigrum has on average been included in one publication per year before 1995 and 4,6 publications from 1997 to 2021 (Figure 3). Among the 116 publications of the targeted pool, 69 publications belong to the field of ecology, involving 8 publications within zoology, 52 publications in plant phenology and physiology, and 9 publications related to other sub-fields of ecology. Besides ecology, 25 publications involve phytochemistry, 17 publications belong to biogeochemistry, and 1 publication is in the field of biogeography. Strikingly none of the targeted publications belong to the field of social science though one study utilized the social phenomena of hiking and berry picking as ecological disturbance factors (Manninen & Peltola, 2013).

Geographically, nearly half of the publications investigated *E. nigrum* in Finland. The country is also the pioneer in this niche of *E. nigrum* research with the first publication in the 1970s. Research in Sweden, Norway, and Russia started later in the 1990s, but the number of publications has increased substantially, especially in Norway and Sweden (Figure 4). The geographic term Fennoscandia represents the publications whose research area cover more than one country, and these publication numbers seem largely constant since the late 1990s.

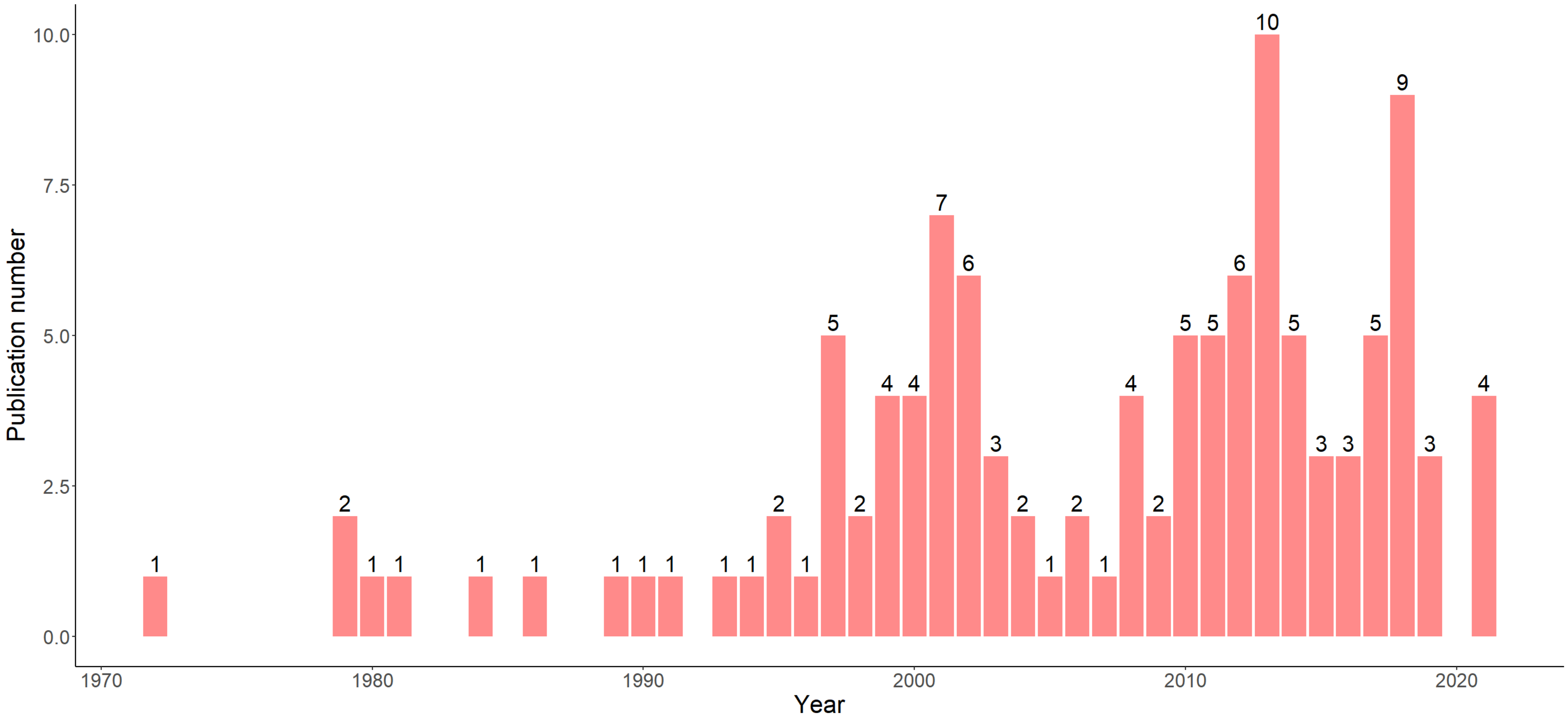

Figure 3: Temporal span of total 116 publications on E. nigrum (1972 – 2021).

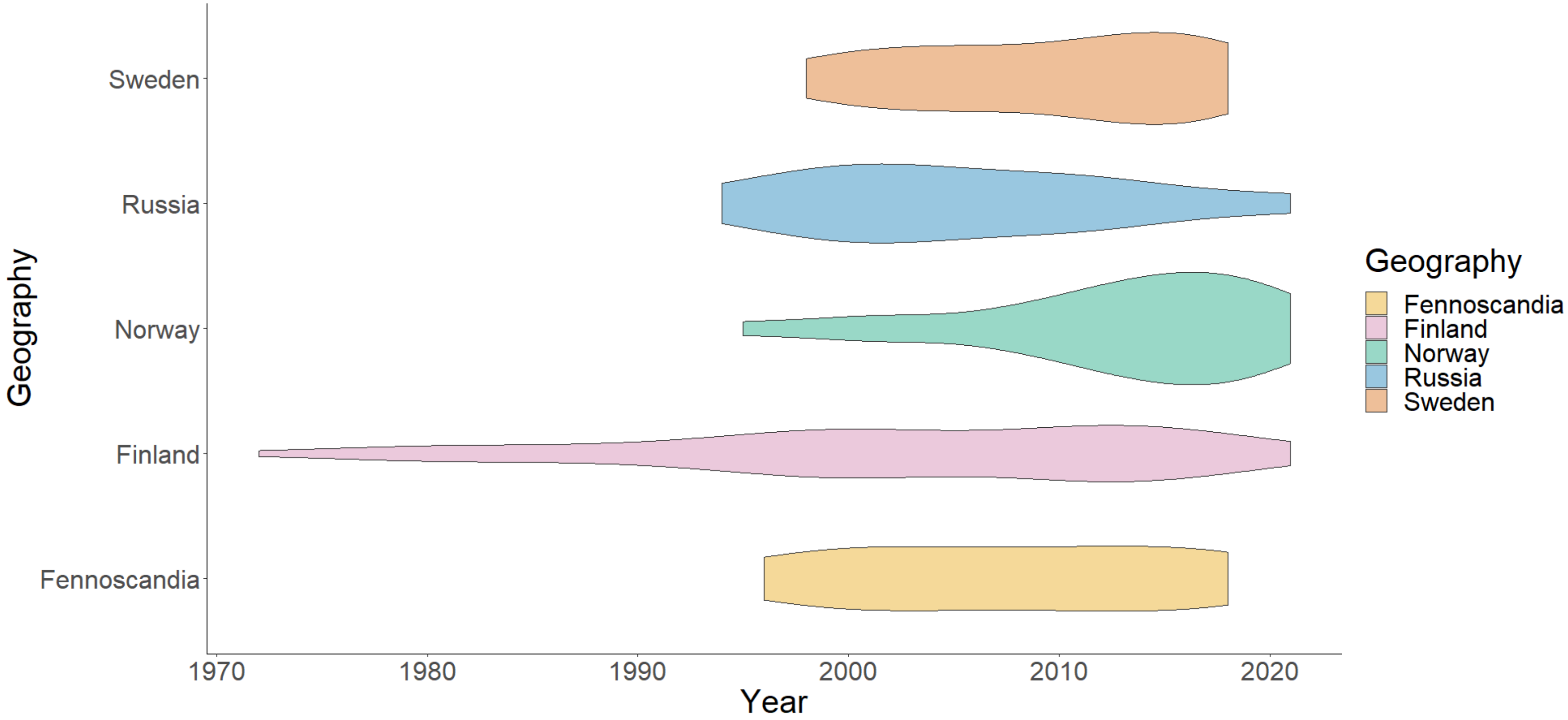

Figure 4: Temporal span of E. nigrum articles within Fennoscandia region.

Based on the analysis, we categorized a total of 11 benefits and detriments of *E. nigrum*. Differences in categorization emerge when we group *E. nigrum* benefits and detriments following the MA and IPBES frameworks. Following the MA framework, 11 benefits and detriments were divided into 5 groups, including provisioning ES (23 articles), regulating ES (5 articles), cultural ES (7 articles), supporting ES (19 articles) and supporting EDS (11 articles). Within the IPBES framework, since the separation of direct-indirect and positive-negative are embedded within the NCP concept, only 3 groups were categorized: material NCP (23 articles), non-material NCP (7 articles), and regulating NCP (22 articles) (see table 3 and figure 5).

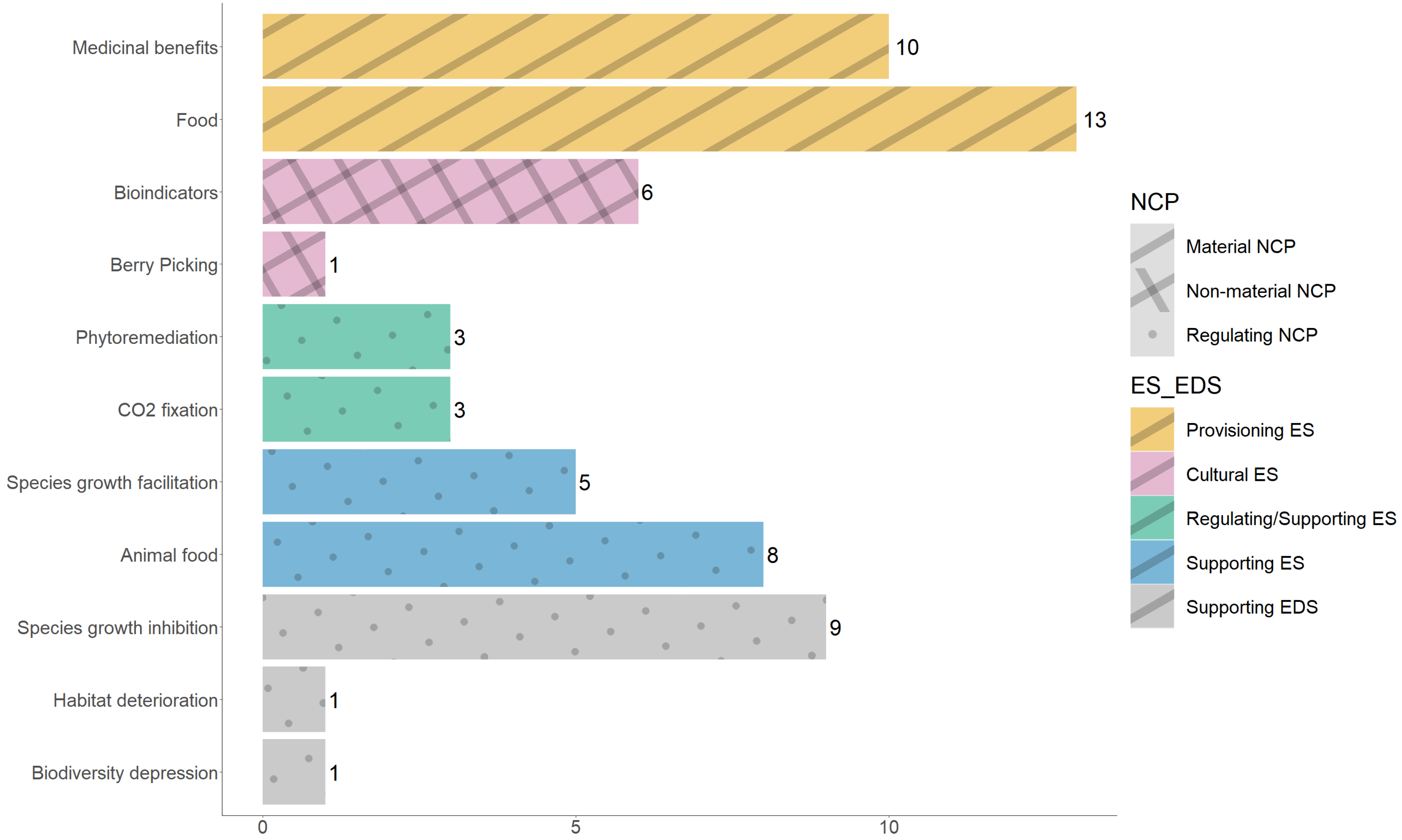

Figure 5: Publication number regarding benefits and detriments of E. nigrum following ES-EDS and NCP categorizations.

Under the MA framework, two benefits of *E. nigrum*, carbon fixation and phytoremediation, were categorized as both regulating and supporting ecosystem services. Regarding carbon fixation, *E. nigrum* expansion increases carbon stocks in aboveground biomass (Silvola & Hanski, 1979; Ylanne et al., 2015). While increased primary production can also translate to increased food for wildlife herbivores, a supporting ES, such bottom-up effects are strongly modulated by e.g. palatability, a functional trait which *E. nigrum* does not possess (Tybirk, Nilsson, Michelsen, Kristensen, Sheytsova, Strandberg, Johansson, Nielsen, Riis-Nielsen, Strandberg, & Johnsen, 2000). Regarding phytoremediation, *E. nigrum* can tolerate and accumulate heavy metals at contaminated sites (Middleton et al., 2018; Monni et al., 2000). Since both humans and nature gain benefits from carbon fixation and phytoremediation, these benefits were categorized as both supporting and regulating ES.

Table 3. List of articles identifying benefits and detriments of E. nigrum and our corresponding categorization into ES/EDS and NCP concepts.

E. nigrum benefits and detriments	MA framework	IPBES framework	Articles
Food (berries)	Provisioning ES	Material NCP	Hakkinen et al., 1999; Hellström et al., 2013; Järvinen et al., 2010; Kallio & Yang, 2014; Koskela et al., 2010; Laaksonen et al., 2011, 2013, 2014; Manninen & Peltola, 2013; Ollanketo & Riekkola, 2000; Sjögren & Arntzen, 2013; Viljakainen et al., 2002; Wallenius, 1999
Medicinal benefits	Provisioning ES	Material NCP	Järvinen et al., 2010; Hellström et al., 2013; Ho et al., 2017; Huttunen et al., 2011; Kallio & Yang, 2014; Koskela et al., 2010; Moskaug et al., 2008; Toivanen et al., 2011; Törrönen et al., 2012
Phytoremediation	Regulating ES/ Supporting ES	Regulating NCP	Helmisaari et al., 2007; Lyanguzova, 2021; Monni et al., 2000
CO_2 fixation	Regulating ES/ Supporting ES	Regulating NCP	Silvola & Hanski, 1979; Silvola & Heikkinen, 1979; Ylanne et al., 2015
Species growth facilitation	Supporting ES	Regulating NCP	Grau et al., 2010; Lindholm & Vasander, 1981; Mod et al., 2014; Pellissier et al., 2010; Svensson et al., 2018
Animal feed	Supporting ES	Regulating NCP	Bokhorst et al., 2018; Dahle et al., 1998; Hertel et al., 2016; Itamies & Varkonyi, 1997; Pulliainen & Tunkkari, 1991; Stenset et al., 2016; Tabell et al., 2019
Biodiversity depression	Supporting EDS	Regulating NCP	Bråthen & Ravolainen, 2015
Habitat deterioration	Supporting EDS	Regulating NCP	Gallet et al., 1999
Species growth inhibition	Supporting EDS	Regulating NCP	González et al., 2015; Grau et al., 2010; Hypponen et al., 2013; Mod et al., 2014; Monni et al., 2000; M.-C. Nilsson et al., 2000; Pellissier et al., 2010; Pilsbacher et al., 2021; Vistnes & Nellemann, 2008
Bioindicators	Cultural ES	Non-material NCP	Bråthen & Ravolainen, 2015; Lyanguzova, 2021; Middleton et al., 2018; Pulkkinen et al., 1989; Reimann et al., 2001; Steyaert et al., 2018
Berry picking	Cultural ES	Non-material NCP	Manninen & Peltola, 2013

5. Discussion

Our systematic literature review of *E. nigrum*'s benefits and detriments provides results which are in line with other reviews of this species. Ecological impacts of *E. nigrum*, such as its ability to degrade local habitats, outcompete neighboring species and depress biodiversity, were the main focus of Tybirk et al (2000) and Nilsson and Wardle (2005). However, since both reviews concentrated on the field of ecology, anthropocentric impacts of *E. nigrum* such as medicinal benefit or educational value were ignored. Lorion and Small (2021), in contrast, focused more on the overall benefits of this species towards nature and humans, yet with only brief mention of the negative impacts of *E. nigrum*. In our study we recognize that under different contexts and perspectives, crowberry can provide either benefits or detriments, or even both. For instance, from a social medical or health perspective, crowberry is a rich source of vitamins and nutrients for human well-being; while within an ecological perspective, *E. nigrum* supports growth of some plants at particular stages yet still induces shifts in vegetation communities. Ours is the first systematic literature review, contributing to a broader impact analysis of *E. nigrum* under different contexts and perspectives.

Among our 11 benefits and detriments, 10 were identified when combining the three other reviews (Lorion & Small, 2021; Nilsson & Wardle, 2005; Tybirk et al., 2000), but none considered carbon fixation as a benefit of *E. nigrum*. In light of *E. nigrum*'s detrimental effects, and the increase of these given climate change (Buizer et al., 2012; Svensson et al., 2018), carbon fixation can be seen as a positive trade-off in relation to the other negative impacts. Additionally, we found no direct EDS of *E. nigrum* in the literature, emphasizing that crowberry only provides indirect negative impacts to humans.

The indirect EDS of crowberry in tundra and boreal ecosystems is illustrated in Figure 6. The x-axis represents the indirect ES/ positive regulating NCP of the ecosystem while the y-axis stands for the direct ES/ positive material and non-material NCP, as well as some regulating NCP that are not on the x-axis. The bell-shaped curve describes a logistic growth for a plant community where the end of the curve is the maximum carrying capacity and the highest point is equivalent to the maximum sustainable yield (msy). As *E. nigrum* inhibits the growth of neighboring vegetation, i.e. a reduction in their intrinsic growth rate (González et al., 2015), this is shown by the downward shift of the curve. Furthermore, crowberry encroachment impacts the potential spread of the vegetation and biodiversity, shown by the decrease in maximum carrying capacity and inward shift of the curve. In total, this shrinks the maximum sustainable growth, leading to a decline in other direct services of the pasture.

Figure 6 emphasizes the importance of species impacts in relation to both indirect and direct ES-EDS/ NCP of the native ecosystems. By allelopathic impact of crowberry and its faster growth rate induced by climate and environmental changes, the biodiverse understorey landscape is homogenized by *E. nigrum.* Thus, not only can the impacts' magnitude, here the abundance of crowberry, amplify its detriments but it also affects other ES-EDS/ NCP of the ecosystems, which then potentially lead to new impacts or elimination of existing ones. For example, on the one hand, direct ES/ NCP provided by the local ecosystem will decrease, such as provisioning ES/ material NCP (berries) and cultural ES/ non-material NCP of the local area (i.e. cultural values from picking other berries, market and non-market values of the beautiful and biodiverse landscape). Crowberry encroachment also inhibits growth of many palatable plants and decreases plant biodiversity of the local ecosystem, which will have further negative consequences on many herbivores whose diets are not based on crowberry's fruit. In Fennoscandia, reindeer – an iconic ungulate of Sami culture – can be affected by this shift of vegetation communities, which then consolidate the indirect impacts of *E. nigrum* to the reindeer husbandry of the Sami people. Thus, indirect detriments of a species may not only decrease other indirect benefits but also direct benefits provided by other ecosystem functions and processes.

On the other hand, high abundance of crowberry might increase harvest and production of crowberry's juice and liquor, which are favoured by the Nordic market (though we found no economic research regarding this gastronomy benefit of *E. nigrum*). From our results, it can also be deduced that more carbon can be captured by crowberry encroachment, just because its wooden roots grow horizontally and vertically. This case study therefore strengthens the argument that identification and evaluation of indirect EDS/ negative regulating NCP are important to achieve complete species assessments.

Figure 6 also underlines the importance of species abundance in species assessments, since species impacts can influence ecosystem functions and processes at different levels of magnitude (since not all impacts have linear effects), which in turn may influence critically and unexpectedly other ES-EDS/NCP. The affected ES-EDS/NCP can further influence the stability of the native ecosystems and impact on people's way of life. These feedback processes of impacts between nature and humans not only highlight the ambiguous tangle between supporting and regulating ES (internalized in NCP) but also underline the importance of indirect ES-EDS/ NCP. Although species abundance may regulate benefits and detriments, quantification issues have, as far as we are aware, largely not been addressed in relation to the ES-EDS and NCP concepts, though both MA and IPBES frameworks acknowledge the dynamics of ecosystem processes and functions. Species abundance, hence, should beneficially be recognized as an element dynamically regulating species' ES-EDS/ NCP.

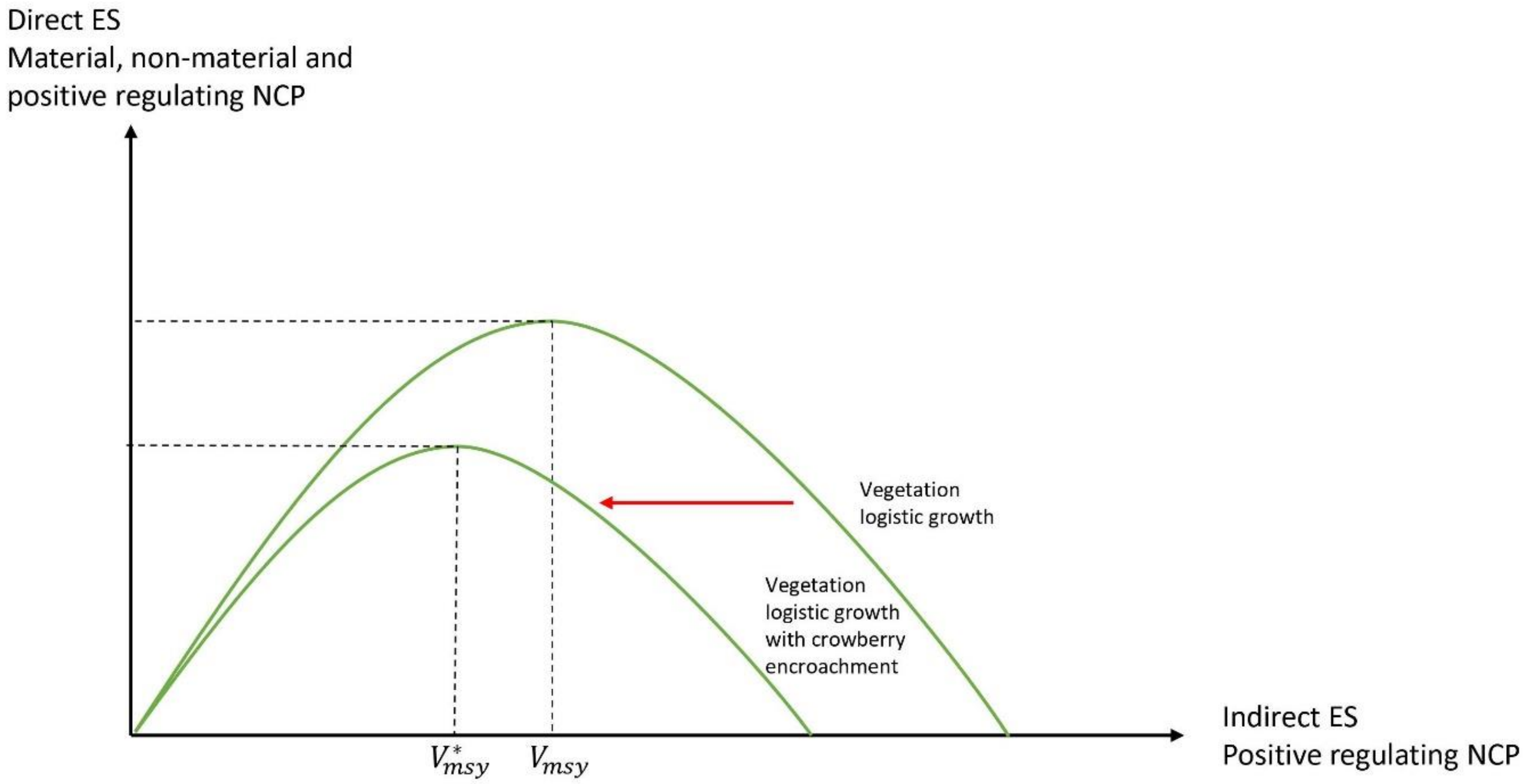

Figure 6: Illustration of negative impact of E. nigrum on a plant community's ES-EDS/ NCP. V_{MSY} describes the stock of plants that provides the maximum provision of services or contributions, while V^*_{MSY} is the stock that yields maximum services or contributions when impacted by crowberry (adapted from Armstrong et al (2014)).

In our comparison between ES-EDS and NCP, we found the latter to be more flexible and comprehensive because of four main points. First, there are two benefits of *E. nigrum*, phytoremediation and CO_2 fixation, which are categorized as both regulating and supporting ES. This is because the MA framework provided limited guidance and explanation for dealing with the blurred line between these two ES categories (La Notte et al., 2017; Wallace, 2007). Other well-known frameworks emanating from the ES concept have dealt with this ambiguity by omitting the supporting ES group such as within the Common International Classification of Ecosystem Services (CICES), due to challenges in relation to identification problems (Haines-Young & Potschin, 2018), or because of their desire to avoid double counting with The Economics of Ecosystems and Biodiversity (TEEB, 2010). However, The IPBES approach solved this issue by merging supporting and regulating ES into regulating NCP, and depending on context or perspective, the impact can be classified as direct or indirect. Although the combination of regulating and supporting ES into regulating NCP may obscure which benefit or detriment is direct or indirect, this re-categorization captures the diversity, complexity, and context-specific dependence of humans on nature. The reason why NCP categorization is more flexible is that as while the ES concept was coined for nature conservation acknowledgement purposes, the NCP concept was created later to be more comprehensive, with broader values, as mentioned above.

Second, it was challenging to categorize the supporting ES of *E. nigrum*, since examples of supporting services in the MA framework often relate to relatively general concepts such as nutrient cycling, soil formation, or primary production, whereas indirect benefits and detriments of *E. nigrum* were analyzed with higher degree of specificity, such as biodiversity depression or species growth inhibition. There is also no clear approach for identifying indirect EDS in the literature. To clarify the indirect impacts of *E. nigrum* we followed the IPBES value assessment guideline regarding the dimensions of nature (IPBES, 2016). Thus indirect impacts of *E. nigrum* are addressed following four categories: (1) individual organisms, (2) biophysical assemblages, (3) biophysical processes, and (4) biodiversity. The IPBES framework, therefore, provides a stronger and clearer structure in linking ecological impacts of nature with human wellbeing. Nevertheless, we also found inconsistency in re-categorization of NCP from ES, especially regarding supporting services. IPBES claimed that they omitted supporting ES from the NCP concept (IPBES, 2017), since these indirect services are now regarded as ecosystem properties and captured by the focal point of nature within the broader IPBES assessment framework. Contrary to this, within the appendix material of Diaz et al. (2018), supporting ES feed into both the value of nature and regulating NCP. Furthermore, within 18 subgroups of NCP, several relate tightly to supporting ES, such as (1) habitat creation and maintenance, (2) pollination and dispersal of seeds and other propagules, and (3) formation, protection and decontamination of soils and sediments. Regulating NCP do indeed capture entirely supporting ES, consistently recognizing the indirect yet indispensable influence of nature. IPBES thus managed to re-orient ES to a pluralistic perspective including ecocentric viewpoints, and also resolved the challenges in EDS definitions and classifications.

Third, we classified EDS according to types of disservices as this proved to be the better approach in our case. While the MA framework divided ES into three main groups of direct services – provisioning, regulating, and cultural ES groups, with EDS classified more closely to the MA constituents of wellbeing, which then enter on another level compared to the services (Figure 1). The impact groups of EDS (Table 1), such as health, security, mobility, and psychological impacts, literally belong to the MA constituents of wellbeing (Millennium Ecosystem Assessment, 2005). The inclusion of economic and financial impacts in EDS, mentioned above, is also confusing since all EDS can provide economic consequences, whether from declines in health, or security or the like. Indeed, economic valuation can be carried out on most direct services (TEEB, 2010), and therefore presumably in relation to EDS as well.

Therefore, in some literature, EDS have been defined by their impacts on human well-being, not as actual disservices in and of themselves. As there is also no consensus in how EDS should be classified, the NCP concept provides a solution to this problem by incorporating also nature's detriments into NCP.

Fourth, even with the above-mentioned ES-EDS mismatch problem, a further semantic problem continues in the valuation phase. The semantic problem lies in the assumption underlying the terminology "services". The purpose of the MA framework was to emphasize the indispensable relationship between nature and humans, so that nature would be accorded a conservation priority in policy development and decision-making. Thus, positivity was embedded within the ES concept. However, more recent works aimed to value nature's benefits, especially represented by the TEEB (2010) initiative, which separated the "services" and "benefits" that ecosystems provide. Following TEEB's categorization (with which studies of ES valuation have been following (Braat & de Groot, 2012b; DeGroot et al., 2010; TEEB, 2010, 2023)), if the concept of "services" – what nature provides – should be understood separately from the concept of "benefits" – what humans receive – then the "service" itself can have different directions of influence on human beings under different contexts. Thus, the terminology "ecosystem services" can be seen as a neutral noun. Yet the term "ecosystem disservices" was coined with the purpose of finding an opposing concept for ES. Even though it was agreed that EDS would also be analyzed differently under specific contexts (Shackleton et al., 2016; Vaz et al., 2017), the term "ecosystem disservices" was still charged with negativity. If the term ES had been considered a neutral noun (DeGroot et al., 2010; Haines-Young & Potschin, 2010; TEEB, 2010) without positive meaning embedded, then the term EDS would not have been necessary. This philosophical and semantic conflict in relation to services will remain unless the importance of both the benefits and detriments that humans receive from nature is recognized.

Though NCP can be considered as a more flexible and comprehensive concept than ES, combining supporting and regulating ES into regulating NCP, may lead to double counting in the valuation phase. Values should only be assessed once; for instance, in the case of *E. nigrum*, values of berries are recognized as provisioning NCP. Yet if researchers additionally evaluate values of crowberry as habitat, which can be recognized as indirect regulating NCP, then this entails double counting (Fu et al., 2011). In these specific situations, researchers can divide NCP into sub-groups, such as direct-indirect subgroups for higher degree of clarification. Moreover, identifying clearly who receives the provided NCP will support direct-indirect clarification. When researchers analyse the impacts accurately, for instance the exact name of the species' benefits or detriments, not the categories these impacts are grouped into, incorrect valuation can also be avoided.

Although we aimed to achieve a comprehensive analysis, some limitations are unavoidable. Since *E. hermaphroditum,* a species now considered synonymous with *E. nigrum* (Royal Botanic Gardens, 2022) was not considered a keyword, some publications may have been left out. Studies comparing both subspecies concluded that they primarily possess the same morphological and phenological characteristics (Altan & Özdemir, 2004; Nilsson et al., 2000), though the negative impact of *E. hermaphroditum* is stronger in some specific situations (Nilsson et al., 2000). Another limitation comes from the exclusion of languages of nations and regions in which *E. nigrum* plays an important role in the local communities, such as in Norwegian – "krekling" or "krøkebær", in Russian – "вороника", in Finnish – "variksenmarja", Swedish – "kråkbär", or other indigenous languages such as the Inuit in Northern America – "paunngak", and the Sami in Fennoscandia – "čáhppesmuorji". Thus, further systematic literature reviews of *E. nigrum* specifically, or other environmental issues, should consider including non-English keywords to embrace diverse worldviews and context-specific perspectives. Last but not least, it is worth noting that among 251 articles only one belongs to social sciences (Hupp et al., 2015), implying that this native invader has largely not been investigated by social scientists before. Further research about *E. nigrum* would beneficially focus more on its socio-economic impacts.

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8 Paper 2 : Controlling the stock or the habitat – The crisis of native invasive encroachment in the grazing land of Norwegian reindeer husbandry

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Research article

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

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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^2 area) is taken as the indicator for pasture sustainability,

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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[1] 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 consumer-resource 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, α_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):

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

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

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[1] 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 α_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:

$$\pi_B = p\left(egM_VR - \frac{eg^2M_V}{\alpha_V}R^2\right) - c_1R \tag{4}$$

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

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

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 $\frac{\partial egVR}{\partial R} = egV$ 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

$$\dot{V} = \alpha_V V\left(1 - \frac{V}{M_V}\right) - gVR - \varphi VK \tag{6}$$

where K denotes the biomass of the native invasive species and φ 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 α_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.[2]

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 $K = M_K$, $V = M_V\left(1 - \frac{g}{\alpha_V}R - \frac{\varphi}{\alpha_V}M_K\right)$, and $S = egM_VR\left(1 - \frac{g}{\alpha_V}R - \frac{\varphi}{\alpha_V}M_K\right)$. $K = 0$ 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:*

$$\begin{cases} V_{E,MSY} = \frac{M_V}{2}\left(1 - \frac{\boldsymbol{M_K\varphi}}{\boldsymbol{\alpha_V}}\right) \\ R_{E,MSY} = \frac{\alpha_V - \boldsymbol{M_K\varphi}}{2g} \\ K_{E,MSY} = \frac{M_K}{2} \\ S_{E,MSY} = \frac{eM_V\alpha_V}{4}\left(1 - \frac{\boldsymbol{M_K\varphi}}{\boldsymbol{\alpha_V}}\right)^{\boldsymbol{2}} \end{cases}$$

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

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

[3]*If condition* (8) *does not hold, then we have a reverse situation where the*

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[2] 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).

[3] as all parameters are positive reals, hence $\frac{\varphi M_K}{\alpha_V} > 0$.

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 $V_{E,MSY} < V_{B,MSY}$, $R_{E,MSY} < R_{B,MSY}$ and $S_{E,MSY} < S_{B,MSY}$.

The profit or social welfare function of the encroachment model becomes

$$\pi_E = p\left[egM_V\left(1 - \frac{g}{\alpha_V}R - \frac{\varphi}{\alpha_V}M_K\right)R\right] - c_1R \tag{9}$$

Intuitively, the native invader's carrying capacity M_K 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 α_V, with higher α_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*

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

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 $\frac{\varphi M_V M_K}{2\alpha_V}$ 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 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 β is the feeding coefficient.[4] Assuming that the manager will control the native invader by burning and/or cutting, equation (7) transforms into

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

where the variable T is the treatment effort and ε 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, $V_{C,MSY}$, and the slaughter volume, $S_{C,MSY}$, 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, $K_{C,MSY}$.

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

$$V_{C,MSY} = \frac{M_V}{2}\left(1 - \frac{M_K\varphi}{\alpha_V}\right) - \left[\frac{\beta F}{2eg}\right] + \left\{\frac{M_V M_K \varphi \varepsilon T}{2\alpha_V \alpha_K}\right\}$$

$$R_{C,MSY} = \frac{\alpha_V - M_K\varphi}{2g} + \left[\frac{\alpha_V \beta F}{2eg^2 M_V}\right] + \left\{\frac{M_K \varphi \varepsilon T}{2\alpha_K g}\right\}$$

$$K_{C,MSY} = \frac{M_K\{(\alpha_K - \varepsilon T)\}}{2}$$

$$S_{C,MSY} = \frac{eM_V\alpha_V}{4}\left(1 - \frac{M_K\varphi}{\alpha_V}\right)^2 - \left[\frac{\alpha_V e}{M_V}\left(\frac{\beta F}{2eg}\right)^2\right] + \left\{\frac{eM_V M_K \varphi \varepsilon T[2\alpha_V\alpha_K + M_K\varphi(\varepsilon T - 2\alpha_K)]}{4\alpha_V \alpha_K^2}\right\}$$

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

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[4] 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*

$$-\frac{\beta F}{2eg}+\frac{M_V M_K \varphi \varepsilon T}{2\alpha_V \alpha_K}>0 \leftrightarrow \frac{T}{F}>\frac{\beta \alpha_V \alpha_K}{egM_V M_K \varphi \varepsilon} \tag{12}$$

Higher intrinsic growth rate of both plants, α_V and α_K, or feeding coefficient β 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 φ together with controlling coefficient ε 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

$$\pi_C = p\left[egM_V R\left(1-\frac{g}{\alpha_V}R-\frac{\varphi}{\alpha_V}M_K\left(1-\frac{\varepsilon}{\alpha_K}T\right)\right)+\beta FR\right]-c_1R-c_2F^2-c_3T^2 \tag{13}$$

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[5] 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^2, making the carrying capacities of both plant species equal to 1, 68 x 10^{10} 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 $\frac{\partial gVR}{\partial R} = gV$, 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 $g = 9 \text{ x } 10^{-7}$ 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 nutrition-rich 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 α_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 φ 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 cost c_1 per reindeer (including transportation, materials, administration costs, etc.) is estimated from the national data on reindeer husbandry in 2020 (Norwegian Government, 2021), by dividing the total cost (excluding labour costs) 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 ε and β 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 ε and β to be equal to compare the effects of both the adaptive measures on the

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[5] 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.

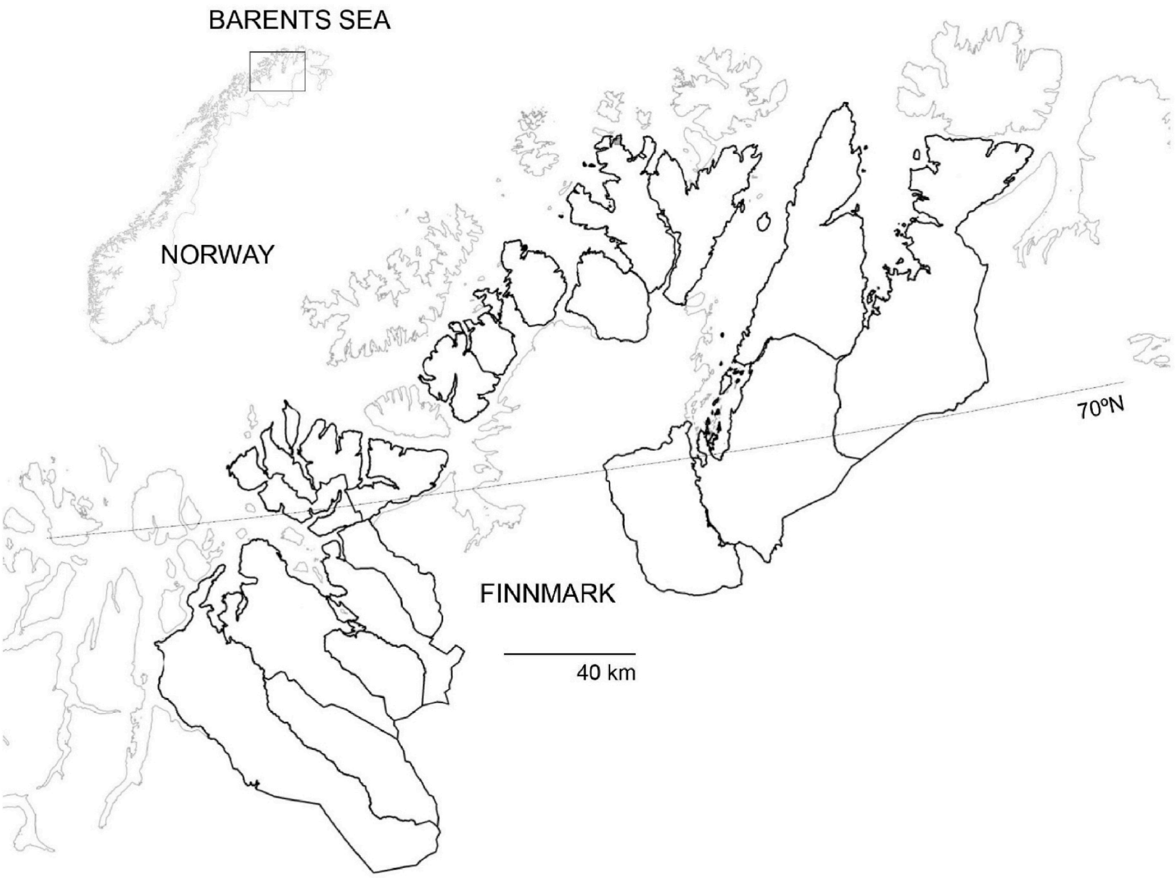

Fig. 1. Geographical map of the 20 chosen herding districts.

Table 1
Ecological and economic parameter values.

Parameters	Unit	Value	Source
α_V		0.6	May 1975; Moxnes (1993); Skonhoft et al. (2010)
α_K		0.15	Murguzur et al. (2019)
M_V	kg	1.68×10^{10}	Calculated from Bråthen and Lortie (2015)
M_K	kg	1.68×10^{10}	Calculated from Bråthen and Lortie (2015)
c_1	NOK/ reindeer	1220	Calculated from Regjeringen (2021)
c_2	NOK/1000 tonne dry feed	6,000,000	Provided by herders
c_3	NOK/labour days	2000	Calibrated
p	NOK/ reindeer	3760	Calculated from Regjeringen (2021)
e		2.8×10^{-5}	Calculated from Regjeringen (2021)
g		9×10^{-7}	Bakka et al., (2021); White and Trudell (1980)
φ		5×10^{-12}	Calculated from Bråthen and Lortie (2015); Bråthen & Ravolainen, 2015; González et al. (2015); Pilsbacher et al. (2020); Tuomi et al., 2022
ε		2×10^{-3}	Calibrated
β		2×10^{-3}	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
V^*	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
K^*		16.8	16.8	12.86	12.85	Million tonne biomass
S^*	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
V^*	12.52	14.8	Million tonne biomass
R^*	76,478	76,257	Reindeer
K^*	16.8	0.58	Million tonne biomass
S^*	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 benefit	5.7	5.7	Million NOK

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 c_2 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 c_3 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 α_V and carrying capacity M_V, price p, maintenance cost c_1, biomass conversion coefficient e and grazing rate g. As α_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

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					
		ΔV_{MEY}	ΔR_{MEY}	ΔS_{MEY}	ΔK_{MEY}	ΔF_{MEY}	ΔT_{MEY}
Intrinsic growth rates	α_V	0.8	**21.1**	**22**	−3.1	**21.1**	10
	α_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**
	c_2	0.0004	−0.01	−0.01	0.004	−9.1	−0.01
	c_3	−0.2	−3.1	−3.3	3.7	−3.1	**−12**
	p	−2.2	**18.8**	**16.8**	**−13.4**	**18.9**	**18.9**
Biomass conversion coefficient	e	−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	φ	−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

Via the results, the feedback loops between ecological factors and 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 capacity, 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.

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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.

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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 $\frac{\partial R_{B,MEY}}{\partial \alpha_V}$, $\frac{\partial R_{B,MEY}}{\partial g}$, and $\frac{\partial S_{B,MEY}}{\partial \alpha_V}$. As vegetation is assumed to be the only source of growth for the herbivore in our model, we expect $\frac{\partial R_{B,MEY}}{\partial \alpha_V} = \frac{egM_Vp - c_1}{2eg^2M_Vp} > 0$ and $\frac{\partial S_{B,MEY}}{\partial \alpha_V} = \frac{eM_V}{4}\left(1 - \frac{{c_1}^2}{p^2e^2g^2{M_V}^2}\right) > 0$, which then requires $pegM_V - c_1 > 0 \leftrightarrow \frac{c_1}{p} < egM_V$, which is exactly the inequality condition (5). The sign of the function $\frac{\partial R_{B,MEY}}{\partial g} = \frac{\alpha_V\left(\frac{2c_1}{eM_Vp} - g\right)}{2g^3}$ 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

$$\frac{2c_1}{eM_Vp} - g < 0 \leftrightarrow \frac{c_1}{p} < \frac{egM_V}{2} \tag{A.1}$$

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 $\frac{\partial V_{E,MEY}}{\partial M_V}$ and $\frac{\partial R_{E,MEY}}{\partial g}$. We expect $\frac{\partial V_{E,MEY}}{\partial M_V} = \frac{\alpha_V - M_K\varphi}{2\alpha_V} > 0$, which then requires that $\alpha_V - M_K\varphi > 0$ or $\frac{M_K\varphi}{\alpha_V} < 1$, which is satisfied by the inequality condition (8). This provides negative signs for other functions, such as $\frac{\partial S_{E,MEY}}{\partial M_K} < 0$ and $\frac{\partial S_{E,MEY}}{\partial \varphi} < 0$. Following the baseline model, we also expect that $\frac{\partial R_{E,MEY}}{\partial g} < 0$, which then requires $\frac{c_1}{p} < \frac{egM_V}{2}\frac{(\alpha_V - M_K\varphi)}{\alpha_V}$, 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			
	$\boldsymbol{V_{B,MEY}}$	$\boldsymbol{R_{B,MEY}}$	$\boldsymbol{S_{B,MEY}}$	$\boldsymbol{V_{E,MEY}}$	$\boldsymbol{R_{E,MEY}}$	$\boldsymbol{S_{E,MEY}}$	$\boldsymbol{K_{E,MEY}}$
α_V	0	$\frac{egM_Vp - c_1}{2eg^2M_Vp}$	$\frac{eM_V}{4}\left(1 - \frac{{c_1}^2}{p^2e^2g^2{M_V}^2}\right)$	$\frac{M_VM_K\varphi}{2{\alpha_V}^2}$	$\frac{egM_Vp - c_1}{2eg^2M_Vp}$	$\frac{eM_V}{4}\left(1 - \frac{{c_1}^2}{p^2e^2g^2{M_V}^2} - \left(\frac{\boldsymbol{M_K\varphi}}{\boldsymbol{\alpha_V}}\right)^{\mathbf{2}}\right)$	
M_V	$\frac{1}{2}$	$\frac{\alpha_Vc_1}{2eg^2{M_V}^2p}$	$\frac{\alpha_V\left(e^2 + \frac{{c_1}^2}{g^2{M_V}^2p^2}\right)}{4e}$	$\frac{1}{2}\left(\frac{\boldsymbol{\alpha_V - M_K\varphi}}{\boldsymbol{\alpha_V}}\right)$	$\frac{\alpha_Vc_1}{2eg^2{M_V}^2p}$	$\frac{\alpha_V\left(e^2 + \frac{{c_1}^2}{g^2{M_V}^2p^2}\right) - \boldsymbol{2e^2M_K\varphi} + \frac{\boldsymbol{e^2{M_K}^2\varphi^2}}{\boldsymbol{\alpha_V}}}{4e}$	
M_K				$-\frac{\boldsymbol{M_V\varphi}}{\boldsymbol{2\alpha_V}}$	$-\frac{\boldsymbol{\varphi}}{\boldsymbol{2g}}$	$-\frac{\boldsymbol{eM_V\varphi(\alpha_V - M_K\varphi)}}{\boldsymbol{2\alpha_V}}$	**1**
c_1	$\frac{1}{2egp}$	$-\frac{\alpha_V}{2eg^2M_Vp}$	$-\frac{\alpha_Vc_1}{2eg^2M_Vp^2}$	$\frac{1}{2egp}$	$-\frac{\alpha_V}{2eg^2M_Vp}$	$-\frac{\alpha_Vc_1}{2eg^2M_Vp^2}$	

(*continued on next page*)

Table A.1 (*continued*)

Parameters	Baseline model			Encroachment model			
	$\boldsymbol{V_{B,MEY}}$	$\boldsymbol{R_{B,MEY}}$	$\boldsymbol{S_{B,MEY}}$	$\boldsymbol{V_{E,MEY}}$	$\boldsymbol{R_{E,MEY}}$	$\boldsymbol{S_{E,MEY}}$	$\boldsymbol{K_{E,MEY}}$
p	$-\frac{c_1}{2egp^2}$	$\frac{\alpha_V c_1}{2eg^2M_Vp^2}$	$\frac{\alpha_V {c_1}^2}{2eg^2M_Vp^3}$	$-\frac{c_1}{2egp^2}$	$\frac{\alpha_V c_1}{2eg^2M_Vp^2}$	$\frac{\alpha_V {c_1}^2}{2eg^2M_Vp^3}$	
e	$-\frac{c_1}{2e^2gp}$	$\frac{\alpha_V c_1}{2e^2g^2M_Vp}$	$\frac{\alpha_V\left({M_V}^2+\frac{{c_1}^2}{e^2g^2p^2}\right)}{4M_V}$	$-\frac{c_1}{2e^2gp}$	$\frac{\alpha_V c_1}{2e^2g^2M_Vp}$	$\frac{\alpha_V\left({M_V}^2+\frac{{c_1}^2}{e^2g^2p^2}\right)-\boldsymbol{2{M_V}^2M_K\varphi}+\boldsymbol{\frac{{M_V}^2{M_K}^2\varphi^2}{\alpha_V}}}{4M_V}$	
g	$-\frac{c_1}{2eg^2p}$	$\frac{\alpha_V\left(-g+\frac{2c_1}{eM_Vp}\right)}{2g^3}$	$\frac{\alpha_V {c_1}^2}{2eg^3M_Vp^2}$	$-\frac{c_1}{2eg^2p}$	$\frac{\alpha_V\left(-g+\frac{2c_1}{eM_Vp}\right)+\boldsymbol{gM_K\varphi}}{2g^3}$	$\frac{\alpha_V {c_1}^2}{2eg^3M_Vp^2}$	
φ				$-\frac{M_VM_K}{2\alpha_V}$	$-\frac{M_K}{2g}$	$-\frac{eM_VM_K(\alpha_V-M_K\varphi)}{2\alpha_V}$	

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 $S = egM_VR - \frac{eg^2M_VR^2}{\alpha_V} + \beta FR - \frac{egM_VM_KR\varphi}{\alpha_V}$. 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

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

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:

$$\pi_{feed} = pS - c_1R - c_2F^2 \tag{B.1}$$

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

$$\pi_{feed} = p\left[egM_VR\left(1-\frac{g}{\alpha_V}\mathrm{R}-\frac{\varphi}{\alpha_V}M_K\right)+\beta FR\right] - c_1R - c_2F^2 \tag{B.2}$$

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:

$$V_{feed,MEY} = \frac{1}{2}\left(\frac{c_1}{peg}+M_V\left(1-\frac{\varphi M_K}{\alpha_V}\right)\right) - \frac{\alpha_V c_1\beta^2 - \alpha_V egM_Vp\beta^2 + egM_VM_Kp\beta^2\varphi}{2\alpha_V egp\beta^2 - 8c_2e^2g^3M_V}$$

$$R_{feed,MEY} = \frac{\alpha_V}{2g}\left(1-\frac{c_1}{pegM_V}-\frac{\varphi M_K}{\alpha_V}\right) + \frac{\alpha_V\beta^2(\alpha_V(egM_Vp-c_1)-egM_VM_Kp\varphi)}{2eg^2M_V\left(4c_2eg^2M_V-\alpha_Vp\beta^2\right)}$$

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

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

$$+\frac{\beta^2(\alpha_V(c_1-egM_Vp)+egM_VM_Kp\varphi)\left({\alpha_V}^2(c_1+egM_Vp)\beta^2+8c_2e^2g^3{M_V}^2M_K\varphi-\alpha_VegM_V\left(8c_2eg^2M_V+M_Kp\beta^2\varphi\right)\right)}{4eM_V\left(-4c_2eg^3M_V+\alpha_Vgp\beta^2\right)^2}$$

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

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

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

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

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

Introducing crowberry treatment provides a positive impact on the profit function by a magnitude of $pegM_V R\frac{\varphi}{\alpha_V}M_K\frac{\varepsilon}{\alpha_K}T$ but also increases the total cost for the herders. Increasing both the controlling coefficient ε 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:

$$V_{ctrl,MEY} = \frac{1}{2}\left(\frac{c_1}{peg} + M_V\left(1 - \frac{\varphi M_K}{\alpha_V}\right)\right) + \frac{M_V {M_K}^2 \varepsilon^2 \varphi^2 (\alpha_V(c_1 - egM_V p) + egM_V M_K p\varphi)}{2\alpha_V g\left(eM_V {M_K}^2 p\varepsilon^2\varphi^2 - 4\alpha_V {\alpha_K}^2 c_3\right)}$$

$$R_{ctrl,MEY} = \frac{\alpha_V}{2g}\left(1 - \frac{c_1}{pegM_V} - \frac{\varphi M_K}{\alpha_V}\right) + \frac{{M_K}^2 \varepsilon^2 \varphi^2 (\alpha_V(c_1 - egM_V p) + egM_V M_K p\varphi)}{2g^2\left(eM_V {M_K}^2 p\varepsilon^2\varphi^2 - 4\alpha_V {\alpha_K}^2 c_3\right)}$$

$$K_{\ ctrl,MEY} = M_K - \frac{{M_K}^2 \varepsilon^2 \varphi(\alpha_V(egM_V p - c_1) - egM_V M_K p\varphi)}{g\left(4\alpha_V {\alpha_K}^2 c_3 - eM_V {M_K}^2 p\varepsilon^2\varphi^2\right)}$$

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

$$+ \frac{eM_V {M_K}^2 \varepsilon^2 \varphi^2 (\alpha_V(c_1 - egM_V p) + egM_V M_K p\varphi)\left(8{\alpha_V}^2 {\alpha_K}^2 c_3 g + egM_V {M_K}^3 p\varepsilon^2\varphi^3 - \alpha_V M_K \varphi(8{\alpha_K}^2 c_3 g + M_K(c_1 + egM_V p)\varepsilon^2\varphi)\right)}{\left(-4\alpha_V g^2\left(4\alpha_V {\alpha_K}^2 c_3 - eM_V {M_K}^2 p\varepsilon^2\varphi^2\right)^2\right)}$$

$$T_{ctrl,MEY} = \frac{\alpha_K M_K \varepsilon\varphi(\alpha_V(c_1 - egM_V p) + egM_V M_K p\varphi)}{g\left(-4\alpha_V {\alpha_K}^2 c_3 + eM_V {M_K}^2 p\varepsilon^2\varphi^2\right)}$$

Appendix D. Optimal analytical results of the comprehensive model:

The optimal solutions for the comprehensive model at are:

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

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

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

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

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

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

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9 Paper 3 : When climate change turns good plant bad – A dynamic multispecies model of reindeer herding in a changing Arctic

When climate change turns good plant bad – A dynamic multispecies model of reindeer herding in a changing Arctic

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Abstract

In many Nordic countries, climate-induced encroachment of the native and allelopathic *Empetrum nigrum* (crowberry) on other palatable vegetation decreases pasture quality for the culturally important reindeer herds. Unfortunately, current pasture management plans do not include pasture quality indicators. To argue for the importance of pasture quality and provide adaptation guidance, we develop a three-species bioeconomic model (reindeer-vegetation-crowberry) with three controls (reindeer slaughter, supplementary feeding of reindeer, and crowberry control). Our model indicates that without human intervention, vegetation biomass and reindeer herd size will decline due to crowberry's allelopathic effects, resulting in 42% loss in reindeer stock and 40% (100 million NOK) profit loss. Human interventions, specifically supplementary feeding and crowberry control, reduces the profit loss by half. To incentivize these interventions, which are partially public goods, the paper proposes a conditional subsidy program that only compensates herders for crowberry control when the shadow value of crowberry becomes negative. This approach can be generalized to other regions experiencing similar ecological changes, in which habitat quality is a crucial yet often overlooked factor.

Introduction

The Arctic’s terrestrial ecosystems are changing (Ims et al., 2013), leading to impacts on the culturally important reindeer husbandry of indigenous Sami people in northern Europe (Bråthen et al., 2018; Heggenes et al., 2017; Tuomi et al., 2024). Due to climate and environmental changes, an evergreen dwarf shrub, *Empetrum nigrum* (crowberry), is encroaching on more palatable vegetation via excretion of several allelopathic substances (e.g., batatasin-III) through its leaf litter and humus, in turn suppressing growth of other plants (González et al., 2021; Pilsbacher et al., 2020). Despite being a native species, crowberry is increasingly considered a pest because this allelopathic encroachment reduces pasture biodiversity (Bråthen et al., 2024; Bråthen & Ravolainen, 2015) and contributes to grazing habitat degradation (Bråthen et al., 2024; Tybirk et al., 2000). A recent study in Northern Norway indicates that pasture land in which crowberry encroaches has increased from 76% to 83% over the last two decades (Tuomi et al., 2024). Private control of crowberry by individual herders is hampered by the fact that costly control actions are a public good while government agencies do not focus on pasture quality. This paper develops and applies a three-species bioeconomic model to identify optimal adaptation strategies in response to a previously overlooked crisis of the reindeer grazing pasture – the deteriorating pasture quality caused by the encroachment of the native pest crowberry.

Reindeer husbandry is a traditional lifestyle of the Sami people (Johnsen et al., 2022; Reinert et al., 2009), and the pasture plays a decisive part in income generated from reindeer herding (Krebs, 2002; Tveraa et al., 2013). In Norway, the traditional Sami herding areas are systematically organized into 89 distinct herding districts, grouped into 6 regions (Ministry of Agriculture and Food, 2017), with more than 200 000 reindeer across the country (Figure 1). Herded using a semi-domesticated approach, the reindeer are allowed to graze freely in a free-range pasture. Sustainable development focused on managing the population to prevent the "tragedy of the commons" on grazing pastures has gained emphasis in recent years (Ministry of Agriculture and Food, 2017). A suitable maximum limit for stock size is established for each herding district by the Directorate of Agriculture, based on pasture quantity. Although the concern for decreasing pasture quality has been mentioned in many reports (Eira et al., 2020; Oskal et al., 2022; Wengen, 2023), the governmental management framework has neither adopted any clear-cut quantitative indicator for measuring pasture quality, nor estimated how biodiversity deterioration negatively impacts the husbandry (Ministry of Agriculture and Food, 2008; Reinert et al., 2009; Tuomi et al., 2024). With the additional pressure from climate change, the presumed driver of crowberry encroachment, homogenization of the pasture by crowberry will decrease the maximum herd size that can be supported on the pasture.

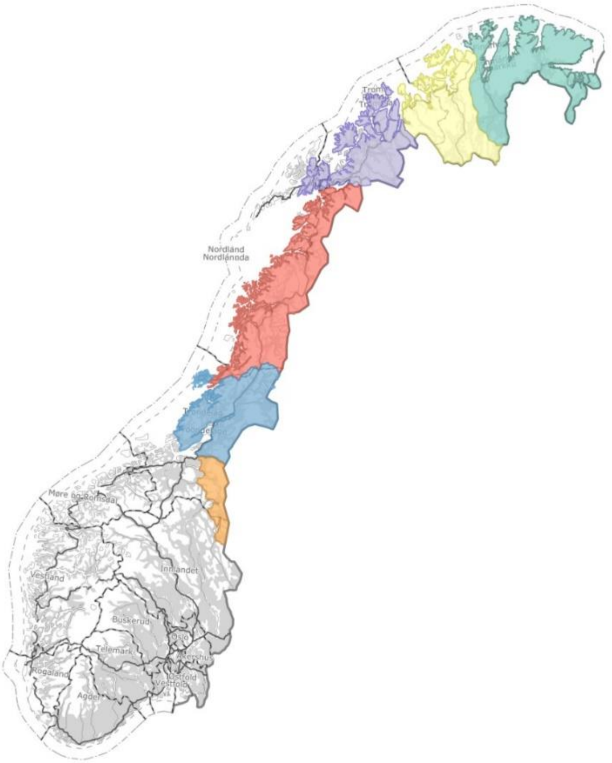

Figure 1: Total defined grazing pasture of the Norwegian reindeer husbandry. Names of the regions from north to south: East Finnmark, West Finnmark, Troms, Nordland, Nord-Trøndelag, and South-Trøndelag and Hedmark. Source:(Agriculture Directorate, 2022b)

The herders must adapt to the new ecological and climate change consequences. In addition to the usual control of reindeer dynamics – slaughter – we investigate the efficiency of the two adaptation measures – crowberry burning and supplementary feeding. Habitat restoration is a common human intervention in species conservation (Ando & Langpap, 2018; Bulte & Horan, 2003). Controlling crowberry, either by burning, plowing, or plucking, can be an adaptative measure. Based on previous literature on the effect of fire to control *Empetrum* on *Empetrum*-dominated understorey vegetation (Nilsson & Wardle, 2005; Wilson et al., 2003), we incorporate crowberry burning in our model to investigate the impacts on the reindeer stock and grazing pasture of removing the native pest.

Rather than restoring the habitat, many herders have been adapting to the new environmental situation by providing supplementary feeding (Helle & Jaakkola, 2008; Horstkotte et al., 2020).[2] Despite ongoing supplementary feeding, there exist no economic studies of this intervention in the Norwegian reindeer husbandry setting. Supplementary feeding in the Finnish reindeer setting was modelled extensively in the studies of Pekkarinen et al (2015, 2021). In the Finnish setting, supplementary feeding is a common practice, regardless of the pasture condition. Thus, energy from supplementary feeding does limit the vegetation intake of reindeer from the pasture in the Finnish setting. Contrary to this, supplementary feeding is conducted in Norway only during harsh winters when the animals cannot find food naturally. Norwegian reindeer energy intake from vegetation, then, is not limited by the manual feeding practice.

There exist very few economic studies of how the changes in pasture quality impacts reindeer husbandry. Some papers have discussed the impact of climate change on the socio-ecological system in Northern Europe, yet with limited economic analysis (Rees et al., 2008; Reinert et al., 2009). Both Rees et al. (2008) and Reinert et al (2009) emphasize how weather variation, especially snow quality will put pressure on the grazing pasture and reindeer stock size. These papers are limited to qualitative analyses of subsidies or governmental management without considering adaptive strategies to mitigate climate change impacts. Other studies of reindeer husbandry show that both ecological and economic dynamics matter (Johannesen et al., 2019; Moxnes et al., 2001; Pekkarinen, 2018). Existing models have incorporated how climate change influences reindeer husbandry without acknowledging the important role of the grazing pasture (Helgesen & Johannesen, 2023). Those studies that do consider grazing focus

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[2] Feeding modifies the natural habitat and can detrimentally alter the herding customs of the Sami (Helle & Jaakkola, 2008; Horstkotte et al., 2020). Though supplementary feeding is unfavourable to the Sami, the Norwegian herders are increasingly forced to provide dry feed in harsh winter conditions due to climate change.

mainly on deteriorating winter pasture quality (Pekkarinen et al., 2021, 2022).[3] None of these above-mentioned studies have discussed the problem of native pests in reindeer husbandry.

Our three-species predator-prey bioeconomic model focuses on how both ecological change in the tundra ecosystem (allelopathic species encroachment) and human interventions (slaughtering, restoring grazing pasture, and feeding the reindeer stock) impact the herd size and grazing pasture. To investigate the explicit ecological and economic impacts of crowberry encroachment on reindeer husbandry, we assume the grazing pasture consists of two plant types: 1) a combination of biodiverse nutrient-rich plants that are treated as a single species (in which lichen is included), and 2) crowberry, a native pest with low palatability. The allelopathic impact of crowberry will increase its competitiveness over the palatable vegetation leading to decreases in the palatable vegetation and the reindeer stocks, while the two adaptation measures will dampen or reverse the impacts of crowberry. A resource manager charged with managing the reindeer husbandry chooses levels of slaughter, feeding and crowberry treatment to maximize the profit from slaughtering and the cultural values of the reindeer herd over time.

Our paper provides both methodological and empirical contributions. We provide the first model of the economic implications of native species encroachment on grazing pasture dynamics. We introduce a novel approach by dynamically quantifying the interactive carrying capacities of two competing plant species. The results of the model highlight a previously under-recognized implication of climate change – native pest encroachment that deteriorates grazing habitat. While other papers have modeled reindeer grazing pasture dynamics in the context of invasive species and general weather effects, ours is the first to account for allelopathic relationships in a bioeconomic model for the reindeer husbandry. Our study

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[3] Current literature on reindeer husbandry dynamics focuses on lichen, a class of fungal-algal symbiotic organism, as an important factor (Pekkarinen, 2018; Tahvonen et al., 2014). However, since reindeer only graze on lichen in the winter (Aagnes et al., 1996; Reinert et al., 2009), modelling solely lichen provides an incomplete picture of pasture quality.

examines whether management strategies aimed at controlling a native pest for ecological reasons can also be economically motivated. This dual motivation, if present, could offer an additional rationale for improving pasture quality through such actions.

By applying the model to the Norwegian reindeer husbandry, we also provide two key insights into the management of this economically and culturally valuable natural resource. First, we provide the first measures of the economic implications of crowberry encroachment. Second, we use our model to provide recommendations for the use of two climate change adaptation measures that can be utilized by reindeer managers to alleviate these impacts. We show that there are ecological and economic benefits when both adaptation measures are used together suggesting that supplementary feeding could be considered as a long-term solution. Third, we propose a conditional subsidy program that only compensates herders for crowberry control when the shadow value of crowberry becomes negative. These results provide support for adopting a new bioeconomic metric for pasture quality that goes beyond simply measuring crowberry biomass.

We present our model in the next section. The model consists of three species-specific state variables and three controls. We then apply our model to the Norwegian husbandry. In the numerical application section, we consider three scenarios: 1) pre-encroachment (pre-EC; optimal slaughter with no allelopathic impact), 2) post-encroachment (post-EC; optimal slaughter with allelopathic encroachment but not adaptation), and 3) adaptive post-EC, which considers optimal slaughter in conjunction with reindeer feeding and crowberry control. The paper ends with a discussion of the implications of our findings and a conclusion section.

Model of reindeer management under crowberry encroachment

Our three-species system consists of one herbivore, the reindeer stock denoted R (number of reindeer), and two plant species, vegetation stock V and crowberry stock K (kilogram area^{-1}).[4] A resource manager must choose how many reindeer to slaughter to maximize profit and cultural values created by the reindeer herd. The slaughtering decision is dynamic since reindeer reproduction, like any other renewable resource, creates an opportunity cost of slaughtering reindeer today. This opportunity cost tempers the incentive to slaughter the entire herd at a given time. The resource manager must also choose the intensity of two adaptation measures in response to climate-induced encroachment of crowberry: 1) supplementary feeding of the reindeer herd and 2) direct control of crowberry. In Norway, the husbandry is under the management of the Norwegian Directorate for Agriculture (Agriculture Directorate, 2022a). To avoid overgrazing, the government regulates the herd size. Hence, we consider the Norwegian government as the resource manager in our optimal control problem.

Ecological dynamics

We adopt the Leslie model (Leslie, 1948) which differs from the Lotka-Volterra model (Lotka, 1920, 1925; Volterra, 1928) in how the predator population carrying capacity depends on prey density. While growth of the predator in Lotka-Volterra models depends on the functional response between predator and prey (be it Holling type 1, 2, or 3, (see Koen-Alonso,

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[4] To focus on the allelopathic interactions between the three species, we ignore age-sex structure. Including age-sex structure, while adding detail, would significantly increase the model's complexity without substantially contributing to the primary objectives of our analysis.

2007)), the Leslie model emphasizes the upper bound of the predator stock, i.e. its carrying capacity, is dependent on prey density (Leslie, 1948). The Leslie model helps us to avoid model instability and capture more realistic interactions between the three species.

Within the non-spatial predator-prey literature, we find no studies where two species are modelled to share a common carrying capacity, in this case determined by the physical area. Given a fixed total areal carrying capacity of the pasture, crowberry encroachment must lower the carrying capacity of other palatable vegetation due to competition. We incorporate these implicit resource constraints by connecting carrying capacities of both species, thereby incorporating a spatial perspective in a non-spatial dynamic model[5]. The general ecological model is then:

$$\dot{V} = \alpha_V V\left(1 - \frac{V + \varphi K}{M}\right) - g_V V R \tag{1}$$

$$\dot{K} = \alpha_K K\left(1 - \frac{K}{M - V}\right) - g_K K R \tag{2}$$

$$\dot{R} = \alpha_R R\left(1 - \frac{R}{d_V V + d_K K}\right) \tag{3}$$

in which V, K, and R are the biomass of vegetation, crowberry, and reindeer respectively[6]. The required initial conditions for three species are: $V(t_0) > 0; K(t_0) > 0; R(t_0) > 0$. To satisfy biological feasibility, all the parameters $\alpha_V, \alpha_K, \alpha_R, \varphi, g_V, g_K, d_V, d_K \in \mathbb{R}^+$. All three species' growth follows a logistic function where M is the pasture carrying capacity while α_V, α_K, and α_R are the intrinsic growth rates of the vegetation, crowberry and reindeer species, respectively. As crowberry grows alongside vegetation, its carrying capacity can be described as $M - V$.

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[5] For spatial optimal control bioeconomic models with prey-predator interactions, see Demir and Lenhart (2021) or Lenhart and Workman (2007)

[6] The term $M - V$ in the denominator of $\dot{K}$ mimics the spatial constraints of the two species. The same adjustment to the carrying capacity does not appear in equation (1), as crowberry impacts vegetation by the allelopathic rate φ following Li and Feng (2010). Furthermore, applying $M - K$ in the denominator of $\dot{V}$ would needlessly complicate the system.

Grazing interactions between reindeer and the two plant stocks are described by the terms $g_V VR$ and $g_K KR$, in which g_V and g_K are the grazing coefficients. Carrying capacity of reindeer is determined by the available pasture, i.e. $d_V V + d_K K$, where d_V and d_K are the impact rates of vegetation and crowberry upon reindeer carrying capacity, respectively. As reindeer only grazes crowberry in early spring, we assume $g_K < g_V$ and $d_K < d_V$. The allelopathic impact of crowberry is captured by the term φK where φ is the allelopathic coefficient, as applied in allelopathic models mentioned by Li and Feng (2010). Appendix A shows the analytical equilibria achieved from solving the three equations (1), (2), and (3).

Climate change initiates a gradual shift in the allelopathic coefficient from $\varphi = 0$ (no crowberry encroachment) to $\varphi > 0$ (crowberry encroachment) (Bråthen et al., 2024; Pilsbacher et al., 2020). One approach to modeling this transition is the fast-slow dynamics framework (Crépin, 2007). This framework explores how fast changing variables, such as populations, interact with slow, and often less noticeable processes, to shift and possibly destabilize an ecosystem's steady states. Applying that framework to our model suggests the system dynamics described in equation (1) – (3) (the fast system) converge to a steady state conditional on a value of φ that gradually changes over time due to climate change (the slow system). Provided that φ continues to increase due to climate change, the result is a corner solution equilibrium where crowberry encroachment forces other native vegetation off the pasture ($V = 0$). Unfortunately, the slow dynamics in this system are poorly understood because of a lack of long time series data on crowberry encroachment. Therefore, our modeling approach allows for an analysis of the system's fast dynamics as new observations of φ emerge (see Appendix B for more detailed analysis of the ecological model).

Analytically, there are seven equilibria, including two axial equilibria[7], three corner solutions and two interior equilibria (Appendix A). As we demonstrate later in the paper, a unique stable interior equilibrium exists given our chosen data. As climate change gradually increaes φ from 0, the interior equilibrium shifts to the corner solution with $V = 0$. This transition is marked by a threshold condition for φ, beyond which the system's stability switches, indicating a critical allelopathy threshold. While climate change often precludes steady state analysis, we believe this new corner solution with $V = 0$ marks a new post climate change equilibrium since the impact of climate change in our model (encroachment on vegetation) has been effectively maxed out. While climate change may continue to impact our system in other ways, the particular climate change pathway we study in this paper (allelopathic encroachment) has come to an end resulting in a new steady state.[8]

Management actions

Crowberry encroachment impacts pasture quantity and quality, leading to the recent practice of supplementary feeding (Horstkotte et al., 2020; Turunen et al., 2016; Tveraa et al., 2013). The resource manager may turn to an alternative, such as crowberry removal by burning, plowing, or plucking. We expand the ecological model to include three controls: reindeer slaughter, supplementary feeding, and crowberry treatment.

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[7] These axial equilibria represent the states where the system's dynamics are aligned along a principal axis.

[8] Climate change may also manifest as changes in climate variability causing possible changes in management to increase system resilience. In cases where environmental stochasticity is an important consideration, dynamic programming can be used to identify adaptive strategies to unpredictable weather variation (Conrad & Smith, 2012; Horan et al., 2023; Sims et al., 2018). Adaptive strategies afforded by a dynamic programming approach may also be useful when considering the uncertainties associated with the slow dynamics of allelopathic encroachment.

Facing allelopathic encroachment of crowberry, the resource manager decides to either incorporate supplementary feeding F or apply crowberry treatment T, or both. Reindeer slaughter enters the reindeer equation of change by the control S and supplementary feeding enters via the term βFR in which β is the feeding coefficient[9]. Equation (3) becomes

$$\dot{R} = \alpha_R R \left(1 - \frac{R}{d_V V + d_K K}\right) + \beta FR - S \tag{4}$$

Similarly, crowberry treatment T enters the model via the term εTK in which ε is the treatment coefficient:[10]

$$\dot{K} = \ \alpha_K K \left(1 - \frac{K}{M - V}\right) - g_K KR - \varepsilon TK \tag{5}$$

The reindeer herd generates revenue through the sale of slaughtered reindeer (at price p). Maintenance and feeding the herd is costly as is any effort directed at controlling crowberry encroachment. Reindeer herding, particularly for the indigenous Sami people, is not only an economic activity but also a bearer of profound cultural and social values (Ministry of Agriculture and Food, 2017). This includes different types of non-use values, such as cultural, bequest and existence values, of the husbandry to the Sami, symbolizing a deep connection to their heritage and identity, as well as the cultural value to the nation, representing a living example of sustainable and traditional land use. Additionally, the size of a reindeer herd often carries social status implications within the community (Johannesen & Skonhoft, 2011), representing non-use value of the species. We, therefore, include the non-use value of reindeer in the objective functional by adding a term linearly dependent on the reindeer population.

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[9] We placed this term outside the logistic growth function of reindeer as no studies have yet examined the relationship between reindeer carrying capacity and supplementary feeding.

[10] Equation (5) assumes the effectiveness of crowberry treatment remains constant over time. Like many invasive species, the long-run effect of crowberry control strategies is unclear and more data to quantify their effectiveness is needed.

Given a discount rate δ, the manager chooses slaughtering S reindeer, feeding reindeer with F tonnes of dry feed and using T days to burn crowberry. The discounted net benefit of reindeer management is maximized in infinite time:

$$max_{S,F,T} \int_0^{\infty} (pS - c_1 R - c_2 F^2 - c_3 T^2 + \gamma R) e^{-\delta t} dt$$

where p is the price per slaughter reindeer, c_1 is the maintenance cost per reindeer[11] and γ is the unit non-use value per reindeer.[12] The feeding cost function $c_2 F^2$ is quadratic in feeding effort F. A quadratic cost function captures the increasing marginal cost of feeding, which arises not only from the scarcity of dry feed – a significant component of feeding costs – but also from the rising opportunity cost of manual feeding labor. We also assume that the additional controlling cost function $c_3 T^2$ is quadratic in treatment effort T where c_3 is the controlling cost effort. Controlling invasive or pest plant species like crowberry via picking, soil preparation, or burning is labor intensive. These characteristics of plant control suggest cost should be convex in effort and largely independent of the population of crowberry (Jardine & Sanchirico, 2018; Kotani et al., 2011).[13]

The current value Hamiltonian is

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[11] The reason why we have a linear maintenance cost function is the slaughter cost is really minimal. The case of linear maintenance cost also arises in literature of livestock management (Aadland, 2004; Skonhoft et al., 2010).

[12] In our model, the term γ reflects the non-use value per reindeer, represented in a linear function as a simple illustrative choice. However, it is conceivable that the non-use value per reindeer declines as herd size increases, implying a concave rather than linear relationship. Given the lack of data needed to parameterize the curvature of a non-use value function, we opted for a linear relationship.

[13] It is possible that the cost of both adaptation measures may stochastically evolve with changing weather. For instance, the cost of feeding can increase sharply during harsh winter conditions, when the demand for dry feed escalates and herders dedicate more time to manually feeding their herd, thereby forgoing other valuable activities (Horstkotte et al., 2020; NIBIO, 2020). We leave this extension for future work.

$$H = pS + (\gamma - c_1)R - c_2F^2 - c_3T^2 + \lambda_R\left[\alpha_R R\left(1 - \frac{R}{d_V V + d_K K}\right) - S + \beta FR\right]$$
$$+\lambda_V\left[\alpha_V V\left(1 - \frac{V + \varphi K}{M}\right) - g_V VR\right] + \lambda_K\left[\alpha_K K\left(1 - \frac{K}{M - V}\right) - g_K KR - \varepsilon TK\right] \qquad (6)$$

subject to (1), (4) and (5) and the initial conditions V_0, R_0, K_0 where $V, R, S, K, F, T \in \mathbb{R}^+$. λ_R, λ_V, and λ_K are the shadow prices of reindeer, vegetation, and crowberry respectively. $\frac{\partial^2 H}{\partial S^2} = 0$ while $\frac{\partial^2 H}{\partial F^2} = -2c_2 < 0$ and $\frac{\partial^2 H}{\partial T^2} = -2c_3 < 0$, which satisfy the concavity condition of the maximization problem.

The first-order-condition (FOC) of this Hamiltonian is $\frac{\partial H}{\partial S} = p - \lambda_R = 0$ which provides ${\lambda_R}^* = p$ for the optimal S^*. Since the resource manager is a price taker, we attain a singular control variable S^* (see Appendix C for proof). The singular solution, a direct result of the linear cost function c_1R, reflects administration and maintenance costs which tend to scale linearly with herd size but do not significantly vary with harvest rates (Norwegian Government, 2021). The FOC for F gives $\frac{\partial H}{\partial F} = -2c_2F + p\beta R = 0$ and thus $F^* = \frac{p\beta}{2c_2}R^*$. The intuition is that the more reindeer there are, the more feeding should take place. For a given number of reindeer, price per slaughtered reindeer, the feeding coefficient, and optimal reindeer stock will incentivize more feeding effort while the feeding cost will dis-incentivize the effort. The FOC for T is: $\frac{\partial H}{\partial T} = -2c_3T - \varepsilon\lambda_K K = 0$, thus $T^* = -\frac{\varepsilon K^* {\lambda_K}^*}{2c_3}$. As all the parameters and variables are positive real numbers, $T^* > 0$ only if the shadow price of crowberry is negative.[14] This implies that when adding one unit of crowberry into the system, the net benefit decreases by an amount of λ_K.

Three intuitive results can be drawn from the three adjoint equations:

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[14] If $T^* = 0$, i.e. if it is optimal to not burn crowberry, then the sign of ${\lambda_K}^*$ follows equation (11) and switches sign when $\varphi > \frac{\alpha_R d_K M \lambda_R^* {R^*}^2}{(d_K K^* + d_V V^*)^2(\alpha_V V^* \lambda_V^*)}$.

$$\dot{\lambda}_R = \delta\lambda_R + c_1 - \gamma - \lambda_R\left(\alpha_R\left(1-\frac{R}{d_V V + d_K K}\right) - \frac{\alpha_R R}{d_V V + d_K K} + \beta F\right) + \lambda_K g_K K + \lambda_V g_V V \quad (7)$$

$$\dot{\lambda}_V = \delta\lambda_V + \frac{\alpha_K K^2 \lambda_K}{(M-V)^2} - \frac{\alpha_R d_V R^2 \lambda_R}{(d_V V + d_K K\,)^2} - \lambda_V\left(-\frac{\alpha_V V}{M} + \alpha_V\left(1-\frac{V+\varphi K}{M}\right) - g_V R\right) \quad (8)$$

$$\dot{\lambda}_K = \delta\lambda_K - \frac{\alpha_R d_K R^2 \lambda_R}{(d_V V + d_K K\,)^2} - \lambda_K\left(\alpha_K\left(1-\frac{K}{M-V}\right) - \frac{\alpha_K K}{M-V} - g_K R - \varepsilon T\right) + \frac{\varphi \alpha_V V \lambda_V}{M} \quad (9)$$

First, with allelopathic encroachment of crowberry, induced by climate and environmental change, the sign of λ_K may switch from positive (pre-encroachment) to negative (post-encroachment), making crowberry a pest (Rondeau, 2001). At the dynamic equilibrium, $\dot{\lambda}_V = \dot{\lambda}_K = \dot{\lambda}_R = 0$. Solving equation (9) for λ_K, we get

$$\lambda_K{}^* = \frac{\dfrac{\alpha_R d_K \lambda_R^* R^{*2}}{(d_K K^* + d_V V^*)^2} - \dfrac{\alpha_V V^* \lambda_V^* \varphi}{M}}{g_K R^* + \varepsilon T^* + \delta - \alpha_K\left(1-\dfrac{2K^*}{M-V^*}\right)} \quad (10)$$

Without allelopathic encroachment, $\varphi = 0$ makes the numerator positive in all cases. For the denominator to be positive, we need the following condition $g_2 R^* + \varepsilon T^* + \delta > \alpha_K\left(1-\frac{2K^*}{M-V^*}\right)$ when $1-\frac{2K^*}{M-V^*} > 0$, which implies that the optimal crowberry stock lies on the LHS of its' logistic growth curve, $K^* < \frac{M-V^*}{2}$. Conversely, with $K^* > \frac{M-V^*}{2}$, the denominator in (10) will always be positive. Therefore, for the sign of $\lambda_K{}^*$ to be negative under the presence of crowberry encroachment, given the denominator is positive, we need

$$\frac{\alpha_R d_K \lambda_R^* R^{*2}}{(d_K K^* + d_V V^*)^2} - \frac{\alpha_V V^* \lambda_V^* \varphi}{M} < 0 \leftrightarrow \varphi > \frac{\alpha_R d_K M \lambda_R^* R^{*2}}{(d_K K^* + d_V V^*)^2(\alpha_V V^* \lambda_V^*)} \quad (11)$$

Hence, if the allelopathic coefficient surpasses the threshold of $\bar{\varphi} = \frac{\alpha_R d_K M \lambda_R^* {R^*}^2}{(d_K K^* + d_V V^*)^2 (\alpha_V V^* \lambda_V^*)}$, the native species becomes a pest from the perspective of the resource manager. This switch in the sign of λ_K is later confirmed in the numerical results (Table 1).

Second, vegetation becomes more valuable when crowberry becomes a pest. Solving the adjoint equation of V, we get

$$
{\lambda_V}^* = \frac{M\left(\frac{\alpha_R d_K p {R^*}^2}{(d_K K^* + d_V V^*)^2} + \left(\alpha_K - g_K R^* - \frac{2\alpha_K K^*}{M - V^*} - \delta - \varepsilon T^*\right){\lambda_K}^*\right)}{\alpha_V V^* \varphi} \tag{12}
$$

Since all parameters and variables are positive real numbers, the denominator is positive. Early in the encroachment process when $\varphi < \bar{\varphi}$ and ${\lambda_K}^* > 0$, an increase in the shadow value of crowberry should decrease the shadow value of vegetation due to the competition between the species. This intuitive result will arise provided the second parenthetical term in the numerator is negative (i.e., the resource manager's discount rate is sufficiently low: $\delta < \alpha_K - g_K R^* - \frac{2\alpha_K K^*}{M - V^*} - \varepsilon T^*$). As encroachment continues and ${\lambda_K}^*$ switches from positive to negative, the shadow value of vegetation continues to increase, signaling its increased value as the only beneficial source of forage. This tradeoffs between the shadow values of the two forage species becomes more pronounced the lower the resource manager's discount rate.

Third, the presence of a native pest that deteriorates pasture quality creates an additional economic benefit of supplementary reindeer feeding. The presence of a native pest that deteriorates pasture quality creates an additional economic benefit of supplementary reindeer feeding.Solving each of the three adjoint equations for δ, we obtain three rate of return equations that characterize the optimal steady state (Clark, 2010)):

$$
\delta = \left[\alpha_R\left(1 - \frac{2R^*}{d_K K^* + d_V V^*}\right) + \beta F^*\right] - \frac{c_1 - \gamma - \frac{2 g_K c_3 T^*}{\varepsilon} + \lambda_V^* g_V V^*}{p} \tag{13}
$$

$$\delta = \left[\alpha_V\left(1 - \frac{2V^* + \varphi K^*}{M}\right) - g_V R^*\right] + \frac{\dfrac{\alpha_R d_V {R^*}^2 p}{(d_K K^* + d_V V^*)^2} + \dfrac{2c_3 \alpha_K K^* T^*}{\varepsilon (M - V^*)^2}}{{\lambda_V}^*} \tag{14}$$

$$\delta = \left[\alpha_K\left(1 - \frac{2K^*}{M - V^*}\right) - g_K R^* - \varepsilon T^*\right] + \frac{\dfrac{\alpha_R d_K {R^*}^2 p}{(d_K K^* + d_V V^*)^2} - \dfrac{\varphi \alpha_V V^* \lambda_V^*}{M}}{\left(-\dfrac{2c_3 T^*}{\varepsilon K^*}\right)} \tag{15}$$

The right-hand sides (RHS) of these three equations indicate the marginal return generated by holding more reindeer, vegetation, or crowberry stocks. Regarding the optimal management for reindeer, equation (13) emphasizes how supplementary feeding will increase reindeer's marginal growth. The reindeer's marginal return is increased with the marginal grazing rate of reindeer on crowberry. λ_V^* will also change as it is a function of the state variables (equation (10)). Therefore, the magnitude of F^* and λ_V^*, will determine the slaughter decision. While higher maintenance cost c_1 leads to an optimal smaller herd, higher crowberry controlling cost c_3 and reindeer non-use value help increase R^*. This is in line with the study of Johannessen et al. (2011) in which higher non-use value will increase the herd size and lower the slaughter rate. Moreover, when the discount rate δ increases, the manager will keep a lower stock level for other alternative investments, and vice versa. If the marginal return from reindeer is lower than the discount rate, the resource manager will slaughter more reindeer and invest the proceeds elsewhere in the economy with a higher rate of return. In the opposite case, the resource manager will conserve more reindeer, postponing harvest, since reindeer conservation earns a higher rate of return than elsewhere in the economy. Sensitivity analysis of the numerical solutions later confirms these findings (see Appendix D).

Derived from (13), when the maintenance cost exceeds a critical threshold

$$c_1 > \gamma + (\alpha_R + \beta F^* - \delta)p + \frac{2c_3 T^*}{\varepsilon}\left[g_K + \frac{g_V M\left(\alpha_K + \dfrac{2\alpha_K K^*}{V - M} - \delta - \varepsilon T^*\right)}{\alpha_V \varepsilon \varphi K^*}\right] \tag{16}$$

equation (13) can no longer hold with equality for any positive reindeer stock.

The required rate of return from vegetation includes vegetation marginal growth minus the marginal grazing rate from reindeer $g_V R^*$ plus the marginal growth of crowberry and reindeer constrained by their carrying capacities. As λ_V is the marginal increase in the objective function with respect to vegetation, an increase in its shadow price will decrease its required rate of return. This in turn stimulates the resource manager to let reindeer graze more on the pasture as it will decrease vegetation's marginal production, all other factors unchanged.

Regarding the marginal return of crowberry, equation (15) implies that crowberry's expected rate of return decreases by marginal constrained growth of reindeer and marginal treatment. Overall, while feeding effort will shift the optimal reindeer stock towards the RHS of the logistic growth curve as we have higher R^*, controlling effort will push the optimal crowberry population K^* towards the LHS of its logistic growth curve.

These dynamic relationships uncover an unintended benefit of feeding effort. Appendix E and F give details of an application of the implicit function theorem to the three equilibrium conditions (13), (14), and (15). While we need specific conditions to know the signs of several implicit functions, we have two certain results; $\frac{\partial R^*}{\partial F^*} > 0$ and $\frac{\partial K^*}{\partial R^*} < 0$ (see appendix E), from which we can deduce $\frac{\partial K^*}{\partial F^*} = \frac{\partial K^*}{\partial R^*}\frac{\partial R^*}{\partial F^*} < 0$. This emphasizes that feeding reindeer indirectly controls the crowberry population, holding all other variables unchanged, since feeding increases the reindeer herd and the reindeer herd grazes on crowberry.

Our model allows for a variety of complex dynamics including various types of cycles. Due to the complex interactions between the multiple state and control variables, the system dynamics and stability will depend on the values of the ecological and economic parameters. In the next section we investigate the dynamics and stability of the ecological system and bioeconomic equilibria using a numerical application of the model to Norwegian reindeer husbandry.

Numerical application

We apply our model to the grazing pasture of the Norwegian reindeer husbandry which is located in the northern part of the country (Figure 1). We outline two cases to illustrate how climate and environmental changes facilitate crowberry encroachment: pre-encroachment with no allelopathic impact (pre-EC, $\varphi = 0$) and post-encroachment with allelopathic impact (post-EC. $\varphi > 0$). Ecological parameters are presented in Appendix A and chosen to 1) be consistent with existing ecological studies, and 2) emphasize how encroachment will impact the reindeer herd and grazing pasture.

Intrinsic growth rates of vegetation α_V and reindeer α_R were adopted from papers modelling the same ecosystem (Moxnes, 1993; Skonhoft et al., 2010). α_V is 0.5 for pre-EC and 0.6 for post-EC cases, due to the arctic greening phenomenon (Myers-Smith et al., 2020; Tuomi et al., 2024), and α_R is equal to 0.7 in both cases (Moxnes, 1993; Skonhoft et al., 2010). Nutrition-rich plants develop palatable leaves and grow faster than nutrition-poor plants, forming unpalatable leaves for energy conservation purposes (Freschet et al., 2010; Wright et al., 2004). Since crowberry grows more slowly than other palatable plants (Hortipedia, 2022; Zverev et al., 2008), α_K was set as one-fifth of α_V in the pre-encroachment case and one-third of α_V in the post-encroachment case. Based on a study of plant biomass and species richness in northern Norway, we computed the carrying capacity of vegetation and crowberry biomass as

1.2 kg per square meter multiplied by estimates of the current total area of the grazing pasture (73 500 km^2)[15,16] (Bråthen & Lortie, 2015).

We tuned the grazing rates g_V and g_K and the comparative coefficients of vegetation d_V and crowberry d_K to reflect differences in reindeer dietary preferences as it only grazes *E. nigrum* in the end of winter when other palatable plants have not regrown (Danell et al., 1994) and at the onset of the growing season when leaf buds are palatable (Iversen et al., 2014). One reindeer consumes between 1 and 10 tonnes of biomass per year, equivalent to $g_V V$ amount of vegetation biomass (Bakka et al., 2021; White & Trudell, 1980). We choose the value of the parameter g_V to be 4x10^{-7} as the magnitude of V is 10^{10}. g_K is then chosen to be 1/50 of g_V because reindeer only consume this evergreen species in the last winter week when other vegetations have not regrown. Collectively, these four parameter values produce a reindeer stock size that is close to the current annual population of more than 200 000 reindeer (Agriculture Directorate, 2022b; Norwegian Government, 2021). We set the marginal impact of crowberry encroachment via seedling recruitment and development (Bråthen & Lortie, 2015; González et al., 2015; Pilsbacher et al., 2020) to $\varphi = 0$ in the pre-encroachment case. In the post-EC scenario we fit $\varphi = 0.8$ from the available data of changes in crowberry density from 2003 and 2020 from Tuomi et al. (2024). Initial condition of $K(t_0)$ is 30% of M, thus $V(t_0) =$

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[15] The total defined grazing pasture of the Norwegian reindeer husbandry is approximately 40% of the whole country area, which accounts for 147 000 km^2 (Agriculture Directorate, 2022b). However, this defined area does not take into account the current human-induced and environmental stress on the pasture (Riseth & Tømmervik, 2017; Stoessel et al., 2022; van Rooij et al., 2023). These stresses have accumulated through decades, shrinking the defined pasture area (Ministry of Agriculture and Food, 2017; NORUT, 2018). One report of the Kvalsund municipality in Finnmark county – where the husbandry plays a culturally significant role – calculated that the actual grazing area is only 54% of the defined area (Eira et al., 2020). Therefore, to acknowledge different stress factors, we assume that the actual grazing area is only 50% of the defined area.

[16] Further analysis on pasture size variations and their impact on allelopathic encroachment intensity revealed that the magnitude of crowberry's negative effects on vegetation remains consistent across different pasture sizes (Bråthen et al., 2018). Additionally, when adjusting for pasture scale by reducing carrying capacities, the required effort for crowberry treatment correspondingly decreases in a proportional manner.

$0.7M$. The value for $R(t_0)$ is set at 250 000 following recent governmental data (Agriculture Directorate, 2009).

Economic parameters are reported in Appendix A and are chosen to be consistent with current economic conditions in Norway. By dividing the reported total product-based income and total cost by the total number of reindeer in 2020, we computed the unit maintenance cost per reindeer c_1 and unit price per slaughtered reindeer p (Norwegian Government, 2021). Government subsidies and economic compensation for lost reindeer from predation and accidents (traffic, etc.) are not included. Based on communications with herders, the average cost of dry feed is 6 NOK per kilogram. We measure our feeding efforts in thousands of tonnes of dry feed on the national scale, resulting in a unit cost c_2 of 6000 NOK per tonne. Since burning crowberry is still being tested, the cost of an effective burning program is unclear. Thus, we decided to use 2000 NOK for the burning effort, as it approximates the salary earned in one normal working day, given the effort unit is labour day. Both effort parameter values, ε and β, are the marginal percentage of change of crowberry and reindeer by burning and feeding respectively. We use Mathematica 13.2 to calculate the results and draw the figures. Finally, to focus more on the allelopathic impact of crowberry, we set the non-use value per reindeer $\gamma = 0$ for the calculations in the result section. Since $\gamma > 0$ will lead to a larger herd size and greater impacts from crowberry encroachment, our main results on the impact of encroachment should be interpreted as a conservative estimate. As a robustness check, we set γ equal to the subsidized amount per reindeer (Norwegian Government, 2021) in Appendix G. Incorporating this value of reindeer existence results in a more realistic slaughter rate, larger herd size, and higher feeding and control efforts in the Adaptive Post-EC scenario (Appendix G).

Results

Regarding the ecological model, there exist seven equilibria whose analytical solutions are presented in Appendix B. Given the chosen set of parameter values, the system reaches either a stable interior equilibrium or a stable corner solution. With $\varphi < 1 + d_K M \left(\frac{g_K}{\alpha_K} - \frac{g_V}{\alpha_V}\right) = 0.98$, the ecological system converges to a stable interior equilibrium where the three state variables co-exist (Appendix B, Figure B.1). If $\varphi > 0.98$, the system converges to a corner solution where V goes to null, thus highlighting the possible elimination of palatable vegetation under extreme encroachment scenarios (Appendix B). The bifurcation analysis of the allelopathic coefficient φ illustrates the gradual shift of the steady-state solution (Figure B.2).

Regarding the bioeconomic model where the reindeer are slaughtered, three scenarios are calculated, which include the pre-EC, post-EC, and adaptive post-EC scenarios where feeding and crowberry control are performed in conjunction with slaughter.[17] Allelopathic crowberry encroachment is only captured in the last two scenarios. In each scenario there exists only one stable equilibrium where all the state and control variables are positive reals (Table 1). For each of these three stable equilibria, there is one positive and two negative eigenvalues which indicates that the stable equilibria are saddle points. This implies that, for given parameter values, there is a single saddle path that must be taken to reach the saddle point. The optimally controlled system may not return to the saddle point equilibrium if environmental fluctuations knock the system off the saddle point (e.g., exogenous weather event that results in reindeer mortality and decreases R). Stability of all equilibria and sensitivity analysis are

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[17] The extreme post-EC case from appendix B is not included in the profit calculation of the bioeconomic model because the extreme value of $\varphi = 1.1$ has not been recorded in any herding district.

provided in Appendix D. In general, the equilibria are insensitive to a 10% increase of each parameter with the exception of the reindeer and crowberry intrinsic growth rates α_R and α_K.

In the pre-EC scenario, dynamic optimized results lead to a reindeer population of approximately 280 000 reindeer. When the objective functional is optimized with regard to S in all scenarios, the slaughter volume (roughly 60% of the optimal reindeer population), is slightly higher than government estimates of the average slaughter rate (Agriculture Directorate, 2009; Norwegian Government, 2021) which is expected due to the exclusion of reindeer non-use value γ. Furthermore, the present stock size of 220 000 reindeer falls within the median range of the pre-EC and post-EC scenarios, indicating that the local socio-ecosystem is gradually moving towards a new equilibrium with crowberry encroachment. In the post-EC scenario, crowberry encroachment causes a 42% decrease in V^*, R^*, and S^* and a 140% increase in K^*. This change in pasture quality results in a 40% decrease (100 million NOK) in profits.

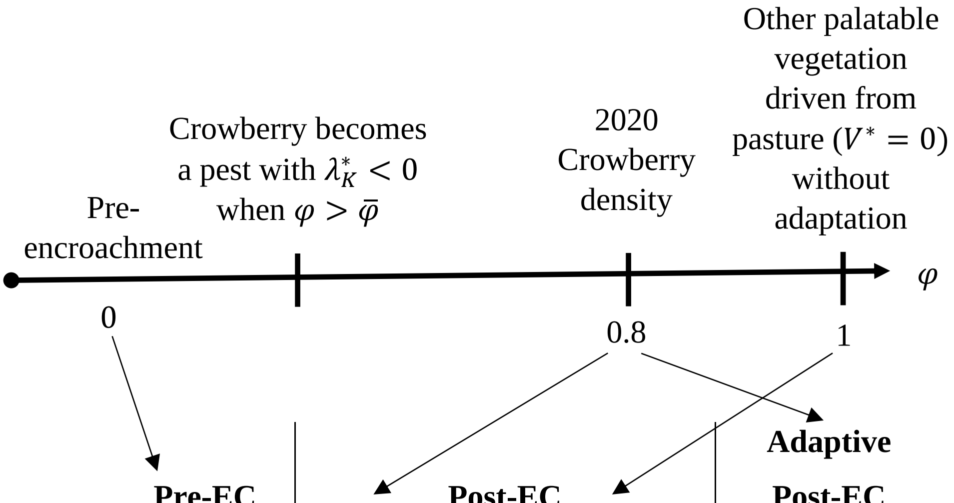
To mitigate this profit loss, the resource manager has two options: 1) supporting the reindeer stock by feeding and 2) restoring the habitat by controlling crowberry. In the adaptive post-EC scenario, the optimal efforts from the two adaptive measures dampen the negative impact of crowberry, as the two state variables V^* and R^* increase by 33% and 53%, while K^* decreases by 50%. The combination of these two adaptation measures reduces the profit loss from crowberry encroachment from 100 million to NOK to 29 million NOK.

Due to the simple functional form of profit, $pS - c_1R$, which is linear in S and R, the optimal shadow price of reindeer $\lambda_R{}^*$ equals the price per slaughtered reindeer p for all scenarios (Table 1). The vegetation shadow price $\lambda_V{}^*$ is positive in all cases, implying the economic gains of adding one kilogram of vegetation to the pasture. Among all scenarios, $\lambda_V{}^*$ in the post-EC scenario shows the highest value of 0.013, implying its scarcity value is highest when crowberry encroachment is not controlled. Furthermore, the crowberry shadow price $\lambda_K{}^*$

shows a change in sign between the pre-EC and the other two post-EC scenarios. The reason is that in the post-EC case, the introduction of the allelopathic impacts causes the cost of an additional kilogram of crowberry to exceed the minimal grazing benefits that crowberry provides. Recall that when $\varphi > \bar{\varphi} = \frac{\alpha_R d_K M \lambda_R^* R^{*2}}{(d_K K^* + d_V V^*)^2 (\alpha_V V^* \lambda_V^*)}$ (equation (11), in which $\bar{\varphi}$ is the switching threshold), the sign of ${\lambda_K}^*$ will turn from positive to negative. Table 1 provides $\bar{\varphi}$ in the three scenarios and confirms this inequality condition. Given available data that indicates φ is approximately 0.8 (Tuomi et al., 2024), crowberry should currently be viewed as a damaging pest in Norway. However, there is still time to adopt adaptation measures and prevent the eradication of vegetation from the grazing pasture. The corner solution $V^* = 0$ is reached when $\varphi = 1$ in the post-EC scenario as opposed to $\varphi = 0.98$ in the ecological model. This suggests that reindeer slaughter delays the threshold at which the palatable vegetation is eradicated. In contrast, the corner solution is never reached in the Adaptive post-EC scenario, highlighting the role of feeding and crowberry control in preventing the eradication of vegetation (Table 2).

We calculate the numerical comparative statics for the relationships between the controls and other variables at the equilibrium point (Figure 2). Varying each control by 10%, we calculated how the equilibrium will change, and plot the changes of each pair of variables. Relationships between the state and control variables are mostly in line with the results of the implicit function theorem in Appendix E and F. The only difference is the relationship between feeding effort and the crowberry population. This is consistent with our theoretical finding that the presence of a native pest that deteriorates pasture quality creates an additional economic benefit of supplementary reindeer feeding. This is an indirect relationship between F and K that manifests through the reindeer dynamics. Figure 2 captures this indirect relationship because it shows how changing one variable changes all other variables. In contrast, the implicit function theorem illustrates the change of only one variable in response to changes in another variable, holding all other variables constant.

Table 1: Saddle point equilibrium for the fast dynamics of the bioeconomic model as the allelopathy parameter gradually changes due to climate change



Variable		**Pre-EC**	**Post-EC**		**Adaptive Post-EC**
V^*	Optimal vegetation population	6.73×10^{10}	4.07×10^{10}	0	5.4×10^{10}
R^*	Optimal reindeer stock	283 572	163 722	8220	251 301
S^*	Optimal slaughter volume	156 897	92 081	4395	148 000
K^*	Optimal crowberry population	1.93×10^{10}	4.6×10^{10}	8.7×10^{10}	2.3×10^{10}
F^*	Optimal feeding effort	--	--	--	63
T^*	Optimal burning effort	--	--	--	73.1
${\lambda_R}^*$	Optimal reindeer's shadow price	3760	3760	3760	3760
${\lambda_V}^*$	Optimal vegetation's shadow price	0.005	0.013	0.06	0.011
${\lambda_K}^*$	Optimal crowberry's shadow price	0.0003	- 0.012	0.0002	- 0.016
$\bar{\varphi}$	Allelopathic threshold	0.024	0.011	--[18]	0.014
Profit (mill NOK)		249.7	149.8	6.7	220.4

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[18] In this case the allelopathic threshold $\bar{\varphi} = \frac{\alpha_R d_K M \lambda_R^* {R^*}^2}{(d_K K^* + d_V V^*)^2(\alpha_V V^* \lambda_V^*)}$ cannot be calculated due to $V^* = 0$ in the denominator

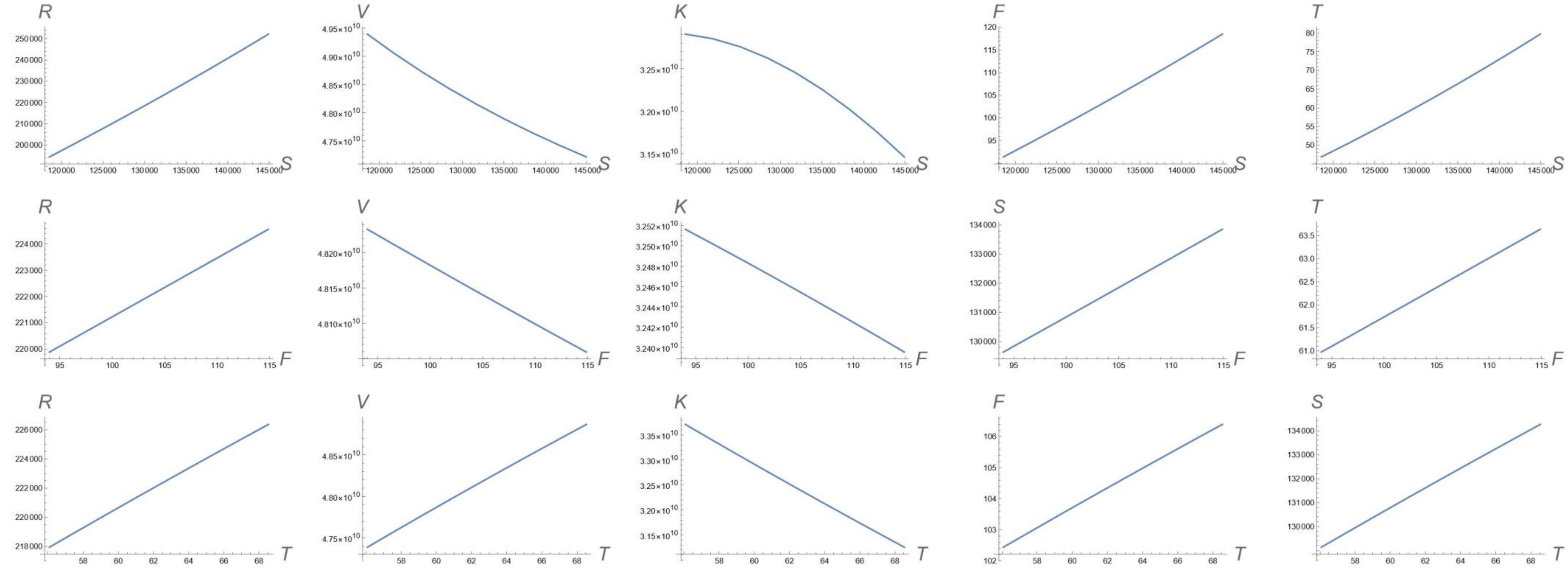

Figure 2: Comparative statics between three control variables and other variables. Comparative statics illustrating the impacts of varying control measures on equilibrium levels of reindeer population, vegetation biomass, and crowberry density under adaptive post-encroachment management strategies. Each row demonstrates how changes in one control variable significantly influence other state and control variables.

Finally, it is important to verify that the cost savings provided from adaptation will persist as the slow dynamics of the change in the allelopathic coefficient continue to evolve. Table 2 shows the unique adaptive post-EC equilibrium when φ changes drastically. The systems equilibrium remains classified as a saddle point as the slow dynamics gradually evolve. Higher φ leads to greater allelopathic effects which drives down the vegetation population. This reduction in competition leaves space for crowberry to expand, which necessitates greater crowberry control by the resource manager. The combination of declining stocks of both forage species reduces the reindeer stock which makes the resource manager reduce feeding and slaughter volume.

Table 2: The effect of changing allelopathic coefficient on the adaptive post-EC saddle point equilibrium for the bioeconomic model

φ	0.8	0.9	1	1.1	1.2
V^*	5.4×10^{10}	5.27×10^{10}	5.16×10^{10}	5.07×10^{10}	4.99×10^{10}
R^*	251 301	244 052	238 147	233 416	229 675
S^*	148 000	143 575	139 951	137 032	134 708
K^*	2.3×10^{10}	2.23×10^{10}	2.15×10^{10}	2.06×10^{10}	1.97×10^{10}
F^*	63	61	59.6	58.5	57.6
T^*	73.1	84.5	95.3	105.2	114.4
Profit (mil NOK)	220.4	210.4	201	192.5	184.8

Discussion

Climate change can impact how native species are assessed. Our results highlight the importance of controlling a native species that becomes a pest. Without the aggressive allelopathic encroachment, crowberry's shadow price is positive because the plant is grazed by valuable reindeer. However, allelopathic encroachment leads to a gradual switch in the sign of crowberry's shadow price turning the valuable native species into a damaging pest. Since this transition from valuable native species to pest has not received much attention (Carey et al., 2012; Valéry et al., 2009), we use our results to highlight four characteristics of any government program designed to mitigate these often unacknowledged impacts of climate change.

First, like many consumable invasive species, reindeer pasture management faces competing market failures (Meadows & Sims, 2023). Historically, reindeer management has focused on avoiding a "tragedy of the commons" where herd sizes increase until all rents associated with grazing are dissipated. This market failure tends to increase the total herd size. The Norwegian government is preventing this first market failure by incentivizing reindeer slaughter through subsidies. Yet this management strategy decreases the reindeer herd size while ignoring the changes in habitat quality due to crowberry encroachment. Hence, crowberry encroachment introduces a second market failure. As crowberry is substantially encroaching the grazing pasture (Tuomi et al., 2024), our chosen value for φ reflects specifically the current encroaching situation. As shown in Table 1 and Appendix B, without rapid control, the actual φ can be expected to exceed the critical threshold when vegetation is eradicated from the pasture. Yet, private herders will underprovide crowberry control since it is a public good (Horan et al., 2002; Perrings et al., 2002). Government support of crowberry control will thus likely be necessary to achieve the socially optimal levels of crowberry control suggested from our theoretical model. Effective management of the reindeer husbandry will require accounting for both market failures. For example, current government efforts to decrease the herd size to avoid overgrazing are reducing the benefits of crowberry control by reducing the number of reindeer to be slaughtered in the future.

Second, any government subsidy program designed to correct the free-rider problem associated with crowberry control will need to develop new metrics for pasture quality. The

Norwegian government's current pasture management strategy focuses on quantity but not quality (Ministry of Agriculture and Food, 2008; Reinert et al., 2009; Tuomi et al., 2024). Such metrics based on total native vegetation could be misleading since it would not account for the shift from palatable vegetation to less palatable crowberry. Percentage of grazing land encroached by crowberry will also be incomplete since biomass measures do not account for changes in the shadow value of crowberry. While crowberry is less valuable as a forage species, incentivizing crowberry control when its shadow value is positive is effectively government-funded reductions in pasture biodiversity. Subsidies for controlling crowberry should not be considered until the crowberry shadow value turns negative. Ensuring that management decisions are well-informed and effective in promoting long-term sustainability for the reindeer husbandry will require closer attention to climate-induced changes in the shadow value of native species.

Third, supplementary feeding of reindeer can be sustainable in the face of encroachment of a native pest. Our adaptive post-EC bioeconomic equilibrium includes positive levels of supplementary feeding indicating an economic justification for long-term feeding efforts. The Norwegian government spends about 20 million NOK annually to subsidize supplementary feeding (County Governor, 2020). The motivation for this government support is to provide supplemental forage to counter the deteriorating pasture quality created by climate change. As our theoretical and empirical results show, feeding also provides an indirect benefit by controlling crowberry encroachment via increased grazing and trampling effects by reindeer (Tybirk et al., 2000). This suggests that the economic argument for supplementary feeding will increase as crowberry encroachment expands.

Fourth, and related to the previous points, government programs to support feeding and crowberry control should be integrated annually to fully account for the tradeoffs and complementarities associated with these adaptation measures. The total calculated adaptation cost in the numerical application of our model is approximately 35 million NOK and is expected to grow as climate change increases the impacts of allelopathy (higher φ). In contrast, recent government support for husbandry under the climate crisis is 20 million NOK, yet this amount is only to subsidize supplementary feeding. These efforts to subsidize supplementary feeding may increase the incentive to control crowberry since feeding and control are shown to be complements in our model. Likewise, any effort to subsidize crowberry control will increase the optimal amount of feeding.

Conclusion

Our study introduces a bioeconomic model that assesses the ecological and economic impacts of native pest species encroachment on grazing lands and highlights the consequences of climate and environmental change affecting grazing habitats. Through our analysis, particularly focusing on Norwegian reindeer herding, we reveal the devastating effects of crowberry encroachment on the herding profit and analyze two climate adaptation strategies for mitigating these impacts. Through our bioeconomic model, we provide several methodological and empirical contributions.

Recently the Norwegian government support for husbandry under the climate crisis has focused only on subsidizing supplementary feeding. This study underscores the need for additional focus on managing native pests, which often cause gradual ecological shifts that may elude immediate attention from resource managers. The study also advocates for the Norwegian government to integrate quantitative indicators of grazing pasture quality into their management strategies, enhancing the effectiveness and sustainability of reindeer husbandry. For example, a subsidy program that is only in effect when the shadow value of crowberry is negative will mitigate the effects of climate change in reindeer husbandry without inadvertently reducing pasture biodiversity through the reduction of a native pest.

Although our analysis captures several critical ecological and economic factors, there are a number of important areas for future work. Other goals need to be included in future studies. For instance, incorporating a spatial perspective in our model could provide further guidance for controlling crowberry where the plant is encroaching the most. Furthermore, many benefits of crowberry are excluded in this paper because we wanted to emphasize the allelopathy characteristic of this native pest. Crowberry has many intrinsic biodiversity benefits, medicinal benefits, gastronomic adoption, and even carbon sequestration benefits (Lorion & Small, 2021; Parmentier et al., 2018; Ylanne et al., 2015). Setting a carbon price for both plant species could shift the optimization solution of the problem, which could be included in future studies (for example see Vondolia et al., 2020). Finally, future studies could benefit from explicitly incorporating dynamic programming and feedback control rules to model stochasticity and uncertainty associated with climate change. Stochastic shocks will become especially important in variations of the model that have multiple stable equilibria where relatively small environmental fluctuations could lead to a shift to an alternative stable steady states. Determining optimal hedging strategies in response to stochastic fluctuations will help identify when managers should double down on conservation or when they should give up and rather allocate limited conservation funding elsewhere.

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Appendix

Appendix A: Ecological model analysis

The equilibrium solutions to the ecological model include seven equilibrium points $P_i \equiv (K_i, R_i, V_i), i \in [1;7]$, including five corner solutions in which there exist two axial equilibria $P_1 \equiv (0,0,M)$ and $P_3 \equiv (Mx,0,0)$. Three other corner solutions are $P_2 \equiv \left(0, \frac{\alpha_V d_V M}{\alpha_V + d_V g_V M}, \frac{\alpha_V M}{\alpha_V + d_V g_V M}\right)$, $P_4 \equiv \left(\frac{M}{\varphi - 1}, 0, \frac{M(\varphi - 1)}{\varphi - 1}\right)$, and $P_5 \equiv \left(\frac{\alpha_K M}{\alpha_K + d_K g_K M}, \frac{\alpha_K d_K M}{\alpha_K + d_K g_K M}, 0\right)$. Conditions for existence of point 4 is $\varphi \neq 1$, and for point 5 is $\alpha_K > d_K g_K M$. There exist two interior equilibria P_6 and P_7 for which the analytical forms are too complex for intuitive interpretation (Table A.1).

Analytical eigenvalues of the axial and corner equilibria are reported in Table A.2. Two axial equilibria are saddle points as the eigenvalues are real numbers of opposite sign. The five other equilibria have complex eigenvalues such that it is difficult to analyze the stability of these equilibria. We therefore use our empirical application to analyze the system. Our goal is to gain more understanding of how changes in the crowberry allelopathy coefficient φ, determines the system’s stability.

Table A.1. Analytical solutions of two interior equilibria

Point 6	V	$\frac{\alpha_V\alpha_K+\alpha_K d_V g_V M-\alpha_K d_K g_V M+\alpha_V d_K g_K M+\alpha_V d_K g_K M-\alpha_V\alpha_K\phi\varphi-\alpha_V d_V g_K M\varphi}{2\alpha_V g_K(d_K-d_V\varphi)}+\frac{\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M+\alpha_V\varphi)(d_V-d_V x\varphi)+(\alpha_K(-d_V+d_K)g_V M+\alpha_V\alpha_K(-1+\varphi)+\alpha_V g_K M(d_V\varphi))^2}}{2\alpha_V g_K(d_K-d_V\varphi)}$
	R	$\frac{\alpha_K(-d_V+d_K)g_V M+\alpha_V\alpha_K(-1+\varphi)+\alpha_V g_K M(d_K-d_K x+d_V\varphi)}{2g_K(d_K g_V M+\alpha_V\varphi)}-\frac{\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M+\alpha_V\varphi)(d_V-d_V\varphi)+(\alpha_K(-d_V+d_K)g_V M+\alpha_V\alpha_K(-1+\varphi)+\alpha_V g_K M(d_V\varphi))^2}}{2g_K(d_K g_V M+\alpha_V\varphi)}$
	K	$\frac{\alpha_K(\alpha_V+d_V g_V M)\big((-d_V+d_K)g_V M+\alpha_V(-1+\varphi)\big)+\alpha_V g_K M\big(\alpha_V(d_V(-2+x)\varphi)+d_V g_V M(d_V\varphi)\big)}{2\alpha_V g_K(d_K g_V M+\alpha_V\varphi)(d_K-d_V\varphi)}-\frac{\alpha_V\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M+\alpha_V\varphi)(d_V+d_K(-1+x)-d_V\varphi)+\big(\alpha_K(-d_V+d_K)g_V M+\alpha_V\alpha_K(-1+\varphi)+\alpha_V g_K M(d_V-d_K+d_V\varphi)\big)^2}}{2\alpha_V g_K(d_K g_V M+\alpha_V\varphi)(d_K-d_V\varphi)}-\frac{d_V g_V M\sqrt{\alpha_V\alpha_K g_K M(d_K g_V M+\alpha_V\varphi)(d_V+d_K(-1+x)-d_V\varphi)+\big(\alpha_K(-d_V+d_K)g_V M+\alpha_V\alpha_K(-1+\varphi)+\alpha_V g_K M(d_K-d_K+d_V\varphi)\big)^2}}{2\alpha_V g_K(d_K g_V M+\alpha_V\varphi)(d_K-d_V\varphi)}$

Point 7	V	$\dfrac{\alpha_V\alpha_K + \alpha_K d_V g_V M - \alpha_K d_K g_V M + \alpha_V d_K g_K M + \alpha_V d_K g_K M - \alpha_V\alpha_K\phi\varphi - \alpha_V d_V g_K M\varphi}{2\alpha_V g_K(d_K - d_V\varphi)} - \dfrac{\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M + \alpha_V\varphi)(d_V - d_V x\varphi) + (\alpha_K(-d_V + d_K)g_V M + \alpha_V\alpha_K(-1+\varphi) + \alpha_V g_K M(d_V\varphi))^2}}{2\alpha_V g_K(d_K - d_V\varphi)}$
	R	$\dfrac{\alpha_K(-d_V + d_K)g_V M + \alpha_V\alpha_K(-1+\varphi) + \alpha_V g_K M(d_K - d_K x + d_V\varphi)}{2g_K(d_K g_V M + \alpha_V\varphi)} + \dfrac{\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M + \alpha_V\varphi)(d_V - d_V\varphi) + (\alpha_K(-d_V + d_K)g_V M + \alpha_V\alpha_K(-1+\varphi) + \alpha_V g_K M(d_V x\varphi))^2}}{2g_K(d_K g_V M + \alpha_V\varphi)}$
	K	$\dfrac{\alpha_K(\alpha_V + d_V g_V M)\big((-d_V + d_K)g_V M + \alpha_V(-1+\varphi)\big) + \alpha_V g_K M\big(\alpha_V(d_V(-2+x)\varphi) + d_V g_V M(d_V\varphi)\big)}{2\alpha_V g_K(d_K g_V M + \alpha_V\varphi)(d_K - d_V\varphi)} + \dfrac{\alpha_V\sqrt{4\alpha_V\alpha_K g_K M(d_K g_V M + \alpha_V\varphi)(d_V + d_K(-1+x) - d_V\varphi) + \big(\alpha_K(-d_V + d_K)g_V M + \alpha_V\alpha_K(-1+\varphi) + \alpha_V g_K M(d_V - d_K + d_V\varphi)\big)^2}}{2\alpha_V g_K(d_K g_V M + \alpha_V\varphi)(d_K - d_V\varphi)} + \dfrac{d_V g_V M\sqrt{\alpha_V\alpha_K g_K M(d_K g_V M + \alpha_V\varphi)(d_V + d_K(-1+x) - d_V\varphi) + \big(\alpha_K(-d_V + d_K)g_V M + \alpha_V\alpha_K(-1+\varphi) + \alpha_V g_K M(d_K - d_K + d_V\varphi)\big)^2}}{2\alpha_V g_K(d_K g_V M + \alpha_V\varphi)(d_K - d_V\varphi)}$

Table A.2. Analytical solutions for traces, determinants, and eigenvalues of P_1, P_2, P_3, P_4, and P_5

	Eigenvalues
Point 1	$-\alpha_V$ α_K α_R
Point 2	$\frac{\alpha_V \alpha_K + \alpha_K d_V g_V M - \alpha_V d_V g_K M}{\alpha_V + d_V g_V M}$ $-\frac{{\alpha_V}^2 + \alpha_V \alpha_R + \alpha_R d_V g_V M + \sqrt{-4\alpha_V \alpha_R (\alpha_V + d_V g_V M)^2 + (\alpha_V(\alpha_V + \alpha_R) + \alpha_R d_V g_V M)^2}}{2(\alpha_V + d_V g_V M)}$ $-\frac{{\alpha_V}^2 + \alpha_V \alpha_R + \alpha_R d_V g_V M - \sqrt{-4\alpha_V \alpha_R (\alpha_V + d_V g_V M)^2 + (\alpha_V(\alpha_V + \mathrm{a3}) + \alpha_R d_V g_V M)^2}}{2(\alpha_V + d_V g_V M)}$
Point 3	$-\alpha_K$ α_R $\alpha_V - \alpha_V \phi$
Point 4	α_R $\frac{\alpha_V + \alpha_K - \alpha_K \varphi - \alpha_V \varphi - \sqrt{(\alpha_K(-1+\varphi) + \alpha_V(-1+\varphi))^2}}{2(-1+\varphi)}$ $\frac{\alpha_V + \alpha_K - \alpha_K \varphi - \alpha_V \varphi + \sqrt{(\alpha_K(-1+\varphi) + \alpha_V(-1+\varphi))^2}}{2(-1+\varphi)}$
Point 5	$-\frac{\alpha_K(\alpha_K + \alpha_R) + \alpha_R d_K g_K M + \sqrt{{\alpha_K}^2(\alpha_K - \alpha_R)^2 + 2\alpha_K \alpha_R(-3\alpha_K + \alpha_R) d_K g_K M + \alpha_R(-4\alpha_K + \alpha_R){d_K}^2 {g_K}^2 M^2}}{2(\alpha_K + d_K g_K M)}$ $\frac{-\alpha_K(\alpha_K + \alpha_R) - \alpha_R d_K g_K M + \sqrt{{\alpha_K}^2(\alpha_K - \alpha_R)^2 + 2\alpha_K \alpha_R(-3\alpha_K + \alpha_R) d_K g_K M + \alpha_R(-4\alpha_K + \alpha_R){d_K}^2 {g_K}^2 M^2}}{2(\alpha_K + d_K g_K M)}$ $\frac{-\alpha_K d_K g_V M x + \alpha_V(\alpha_K + d_K g_K M x - \alpha_K \varphi)}{\alpha_K + d_K g_K M}$

Table A.3: Ecological parameters for both ecological and bioeconomic models

Parameters	Indicators	Unit	Value		Sources
			Pre-encroachment	Post-encroachment	
α_V	Vegetation intrinsic growth coefficient	Kg biomass/ total area	0.5	0.6	Moxnes, 1993; Skonhoft et al., 2010, Myers-Smith et al., 2020
α_K	Crowberry intrinsic growth coefficient		0.1	0.2	Murguzur et al., 2019, Tuomi et al., 2022
α_R	Reindeer intrinsic growth coefficient		0.7		Moxnes, 1993; Skonhoft et al., 2010
M	Pasture carrying capacity		8.7 x 10^{10}		Calculated from Bråthen and Lortie 2015
g_V	Grazing coefficient on vegetation		4 x 10^{-7}		Bakka et al., 2021; White & Trudell, 1980
g_K	Grazing coefficient on crowberry		8 x 10^{-9}		Danell et al., 1994
d_V	Impact coefficient of vegetation on reindeer carrying capacity from vegetation		2 x 10^{-5}		Calibrated
d_K	Impact coefficient of crowberry on reindeer carrying capacity		4 x 10^{-7}		Calibrated
φ	Allelopathic coefficient		0	0.8	Calculated from Bråthen & Lortie, 2015; Pilsbacher et al., 2020; Tuomi et al., 2022
$V(t_0)$	Initial condition of vegetation	Kg biomass	6.09 x 10^{10}		Bråthen et al., 2018
$K(t_0)$	Initial condition of crowberry	Kg biomass	2.61 x 10^{10}		Bråthen et al., 2018
$R(t_0)$	Initial condition of reindeer	Reindeer	250 000		Landbruksdirektoratet, 2009

Table A.4: Economic parameters for the bioeconomic model

Parameters	**Meaning**	**Unit**	**Value**	**Source**
ε	Burning coefficient	/effort unit	8 x 10^{-4}	Calibrated
β	Feeding coefficient	/effort unit	8 x 10^{-4}	Calibrated
c_1	Maintenance cost	NOK/ reindeer	1200	Calculated from Regjeringen, 2021
c_2	Supplementary feeding cost	NOK/ tonne dry feed	6000	Discussion with herders, Pekkarinen et al. 2015
c_3	Crowberry burning cost	NOK/ treatment effort	2000	Calibrated
p	Price per reindeer	NOK/ reindeer	3760	Calculated from Regjeringen, 2021
γ	Non-use value per reindeer	NOK/ reindeer	2540	Calculated from Regjeringen, 2021
δ	Discount rate		0.05	Regjeringen, 2012

Appendix B: Impact of crowberry encroachment in the ecological system

Besides the fitted value for $\varphi = 0.8$, we choose another more extreme value for $\varphi = 1.1$ to represent the extreme post-EC case in which the high-quality palatable vegetation goes extinct due to crowberry encroachment. Table B.1 shows the existence of a unique stable equilibrium in all three cases. While point P_7 is the stable equilibrium in the pre- and post-EC cases, it turns into a saddle point in the third case when $\varphi = 1.1$.

Table B.1: Multiple equilibria for the ecological model in three cases: pre-EC, post-EC, and extreme post-EC cases.

Unit for biomass V and K is kg/ whole area while R is reindeer number.

Equilibria	**Pre-EC ($\boldsymbol{\varphi = 0}$)**				**Post-EC ($\boldsymbol{\varphi = 0.8}$)**				**Extreme Post-EC ($\boldsymbol{\varphi = 1.1}$)**			
	$\boldsymbol{K}$	$\boldsymbol{R}$	$\boldsymbol{V}$	**Stability**	$\boldsymbol{K}$	$\boldsymbol{R}$	$\boldsymbol{V}$	**Stability**	$\boldsymbol{K}$	$\boldsymbol{R}$	$\boldsymbol{V}$	**Stability**
$\boldsymbol{P_1}$	0	0	8.7 x 10^{10}	Saddle	0	0	8.7 x 10^{10}	Saddle	0	0	8.7 x 10^{10}	Saddle
$\boldsymbol{P_2}$	0	727 425	3.64 x 10^{10}	Saddle	0	805 556	4.03 x 10^{10}	Saddle	0	805 556	4.03 x 10^{10}	Saddle
$\boldsymbol{P_3}$	7.83 x 10^{10}	0	0	Saddle	7.83 x 10^{10}	0	0	Saddle	7.83 x 10^{10}	0	0	Saddle
$\boldsymbol{P_4}$	-8.7 x 10^{9}	0	8.7 x 10^{10}	Saddle	-4.35 x 10^{10}	0	1.22 x 10^{11}	Saddle	8.7 x 10^{10}	0	-8.7 x 10^{9}	Saddle
$\boldsymbol{P_5}$	7.81 x 10^{10}	31 242	0	Saddle	7.82 x 10^{10}	31 281	0	Saddle	7.82 x 10^{10}	31 281	0	**Stable**
$\boldsymbol{P_6}$	-6.36 x 10^{15}	-1.06 x 10^{9}	7.4 x 10^{13}	Saddle	5.57 x 10^{12}	-3.94 x 10^{7}	-2.08 x 10^{12}	Saddle	2.24 x 10^{12}	-2.16 x 10^{7}	-1.12 x 10^{12}	Saddle
$\boldsymbol{P_7}$	3.99 x 10^{10}	734 098	3.59 x 10^{10}	**Stable**	6 x 10^{10}	372 433	1.74 x 10^{10}	**Stable**	7.91 x 10^{10}	14 374	-6.64 x 10^{8}	Saddle

Regarding the extreme post-EC case, only the corner solution P_5 is stable, emphasizing the system shift from an interior to a corner solution without the palatable vegetation. Though the eigenvalues of P_7 are too complex to analyze analytically when $\varphi = 1.1$, we can analyze the eigenvalues of P_5. Among three eigenvalues (Table A.2), only one contains φ, which is

$$\frac{-\alpha_K d_K g_V M + \alpha_V(\alpha_K + d_K g_K M - \alpha_K x\varphi)}{\alpha_K + d_K g_K M}$$

Since P_5 is stable in the extreme case while a saddle point in the two former cases, we need

$$-\alpha_K d_K g_V M + \alpha_V(\alpha_K + d_K g_K M - \alpha_K \varphi) < 0 \leftrightarrow \varphi > 1 + d_K M\left(\frac{g_K}{\alpha_K} - \frac{g_V}{\alpha_V}\right)$$

for the eigenvalue of P_5 to be negative. Thus, when φ reaches the encroachment threshold of $1 + d_K M\left(\frac{g_K}{\alpha_K} - \frac{g_V}{\alpha_V}\right)$, the system's unique stable equilibrium will turn from an interior to a corner solution of only crowberry and reindeer. At this threshold, the allelopathic encroachment leads to the extinction of the palatable vegetation. The extinction threshold varies based on the magnitudes of the ecological parameters. Specifically, the higher grazing rate of reindeer and impact rate of crowberry, g_K and d_K, the harder crowberry encroachment can drive the system to a corner solution. Numerical results of the eigenvalues in three cases are reported in table B.2.

The number of reindeer in the pre-EC case in P_7 reaches 734 000 reindeers, which serves as the carrying capacity of reindeer in the bioeconomic model. Crowberry encroachment inflicts a 50% decline in reindeer population in the post-EC case, while vegetation is reduced 50%

due to allelopathic impact. Together with reindeer's selective herbivory towards vegetation, the crowberry population increases up to 70% of the total pasture carrying capacity in the post-EC case. The ecological model can be visualized in a three-dimensional phase-space plot, which includes three iso-planes to enhance the depiction of equilibrium points and their stability.

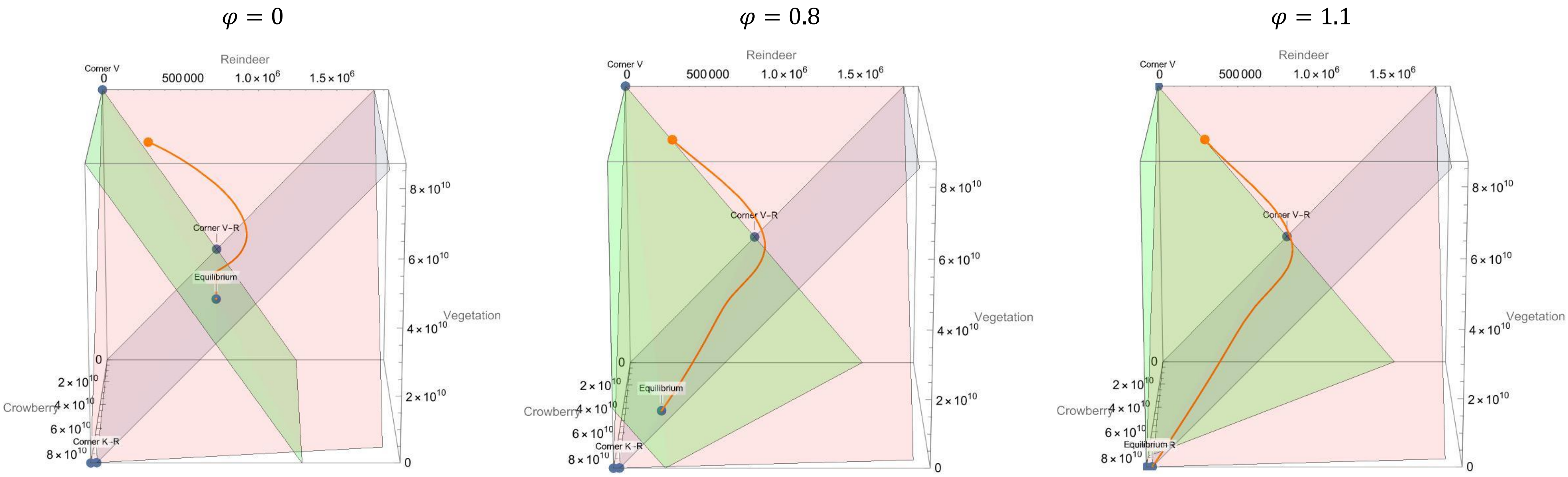

Figure B.1: Visualization of the three-dimensional phase-space of the system, showing the iso-planes of three species and the dynamic trajectory to a stable equilibrium. The green, red, and blue surfaces represent the iso-planes of vegetation, crowberry, and reindeer, respectively. The orange trajectory illustrates system convergence from the starting point (orange dot) to the intersection of all three iso-planes in the three cases: $\varphi = 0$, $\varphi = 0.8$, *and* $\varphi = 1.1$. *The other blue dots are the non-negative equilibria of the system. Initial conditions follow those described in the dataset.*

Figure B.1 illustrates the impact of the allelopathic coefficient φ on the system's stability. Each isophase plane corresponds to a condition wherein the growth rate of a particular species is constant, indicating a state of equilibrium for that species. The intercept of these planes marks the equilibria of the system. Notably, since φ directly influences the growth dynamics of vegetation (equation (1)), altering φ results in corresponding shifts solely in the vegetation's iso-plane, while the iso-planes of crowberry and reindeer remain unchanged. The shift in vegetation’s iso-plane indicates the decrease in vegetation when φ increases, shifting the stable equilibrium of the system from an interior solution to a corner solution with $V = 0$. A cross-section of this phase-space is the phase-plane of each pair of two species.

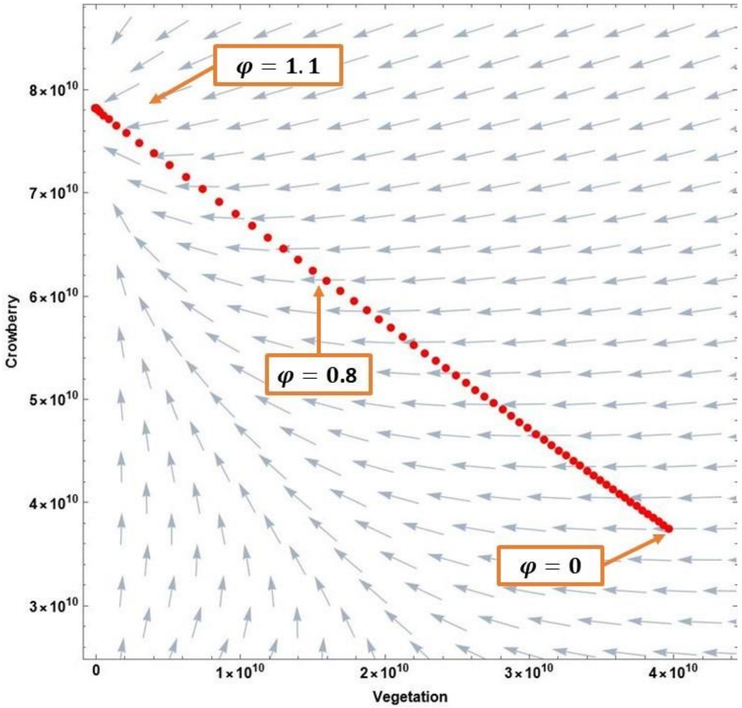

Figure B.2: Phase-plane bifurcation analysis of vegetation and crowberry dynamics with varying allelopathic coefficient φ.

Figure B.2 visualizes the dynamics between vegetation and crowberry populations, where the directional vector field, illustrated by blue arrows, conveys the trajectory and velocity of population changes at $\varphi = 1.1$. The series of red dots depict the gradual shift of the system's equilibrium in response to the incremental bifurcation of the allelopathic coefficient φ. Notably, the equilibrium shift indicates a consistent and progressive movement rather than an abrupt and drastic change, mirroring the ecological behavior of the crowberry – a native species whose spread is gradually amplified by climate change (Bokhorst et al., 2018; Gonzalez et al., 2021). The absence of rapid encroachment, due to the ecological characteristics of this plant, circumvents any abrupt disruptions to the system's equilibrium. (Bråthen et al., 2018; Maliniemi et al., 2018; Tuomi et al., 2024). We acknowledge that incorporating more complex ecological factors, such as an Allee effect (Drake & Lodge, 2006; Salau & Fenichel, 2015), into our model might result in an abrupt shift.

Figure B.3 and B.4 shows the time convergence of three species between 2 cases, pre-EC and post-EC, under different initial conditions. Figure B.5. depicts the system convergence to the stable interior equilibrium from different initial conditions.

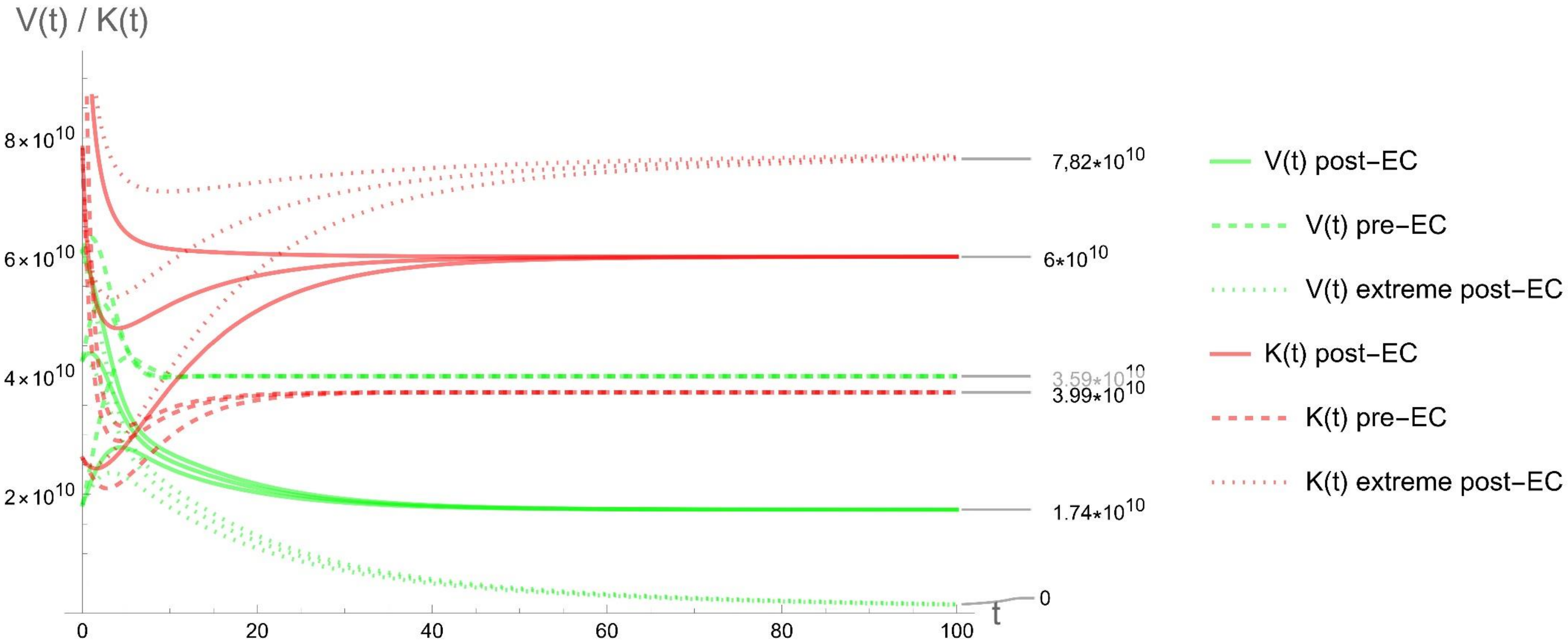

Figure B.3: Dynamic convergence of vegetation and crowberry in three cases with different initial conditions

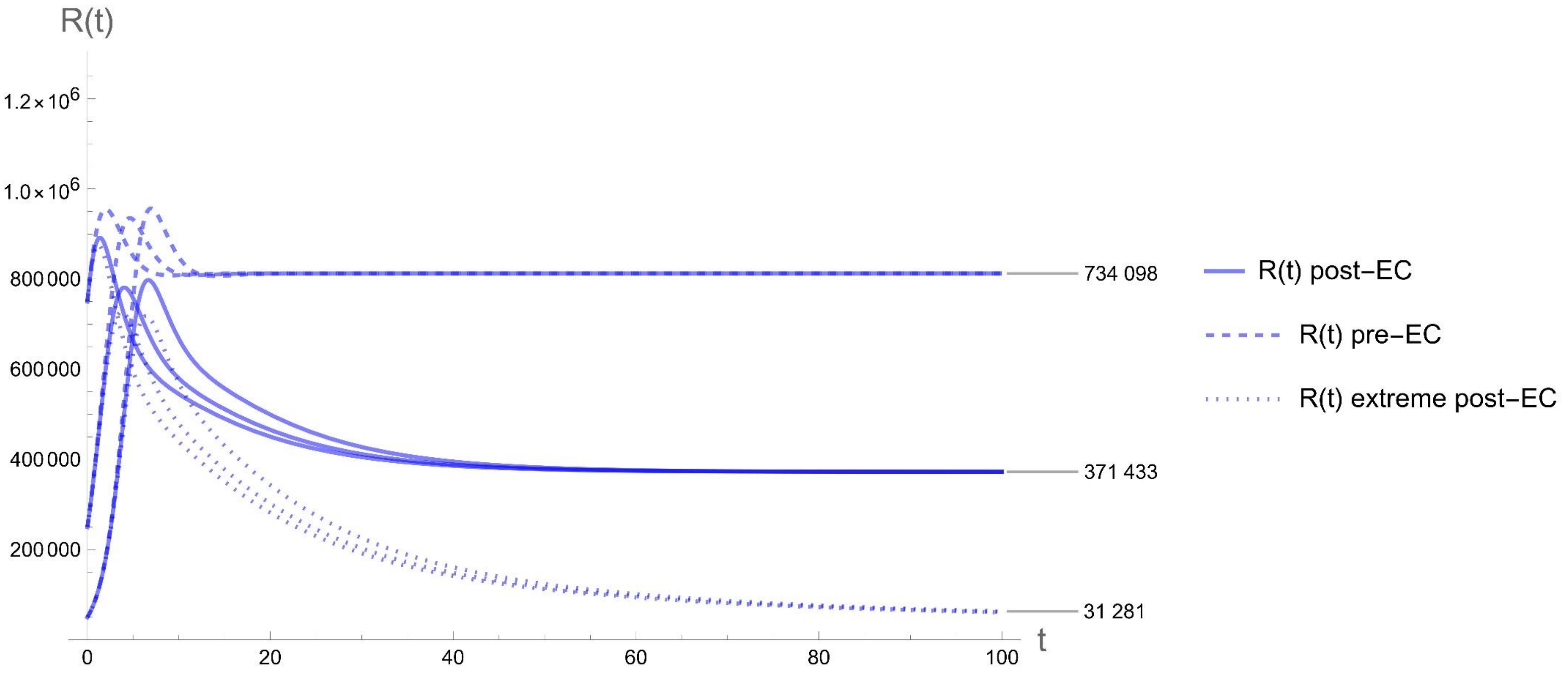

Figure B.4: Dynamic convergence of reindeer in three cases with different initial conditions

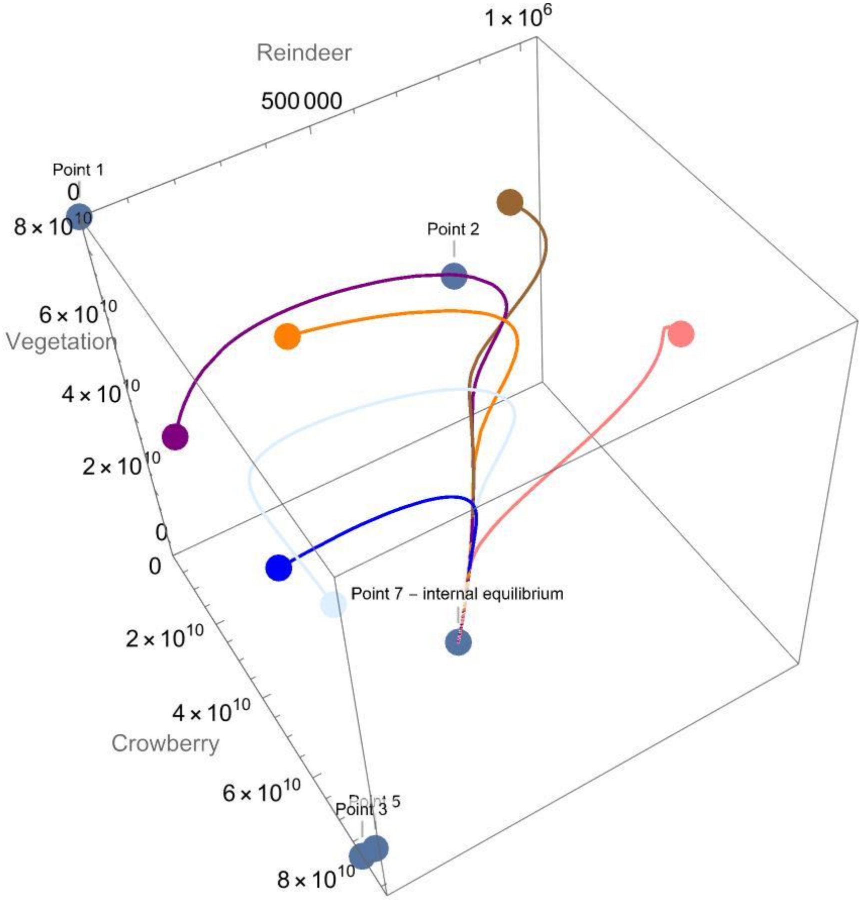

Figure B.5: Convergence to the stable interior equilibrium with different initial conditions

Table B.2: Numerical solutions for stability of seven ecological equilibria in the pre- , post- , and extreme post-encroachment cases

	Pre-EC		**Post-EC**		**Extreme Post-EC**	
	Eigenvalues	**Stability**	**Eigenvalues**	**Stability**	**Eigenvalues**	**Stability**
Point 1	– 0.5	Saddle point	– 0.6	Saddle point	– 0.6	Saddle point
	0.1		0.2		0.2	
	0.7		0.7		0.7	
Point 2	0.094	Saddle point	0.194	Saddle point	0.194	Saddle point
	– 0.455 – 0379i		– 0.489 – 0.425i		– 0.489 – 0.425i	
	– 0.455 + 0379i		– 0.489 + 0.425i		– 0.489 + 0.425i	
Point 3	0.7	Saddle point	0.7	Saddle point	0.7	Saddle point
	0.5		– 0.2		– 0.2	
	– 0.1		0.168		0.006	
Point 4	0.7	Saddle point	– 1.007	Saddle point	0.7	Saddle point
	– 0.5		0.7		-0.13	
	– 0.1		– 0.033		-0.009	
Point 5	– 0.7	Saddle point	– 0.7	Saddle point	-0.7	Stable point
	0.488		– 0.2		-0.2	
	– 0.1		0.156		-0.006	
Point 6	– 424.328	Saddle point	14.078	Saddle point	7.73	Saddle point
	– 11.547		– 1.296		-1.26	
	1.237		0.373		0.2	
Point 7	– 0.453 + 0,375i	Stable point	– 0.464 + 0.162i	Stable point	-0.71	Saddle point
	– 0.453 – 0,375i		– 0.464 + 0.162i		-0.19	
	– 0.093 + 0. i		– 0.09 + 0. i		0.006	

Sensitivity analysis provides insight regarding how sensitive the variables are in relation to a 10% increase in a single parameter (Table B.3). The results provide signs of change as expected, with the exception of the relationship between changes in α_R and the variables. K in both cases and V and R in post- and extreme post-EC cases are sensitive in relation to only the parameters governing carrying capacity M. Due to reindeer's selective herbivory, V and R are robust to a 10% change in M, but not K. Also due to selective herbivory, a 10% increase in g_V and g_K leads to different signs for the change in reindeer stock, for pre- and post-EC. Moreover, a 10% increase in α_K causes sign difference for the change of R in all cases.

Table B.3: Sensitivity analysis in pre-encroachment and post-encroachment cases in relation to 10% increase in each parameter (in percentage)

Indicators	**Parameters**	**Pre-EC**			**Post-EC**			**Extreme Post-EC**		
		$\Delta\, \boldsymbol{V}^*$	$\Delta\, \boldsymbol{R}^*$	$\Delta\, \boldsymbol{K}^*$	$\Delta\, \boldsymbol{V}^*$	$\Delta\, \boldsymbol{R}^*$	$\Delta\, \boldsymbol{K}^*$	$\Delta\, \boldsymbol{V}^*$	$\Delta\, \boldsymbol{R}^*$	$\Delta\, \boldsymbol{K}^*$
Intrinsic growth rates	α_V	5.78	5.54	-5.22	9.33	8.55	-2.8	-10.15	**11.94**	-0.12
	α_K	-0.007	0.005	0.57	-0.3	-0.26	0.23	0.55	-0.64	0.01
	α_R	0	0	0	0	0	0	0	0	0
Carrying capacity	M	3.75	3.99	**15.007**	0.73	1.49	**12.63**	**19.28**	-0.92	10.1
Grazing coefficients	g_V	-5.69	-5.46	5.18	-8.72	-8	2.62	8.93	-10.5	0.1
	g_K	0.008	-0.006	-0.63	0.33	0.29	-0.25	-0.62	0.71	-0.01
Comparative rate to reindeer carrying capacity	d_V	-5.55	3.9	4.45	-7.88	1.39	2.23	-10.11	1.11	-0.11
Comparative rate to reindeer carrying capacity	d_K	-0.13	0.09	0.11	-0.59	0.1	0.17	**20.66**	-2.26	0.23
Allelopathy coefficient	φ	0	0	0	**-22.49**	**-20.61**	6.77	**119.8**	**-140.89**	**13.99**

The reason why both the pasture and reindeer are sensitive to the allelopathy coefficient φ lies in the analytical solutions, as K increases exponentially with higher φ while V and R develops in the opposite direction. As a function of φ, point 7 takes the form of

$$K_7 = \frac{2.89 \times 10^{12} - 1.35 \times 10^{12}\varphi - 1.13 \times 10^{13}\sqrt{0.07 + (-0.06 + 0.01\varphi)\varphi}}{(0.02 + \varphi)(-0.02 + \varphi)}$$

$$R_7 = \frac{-2.67 \times 10^{7} + 1.33 \times 10^{7}\varphi + 1.04 \times 10^{8}\sqrt{0.07 + (-0.07 + 0.01\varphi)\varphi}}{0.02 + \varphi}$$

$$V_7 = \frac{-1.34 \times 10^{12} + 6.64 \times 10^{11}\varphi + 5.21 \times 10^{12}\sqrt{0.07 + (-0.06 + 0.01\varphi)\varphi}}{-0.02 + \varphi}$$

Given all the chosen parameters are fixed, K, R, and V are nonlinear functions of φ where K increases exponentially when φ ranges from 0 to 1,5, while V and R follows the opposite growth direction (Figure B.6 and B.7).

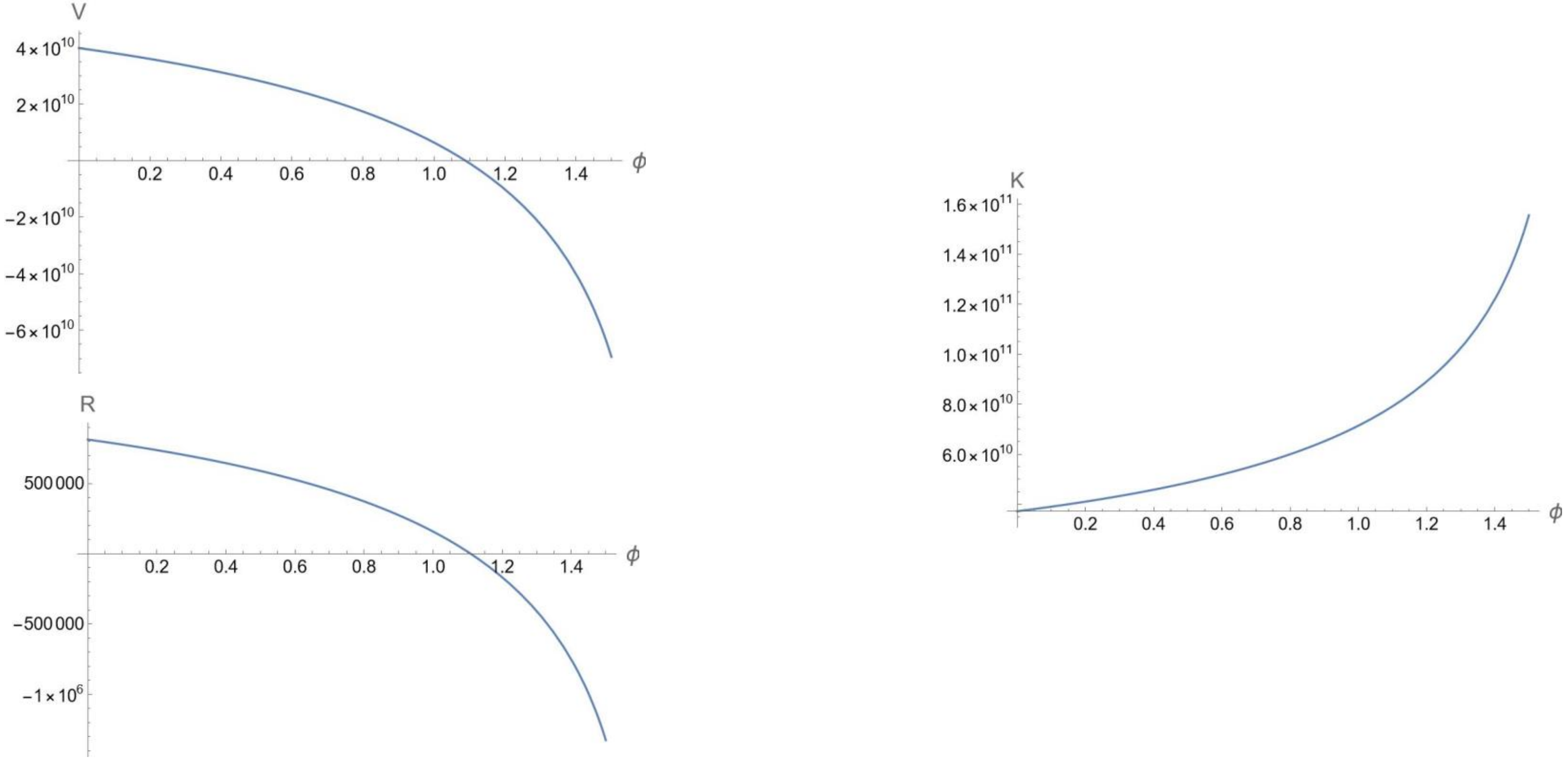

Figure B.6: Relationship between different choice of φ and the equilibrium point

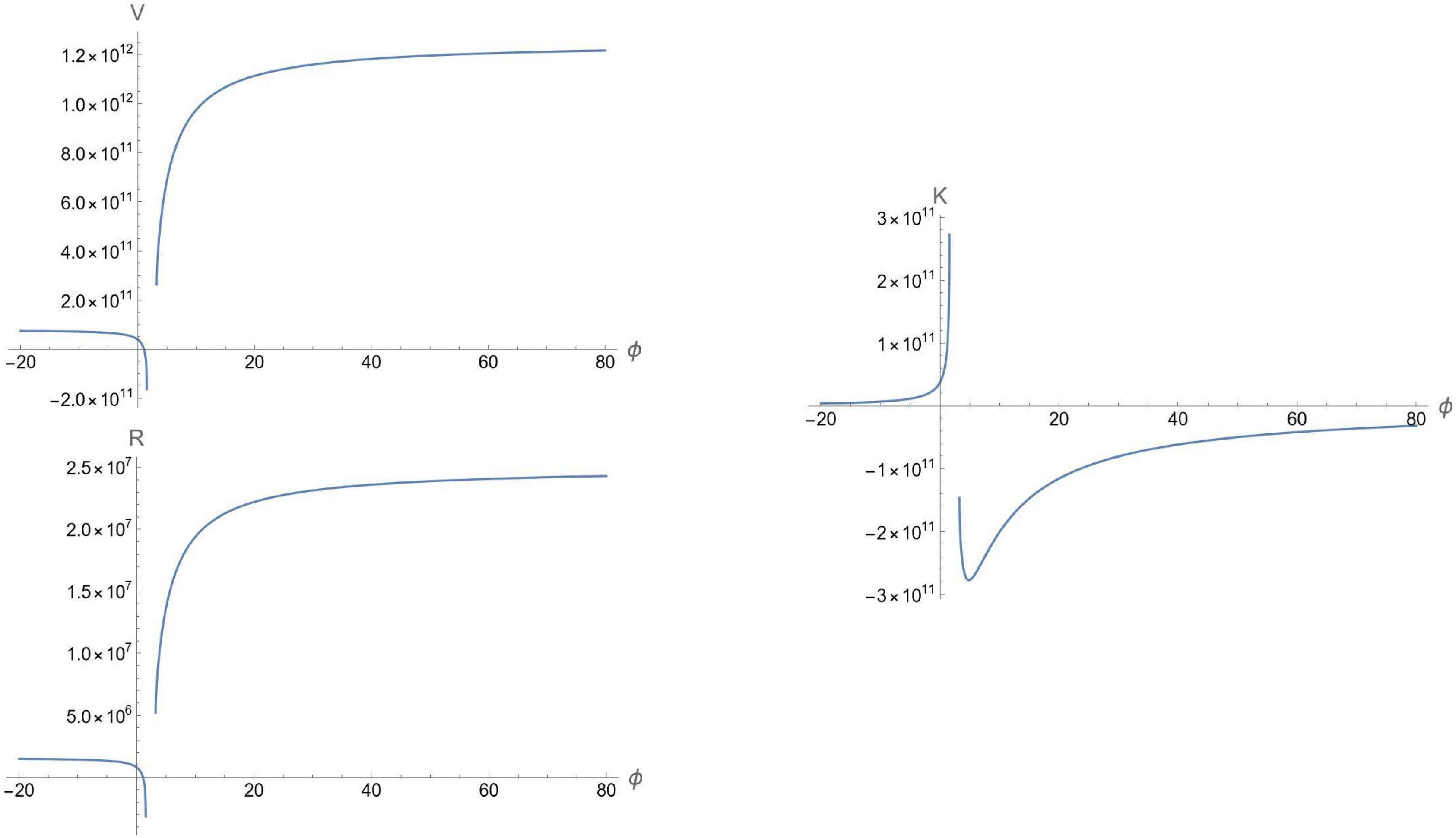

Figure B.7: Bifurcations of φ in relation to the equilibrium point

Appendix C: Proof for singular control S

Due to the linear S control in the objective functional, S disappears from the FOCs and the adjoint equations. To determine the functional form of S^*, we can take the second time derivative of the first adjoint equation. We use the first adjoint equation in the adaptive scenario since it includes all three control variables. Setting this equation equals to 0, we obtain:

$$\begin{aligned}
S^* = \frac{1}{p\left(-\frac{4\alpha_R}{d_K K^* + d_V V^*} + \frac{p\beta^2}{c_2}\right)} \Bigg[& \frac{4{\alpha_R}^2 p R^*(R - d_K K^* - d_V V^*)}{(d_K K^* + d_V V^*)^2} + \frac{F^* p^2 R^* \beta^3}{c_2} - 2 g_V V^* \delta \lambda_V^* - \frac{2\alpha_K {K^*}^2 (g_V V^* - g_K V^* + g_K M)\lambda_K^*}{(V^* - M)^2} - 2 g_K K^* \delta \lambda_K^* \\
& - \frac{2\alpha_V V^* \lambda_V^* (g_V V^* + g_K K^* \varphi)}{M} \\
& + \frac{\alpha_R R^*}{c_2 M (d_K K^* + d_V V^*)^2 (Mx - V^*)} \Big[-4\alpha_K c_2 d_K K^* M p (K^* + V^* - M) \\
& - (M - V^*) \Big(-M p^2 (d_K K^* + d_V V^*)(d_K K^* + d_V V^* - R^*)\beta^2 + 2 c_2 d_K K^* M (2p(g_K R^* + F^* \beta + T^* \varepsilon) - g_K p R^*) \\
& + 2 c_2 d_V V^* \big(2F^* M p \beta + g_V p M R^* + 2\alpha_V p (V^* + K^* \varphi - M)\big)\Big)\Big]\Bigg]
\end{aligned}$$

We check whether S^* is a singular control by testing the Legendre-Clebsch condition (Krener, 1977), obtaining:

$$\frac{d}{dS}\frac{d^2}{dt^2}\frac{\partial H}{\partial S} = \frac{p\alpha_R 2(-1)}{(d_K K^* + d_V V^*)} < 0$$

which satisfies the condition for a maximization problem with singular control, and S^* will be singular through time (see similar example in Clayton et al., 2010).

Appendix D: Stability and Sensitivity results of bioeconomic models

In general, the results are insensitive to the 10% increase of each parameter, except α_R, α_K, and φ in some scenarios (Table D.1 and D.2). One seemingly unexpected sign in all scenarios is that 10% increase of α_R leads to an increase in V^* and a decrease in K^*, which does not seem to follow the selective herbivory in our model. However, from table D.2, it becomes clear that the increase in α_R leads to a larger increase in crowberry control than supplementary feeding which triggers the divergence of the V and K values. Another unexpected sign is that V^* increases when α_K increases in the post-EC case whereas R^* and S^* show negative signs. This can be explained as higher α_K boosts crowberry encroachment, leaving the reindeer stock less nutritious food which then alleviates less stress on vegetation stock. Model sensitivity to a 10% increase in φ can be explained by the non-linear effect of crowberry encroachment (see Appendix B).

Combination of both measures reinforces the robustness of the model as the variables are insensitive to 10% change of the parameters. Besides, a 10% increase in maintenance cost c_1 decreases the gained profit, reducing treatment effort, making the sign of change in T^* negative. Another seemingly unexpected sign is that 10% higher reindeer price decreases the optimal vegetation biomass. The reason is that as reindeer meat is valued 10% higher, enhanced feeding effort F^* and controlling effort T^* are needed to increase the herd size, thus decreasing K^*. Table D.3 shows the stability of the equilibrium in three scenarios.

Table D.1: Sensitivity results between pre-encroachment and post-encroachment cases in relation to 10% increase of each parameter (in percentage). Sensitivity higher than 10% is marked in bold.

Parameters	**Pre-EC**							**Post-EC**						
	$\Delta \boldsymbol{V}^*$	$\Delta \boldsymbol{R}^*$	$\Delta \boldsymbol{S}^*$	$\Delta \boldsymbol{K}^*$	$\Delta \boldsymbol{\lambda_R}^*$	$\Delta \boldsymbol{\lambda_V}^*$	$\Delta \boldsymbol{\lambda_K}^*$	$\Delta \boldsymbol{V}^*$	$\Delta \boldsymbol{R}^*$	$\Delta \boldsymbol{S}^*$	$\Delta \boldsymbol{K}^*$	$\Delta \boldsymbol{\lambda_R}^*$	$\Delta \boldsymbol{\lambda_V}^*$	$\Delta \boldsymbol{\lambda_K}^*$
α_V	1.94	2.727	2.503	-6.671	0	-8.213	1.69	4.861	5.438	5.246	-4.314	0	-8.044	6.163
α_K	-0.001	0.005	0.003	0.216	0	-0.035	-6.331	0.061	-0.293	-0.207	0.008	0	1.524	-5.947
α_R	8.077	**11.609**	**10.584**	**-27.722**	0	**-32.6**	7.238	**12.7**	**14.439**	**13.866**	**-11.239**	0	**-19.995**	**15.93**
M	7.803	6.808	7.083	**17.303**	0	-0.167	-1.833	5.069	4.054	4.349	**14.311**	0	0.698	-3.817
g_V	-1.998	-2.9	-2.65	6.882	0	-0.169	-1.978	-4.597	-5.546	-5.27	4.085	0	0.792	-3.89
g_K	0.001	-0.002	-0.001	-0.234	0	0.002	0.152	0.122	0.152	0.143	-0.174	0	-0.1	0.074
d_V	-1.981	6.752	7.031	6.584	0	9.902	-1.859	-4.351	3.935	4.237	3.804	0	**10.765**	6.084
d_K	-0.016	0.055	0.051	0.053	0	-0.091	10.03	-0.135	0.122	0.114	0.118	0	-0.013	-0.289
φ	0	0	0	0	0	0	0	**-26.482**	**-25.314**	**-25.33**	**23.52**	0	**36.447**	**10.34**
p	-1.758	5.991	3.787	5.843	10	**29.948**	**28.041**	-3.956	3.578	1.637	3.457	10	**30.94**	**25.759**
c_1	2.039	-6.949	-4.787	-6.797	0	**-18.237**	**-16.847**	4.813	-4.343	-2.34	-4.209	0	**-18.978**	**-15.079**
δ	0.287	-0.978	-0.649	-0.956	0	-3.798	-5.699	0.305	-0.275	-0.137	-0.266	0	-6.511	-8.146

Table D.2: Sensitivity results in comprehensive scenarios in relation to 10% increase of each parameter (in percentage)

Parameters	**Adaptive post-EC**								
	$\Delta\, \boldsymbol{V}^*$	$\Delta\, \boldsymbol{R}^*$	$\Delta\, \boldsymbol{S}^*$	$\Delta\, \boldsymbol{K}^*$	$\Delta\, \boldsymbol{F}^*$	$\Delta\, \boldsymbol{T}^*$	$\Delta\, \boldsymbol{\lambda_R}^*$	$\Delta\, \boldsymbol{\lambda_V}^*$	$\Delta\, \boldsymbol{\lambda_K}^*$
α_V	3.806	5.357	5.399	-4.962	5.357	1.076	0	-7.086	6.353
α_K	-1.772	-2.494	-2.494	4.524	-2.494	-2.727	0	3.801	-6.937
α_R	9.72	**14.1**	**14.206**	**-12.517**	**14.1**	2.079	0	**-17.561**	**16.683**
M	7.225	7.037	7.766	**11.303**	7.037	9.695	0	-0.319	-1.445
g_V	-3.559	-5.289	-5.245	4.523	-5.288	-0.277	0	-0.976	-4.592
g_K	0.063	0.017	0.104	-0.171	0.107	-0.083	0	-0.045	0.088
d_V	-2.435	6.969	7.7	1.055	6.969	9.815	0	9.623	8.668
d_K	-0.093	0.07	0.069	0.137	0.07	-0.123	0	0.016	-0.26
φ	-5.706	-6.712	-6.964	3.556	-6.712	**17.985**	0	6.86	**13.934**
p	0.008	9.423	8.596	-4.692	**20.366**	**24.576**	10	**26.082**	**30.709**
c_1	1.377	-7.201	-5.68	1.022	-7.201	**-14.471**	0	**-14.745**	**-15.336**
c_2	0.185	-1.057	-1.603	0.182	**-10.052**	-2.149	0	-2.205	-2.327
c_3	-1.113	-1.366	-1.403	2.742	-1.366	-7.13	0	1.572	-0.57
β	-0.419	2.525	3.882	-0.476	**12.777**	5.166	0	5.323	5.669
ε	2.307	2.872	2.95	-5.702	2.872	5.034	0	-3.218	1.259
δ	-0.659	-1.469	-1.371	1.951	-1.469	-5.951	0	-4.145	-7.75

Table D.3: Stability results of the dynamic optimized equilibrium under different scenarios

Scenario	**Eigenvalues**	**Stability**
pre-EC	0.385 ; - 0.365 ; - 0.1	Saddle point
post-EC	- 0.448 ; 0.411 ; - 0.017	Saddle point
Adaptive post-EC	- 0.448 ; 0.413; - 0.031	Saddle point

Appendix E: Analysis of some implicit-function theorems

From the reindeer equilibrium condition (equation (13)) we have three implicit functions (*E1*), (*E2*), and (*E3*) with:

$$\frac{\partial V^*}{\partial R^*} = \frac{2\alpha_R(d_K K^* + d_V V^*)\lambda_R^*}{2\alpha_R d_V R^* \lambda_R^* - g_1(d_K K^* + d_V V^*)^2 \lambda_V^*} \tag{E1}$$

We expect that the sign of the implicit function of vegetation w.r.t reindeer $\frac{\partial V^*}{\partial R^*} < 0$ if $\frac{\lambda_V^*}{\lambda_R^*} > \frac{2\alpha_R d_V R^*}{g_V(d_K K^* + d_V V^*)^2}$ (derived from the denominator).

$$\frac{\partial K^*}{\partial R^*} = \frac{2\alpha_R(d_K K^* + d_V V^*)\lambda_R^*}{2\alpha_R d_K R^* \lambda_R^* - g_2(d_K K^* + d_V V^*)^2 \lambda_K^*} \tag{E2}$$

As $\lambda_K^* < 0$ when $\varphi > \frac{\alpha_R d_K M \lambda_R^* {R^*}^2}{(d_K K^* + d_K V^*)^2(\alpha_V V^* \lambda_V^*)}$, $\frac{\partial K^*}{\partial R^*} > 0$. Intuitively, due to reindeer's selective herbivory, reindeer will suppress the high quality pasture, leaving the native pest to grow wild. If $\lambda_K^* > 0$ then $\frac{\partial K^*}{\partial R^*} > 0$ only when $\frac{\lambda_K^*}{\lambda_R^*} < \frac{2\alpha_R d_K R^*}{g_2(d_K K^* + d_V V^*)^2}$ (derived from the denominator).

$$\frac{\partial R^*}{\partial F^*} = \frac{d_K \beta K^* + d_V \beta V^*}{2\alpha_R} \tag{E3}$$

From (*E3*) we can have $\frac{\partial F^*}{\partial R^*} > 0$, which indicates that if there is more reindeer, under the climate change situation, more effort is needed.

We get two implicit functions from the equilibrium condition of vegetation equation (14):

$$\frac{\partial K^*}{\partial V^*} = \frac{2\left(\alpha_R {d_V}^2 M R^{*2}(M - V^*)^3 \lambda_R^* + (d_K K^* + d_V V^*)^3\left(-\alpha_V (V^* - M)^3 \lambda_V^* + \alpha_K K^{*2} M \lambda_K^*\right)\right)}{(V^* - M)\left(2\alpha_R d_V d_K M R^{*2}(V^* - M)^2 \lambda_R^* + (d_K K^* + d_V V^*)^3 (2\alpha_K M K^* \lambda_K^* + \alpha_V (V^* - M)^2 \lambda_V^* \varphi)\right)} \tag{E4}$$

$$\frac{\partial R^*}{\partial V^*} = \frac{2\left(\alpha_R {d_V}^2 M R^{*2}(M - V^*)^3 \lambda_R^* + (d_K K^* + d_V V^*)^3\left(-\alpha_V (V^* - M)^3 \lambda_V^* + \alpha_K K^{*2} M \lambda_K^*\right)\right)}{M(d_K K^* + d_V V^*)(M - V^*)^3 (2\alpha_R d_V R^* \lambda_R^* - g_V (d_K K^* + d_V V^*)^2 \lambda_V^*)} \tag{E5}$$

The sign of equation (*E4*) is unsure but we expect it to be negative as crowberry shares the common area with vegetation. However, it can also be positive because crowberry acts as a "predator" on vegetation with its allelopathic effect. The sign of equation (*E5*) depends on the sign of the last parenthesis of the nominator $\left(-\alpha_V (V^* - M)^3 \lambda_V^* + \alpha_K K^{*2} M \lambda_K^*\right)$, given that the denominator is positive as we have the above-mentioned inequality condition $\frac{\lambda_V^*}{\lambda_R^*} > \frac{2\alpha_R d_V R^*}{g_V (d_K K^* + d_V V^*)^2}$. As vegetation is the feed for reindeer, we expect that $\frac{\partial R^*}{\partial V^*} > 0$. Letting $-\alpha_V (V^* - M)^3 \lambda_V^* + \alpha_K K^{*2} M \lambda_K^* > 0$ and re-arranging, we have the condition for positive numerator $-\frac{\lambda_V^*}{\lambda_K^*} < \frac{\alpha_K K^{*2} M}{\alpha_V (M - V^*)^3}$. To attain a positive denominator the condition is in the opposite with equation (*E1*) that $\frac{\lambda_V^*}{\lambda_R^*} < \frac{2\alpha_R d_V R^*}{g_V (d_K K^* + d_V V^*)^2}$. This implies that the sign of $\frac{\partial R^*}{\partial V^*}$ and $\frac{\partial V^*}{\partial R^*}$ must be the same.

Three implicit functions are obtained from the equilibrium condition of crowberry (equation (15)):

$$\frac{\partial T^*}{\partial K^*} = \frac{2\left(\frac{\alpha_K}{V^* - M} - \frac{\alpha_R {d_K}^2 R^{*2} \lambda_R^*}{(d_K K^* + d_V V^*)^3 \lambda_K^*}\right)}{\varepsilon} \tag{$E6$}$$

The expected sign of $\frac{\partial T^*}{\partial K^*}$ is positive as the resource manager needs to increase the removal effort when crowberry increases. To satisfy this condition, we need $-\frac{\lambda_R^*}{\lambda_K^*} > \frac{\alpha_K (d_K K^* + d_V V^*)^3}{(M - V^*) \alpha_R {d_K}^2 R^{*2}}$.

$$\frac{\partial R^*}{\partial K^*} = \frac{2\left(\alpha_R {d_K}^2 R^{*2} (M - V^*) \lambda_R^* + \alpha_K (d_K K^* + d_V V^*)^3 \lambda_K^*\right)}{(d_K K^* + d_V V^*)(V^* - M)(-2\alpha_R d_K R^* \lambda_R^* + g_2 (d_K K^* + d_V V^*)^2 \lambda_K^*)} \tag{$E7$}$$

As crowberry is a native pest to the husbandry, we expect that $\frac{\partial R^*}{\partial K^*} < 0$. Setting the nominator negative, we need the condition $\frac{\lambda_R^*}{\lambda_K^*} < \frac{\alpha_K (d_K K^* + d_V V^*)^3}{(M - V^*) \alpha_R {d_K}^2 R^2}$, which is always given the negative λ_K^*. To attain a positive denominator, we need $2\alpha_R d_K R^* \lambda_R^* - g_K (d_K K^* + d_V V^*)^2 \lambda_K^* > 0 \leftrightarrow \frac{\lambda_K^*}{\lambda_R^*} < \frac{2\alpha_R d_K R^*}{g_K (d_K K^* + d_V V^*)^2}$ which is always hold. Thus $\frac{\partial R^*}{\partial K^*} < 0$, and from the same calculation that $\frac{\partial K^*}{\partial R^*} < 0$, reflecting the negative impact of crowberry on reindeer stock size. We also have

$$\frac{\partial V^*}{\partial K^*} = -\frac{2M(Mx - V^*)\left(\alpha_R {d_K}^2 R^{*2} (M - V^*) \lambda_R^* + \alpha_K (d_K K^* + d_V V^*)^3 \lambda_K^*\right)}{2\alpha_R d_V d_K M {R^*}^2 (V^* - M)^2 \lambda_R^* + (d_K K^* + d_V V^*)^3 (2\alpha_K K^* M \lambda_K^* + \alpha_V (V^* - M)^2 \lambda_V^* \varphi)} \tag{$E8$}$$

We expect the sign of equation (*E8*) to be negative, thus we need both numerator and denominator to be positive. Then the condition for the numerator is $-\frac{\lambda_V^*}{\lambda_K^*} < \frac{\alpha_K (d_K K^* + d_V V^*)^3}{(M - V^*) \alpha_R {d_K}^2 R^{*2}}$, which then contrasts with the condition for equation (*E6*). For the denominator the last parenthesis needs to be positive, which then leads to $-\frac{\lambda_K^*}{\lambda_V^*} < \frac{\alpha_V (V^* - M)^2 \varphi}{2\alpha_K K^* M}$.

Appendix F: Indirect deductions of the implicit-function theorem

$$\frac{\partial F^*}{\partial V^*}=\frac{\partial F^*}{\partial K}\frac{\partial K}{\partial V^*}<0$$

$$\frac{\partial F^*}{\partial K^*}=\frac{\partial F^*}{\partial R^*}\frac{\partial R^*}{\partial K^*}<0$$

$$\frac{\partial T^*}{\partial R^*}=\frac{\partial T^*}{\partial K^*}\frac{\partial K^*}{\partial R^*}>0$$

$$\frac{\partial R^*}{\partial T^*}=\frac{\partial R^*}{\partial K^*}\frac{\partial K^*}{\partial T^*}>0$$

$$\frac{\partial V^*}{\partial F^*}=\frac{\partial V^*}{\partial K^*}\frac{\partial K^*}{\partial F^*}<0$$

$$\frac{\partial F^*}{\partial T^*}=\frac{\partial F^*}{\partial K^*}\frac{\partial K^*}{\partial T^*}>0$$

$$\frac{\partial T^*}{\partial V^*}=\frac{\partial T^*}{\partial R^*}\frac{\partial R^*}{\partial V^*}>0$$

$$\frac{\partial T^*}{\partial F^*}=\frac{\partial T^*}{\partial R^*}\frac{\partial R^*}{\partial F^*}>0$$

$$\frac{\partial K^*}{\partial F^*}=\frac{\partial K^*}{\partial R^*}\frac{\partial R^*}{\partial F^*}>0$$

$$\frac{\partial V^*}{\partial T^*}=\frac{\partial V^*}{\partial K}\frac{\partial K^*}{\partial T^*}>0$$

Appendix G: The role of reindeer's non-use value in managing crowberry

Table G.1. Differences in the results at equilibrium with and without reindeer's non-use value

	Without reindeer's non-use value		**With reindeer's non-use value**	
	Post-EC	**Adaptive Post-EC**	**Post-EC**	**Adaptive Post-EC**
V^*	4.07 x 10^{10}	5.4 x 10^{10}	2.16 x 10^{10}	4.8 x 10^{10}
R^*	163 722	251 301	234 102	587 627
S^*	92 081	148 000	79 956	229 873
K^*	4.6 x 10^{10}	2.3 x 10^{10}	6.5 x 10^{10}	6.0 x 10^{9}
F^*	--	63	--	147.3
T^*	--	73.1	--	205.3
$\lambda_R{}^*$	3760	3760	3760	3760
$\lambda_V{}^*$	0.013	0.011	0.13	0.05
$\lambda_K{}^*$	- 0.012	- 0.016	- 0.06	- 0.17
$\bar{\varphi}$	0.011	0.014	0.014	0.02
Social welfare (mil NOK)	149.8	220.4	614.32	1 437.3

Incorporation of reindeer non-use value shows more realistic slaughter results in which the slaughter percentage is roughly 35% of the total herd. The non-use value also emphasizes the importance of existence of reindeer in that the herd size in both Post-EC and Adaptive Post-EC scenarios are larger than the results of the same scenarios where non-use value of reindeer is omitted. Especially, in the Adaptive Post-EC scenario, due to reindeer non-use value, more feeding and controlling efforts are invested than for the scenario without reindeer non-use value, leading to a minimal crowberry population.

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10 Paper 4 : Dr. Jekyll and Mr. Hyde – How different ecosystem (dis)services perspectives alter management decisions of a native invasive encroachment

Dr. Jekyll and Mr. Hyde

How different ecosystem (dis)services perspectives alter management decisions of a native invasive encroachment

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Abstract

As a consequence of climate change, the encroachment of the native species *Empetrum nigrum* (crowberry) is exerting multifaceted effects on the Arctic socio-ecological system in Norway. The native invader detrimentally affects the quality of the reindeer grazing land, yet is beneficial for carbon sequestration, i.e. providing both ecosystem services and disservices. Though the Norwegian reindeer husbandry acknowledges the importance of pasture quality, the government has not adopted any quantitative indicator to evaluate the current situation. Employing optimal control in a bioeconomic model of three species – reindeer, vegetation, and crowberry – we explore the effectiveness of three controls: slaughter and feeding of reindeer, and burning crowberry, in the short run (5 years) and long run (30 years). Our study seeks to determine the optimal crowberry burning effort and assess whether incorporating carbon sequestration alters the preferred burning strategy. Our results emphasize the critical role of crowberry burning in rejuvenating vegetation, a key indicator of pasture quality, especially in the long run. Burning crowberry remains optimal when carbon sequestration is included, yet at a lower level than when this value is excluded. We also highlight the incorporation of a salvage value for the palatable pasture, advocating for a balanced approach to burning that optimizes economic net benefit while sustaining pasture quality. Incorporating salvage values into the social welfare function emphasizes both the potential future use and the preservation of the grazing pasture for future generations. Our results suggest that the decision-maker should continue burning crowberry in the long run while taking into account the plant’s carbon sequestration, to maximize social welfare.

Recommendations for Resource Manager

1. Continuously burning crowberry rejuvenates the vegetation and sustains the high biodiversity nutrient-rich pasture for the reindeer husbandry

2. Acknowledging crowberry’s carbon sequestration value is crucial for an overall management strategy that balances its negative and positive impacts to the ecosystem; as this value can shift resource managers' view of the native invasive species from a pest to a beneficial resource.

3. Recognizing vegetation's salvage value will lead to higher crowberry burning efforts, emphasizing long-term pasture sustainability over short-term profits while also bequesting use and non-use values of the pasture to future generations.

4. Securing financial support to cover initial burning costs is essential, especially in the short run to ensure economic feasibility for the herders.

Introduction

The introduction of the ecosystem service (ES) and ecosystem disservice (EDS) concepts provides conceptual frameworks to understand the dynamic interactions, both positive and negative, between species and human beings (Braat & de Groot, 2012; Wu et al., 2021). Accounting for both positive and negative contributions of nature to humans has been researched thoroughly for many ecosystems, and in many cases a species or group of species can provide both positive and negative contributions to society (Shackleton & Shackleton, 2018; Vaz et al., 2017). One example is ES-EDS assessment of urban forests (Escobedo et al., 2011, 2018; Lyytimäki, 2017). Another example is assessment of invasive species, with the invasive red king crab in the Barents Sea being one case. This species impacts negatively the harvest of some traditional Norwegian coastal fisheries, yet the harvested red king crab is highly profitable and has been vital for local communities (Falk-Petersen & Armstrong, 2013; Skonhoft & Kourantidou, 2021). Similarly, the invasion of zebra and quagga mussels in North American aquatic ecosystems has caused substantial ecological disturbances, yet their presence has unexpectedly improved water clarity, which is appreciated by local populace (Davoren & Shackleton, 2021; Finnoff et al., 2006; Leung et al., 2002). One subset of invasive species are the native invasives, which though naturally present in the local ecosystems, due to climate or environmental change possess increasing competitiveness as an invasive species (Carey et al., 2012; Valéry et al., 2009). In this paper we will study one such species, the Arctic evergreen dwarf shrub *Empetrum nigrum* (crowberry).

Crowberry is found to provide both ES and EDS (Bråthen et al., 2007; Pilsbacher et al., 2020). On the one hand, crowberry provides an indirect EDS to human well-being by releasing allelopathic substances that inhibit the growth of neighboring plants, thereby reducing the quality and quantity of available pasture (Gonzalez et al., 2019; Ravolainen et al., 2010). With climate change increasing the spread of crowberry, this allelopathic encroachment poses a direct challenge to the traditional and culturally significant reindeer husbandry of the indigenous Sami people. (Krebs, 2002; Tveraa et al., 2007, 2013). On the other hand, crowberry is found to provide positive carbon sequestration services as this dwarf shrub evergreen species grows its wooden roots deeply and expands horizontally, forming thick wooden layers (Silvola et al., 1979; Silvola & Hanski, 1979; Ylanne et al., 2015). In fact, carbon sequestration services of the local ecosystems has provided arguments against nature exploitation in the region (Directorate, 2023; West et al., 2018). Crowberry encroachment hence could act as a potential carbon sink. Crowberry, reminiscent of the dual nature in Stevenson's "Dr. Jekyll and Mr. Hyde" (1886) exhibits both beneficial and detrimental impacts on its ecosystem, providing critical carbon sequestration services while simultaneously challenging traditional reindeer husbandry through allelopathic encroachment.

In this paper, we investigate the positive and negative impacts of a native invader – *Empetrum nigrum* (crowberry) – on the Norwegian reindeer husbandry. Reindeer husbandry has been the emblematic lifestyle of the Sami people in Norway, mainly carried out in mountain pastures and rangelands from the central to northernmost regions of the country (Ministry of Agriculture and Food, 2017). Preserving the reindeer husbandry by protecting the grazing pasture has been a key objective, which often conflicts with other regional and national industries, from transportation to energy transition and tourism (Eftestøl et al., 2023; Ministry of Agriculture and Food, 2017; Ravna, 2022). As the husbandry is managed via sustainable development of the grazing pasture, the government uses the number of reindeer per grazing area (km^2) as the management indicator (Norwegian Government, 2021, 2023). Under the influence of crowberry, the quality of pasture is declining (Bråthen et al., 2024), potentially leading to future reductions in herd size. However, economic studies that specifically address these changes in pasture quality and their impact on reindeer husbandry are lacking. Besides, to our knowledge, there exists no research on the ecological and economic importance of crowberry's carbon sequestration service in managing the Arctic pasture and landscape.

Besides the potential challenge inflicted by the native invasive crowberry, the husbandry is currently experiencing significant changes due to climate warming and other environmental pressures. Studies show that ecological change in the Arctic will impact the Sami reindeer husbandry in northern Europe (Bråthen et al., 2018; Heggenes et al., 2017). Specifically, an increase in rain-on-snow events in winter due to greater weather volatility leads to pasture lock, causing negative impact on reindeer herds (Albon et al., 2017; Hansen et al., 2019). Many herders have adapted to the pasture lock phenomenon by providing supplementary feeding, though this practice is not considered a sustainable long-term solution as it can alter the herding customs of the Sami people and affect the animals (Helle & Jaakkola, 2008; Horstkotte et al., 2020; Turunen et al., 2016).

Several bioeconomic models for the husbandry have been developed with an aim to provide optimal pasture management and optimal slaughtering decisions (Johannesen et al., 2019; Johannesen & Skonhoft, 2011; Pekkarinen et al., 2015; Pekkarinen, Kumpula, et al., 2022; Tahvonen et al., 2014). Moxnes (1993) developed an age-sex structured continuous-time bioeconomic reindeer-lichen model, focusing on the importance of lichen in winter grazing. Later works by Moxnes et al. (2001), Tahvonen et al. (2014), and Pekkarinen et al. (2015, 2017, 2021; 2022; 2022) include reindeer age-sex structured discrete-time models with various types of diets, particularly ground and arboreal lichens. Furthermore, Pekkarinen et al. (ibid.) first studied the economic and ecological impacts of supplementary feeding on Finnish reindeer husbandry, after this practice was introduced in the 1960s[2]. Their consumer-resource models

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[2] Supplementary feeding is commonly practiced in Finnish reindeer husbandry, regardless of the pasture crisis situation; whereas in Norway, it is conducted only during harsh winters when animals cannot find food naturally (Horstkotte et al., 2020).

depict in much detail the 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. Johannesen et al. (2019) developed a wolf-reindeer bioeconomic model that accounts for intraspecific competition and predation. The authors also incorporated age-sex structure as in previous models but used the total number of grazing animals as a proxy for food scarcity of reindeer. Although this proxy can capture the partial effect of reindeer on pasture, it oversimplifies food competition, which could include exogenous ecological factors constraining reindeer populations such as shifts in vegetation community composition of the grazing pasture (Krebs, 2002).

Acknowledging the gaps in the literature, specifically the lack of habitat incorporation in bioeconomic reindeer models and the limited investigation of ES and EDS of crowberry on reindeer pastures, our study employs optimal control theory to explore the dynamics of vegetation, crowberry, and reindeer under three management controls: slaughtering and feeding reindeer, and burning crowberry. Regarding the third control, there are different ways to manage invasive plant species (such as plowing, plucking, etc.), yet in the case of *E. nigrum*, only burning has been studied[3] (Brathen et al., 2010; Pakeman et al., 2003; Penney et al., 2008).

Our approach, leveraging optimal control theory, not only fills these critical research gaps but also brings to the forefront the decision-making process in reindeer husbandry under climate change. The aggressive allelopathic encroachment of crowberry may be expected to encourage management control; however, the optimal strategy for this control may vary significantly depending on whether the carbon sequestration benefits of crowberry are taken into account in the decision-making process. We define the decision-maker in our study as the

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[3] Though cutting and burning practices for *Empetrum nigrum* (crowberry) are under testing (Tuomi et al., 2022), similar methods have been adopted for the heath of *Calluna vulgaris* (ling or heather) in Norway, and have proved to be effective in removing this drawf shrub in order for other nutrient-rich plants to establish (Calvo et al., 2020; Log, 2020; Måren et al., 2010; Nilsen et al., 2005; Pakeman et al., 2003; Vandvik et al., 2005; Whittaker & Gimingham, 1962).

Department of Reindeer herding (*Avdeling reindrift*, a subdivision of the Directorate of Agriculture), that determines whether it is beneficial to control crowberry, and assess the optimal dynamics of slaughter and feeding of reindeer under crowberry encroachment, and whether acknowledgment of crowberry's carbon sequestration will impact management decisions. In the next section we present a dynamic reindeer-habitat and invasive species control model. Optimal control problems are considered under two scenarios in the theoretical section: 1) when the control to burn crowberry is accounted for (burning scenario), and 2) when carbon sequestration of both palatable vegetation and crowberry are incorporated (carbon scenario). In the numerical application section, we divide the two analytical scenarios into five distinct cases, including a baseline scenario without crowberry burning to assess the impact of crowberry control. The burning and carbon scenarios are each divided into two sub-scenarios, one with and one without a vegetation salvage term describing value of the vegetation at the final time. This allows comparison of optimal management effects when a salvage value of vegetation is incorporated. The final section is left for discussion, in which we emphasize the critical role of incorporating salvage values in decision-making, and the need for a balanced approach that accounts for both short-term and long-term benefits to achieve sustainable reindeer husbandry.

Bioeconomic models

Burning scenario

We propose a three-species model for the Norwegian reindeer husbandry, consisting of one predator, reindeer R, feeding on two vegetation stocks, the palatable vegetation V[4] and the

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[4] Though we do acknowledge that biodiverse vegetation consists of many different plant species, we model one species as the general representative due to similarities in palatability and carbon content (Murguzur et al., 2019).

less palatable and native invasive crowberry K. The former is much preferred by reindeer, as crowberry has much lower nutritional value (Freschet et al., 2010; Hortipedia, 2022; Wright et al., 2004; Zverev et al., 2008). Reindeer is harvested with a controlled slaughter rate (or share) S with $S \in [0, S_{max}]$ with $S_{max} \leq 1$. Growth of the three species is assumed to follow logistic patterns where the two plants share a common carrying capacity M (where the unit is biomass) and carrying capacity of reindeer depends proportionally on the plant populations $d_V V + d_K K$. Furthermore, crowberry provides an ecosystem disservice as it inflicts an allelopathic impact on the palatable vegetation, decreasing growth of vegetation through the allelopathic term φ.

Our model reads:

$$\dot{V} = \alpha_V V \left(1 - \frac{V + \varphi K}{M}\right) - g_V V R \tag{1}$$

$$\dot{K} = \alpha_K K \left(1 - \frac{K}{M - V}\right) - g_K K R - \varepsilon B K \tag{2}$$

$$\dot{R} = (\alpha_R + \beta F) R \left(1 - \frac{R}{d_V V + d_K K}\right) - S R \tag{3}$$

with $\alpha_V, \alpha_K, \alpha_R, g_V, g_K, \varphi, \beta, M, d_V,$ and d_K all positive real numbers. The coefficients $\alpha_V, \alpha_K, \alpha_R$ are the intrinsic growth rates of $V, K,$ and $R,$ respectively. While g_V and g_K are the grazing coefficients of the interaction of reindeer with vegetation and crowberry, respectively, d_V and d_K are coefficients providing the contribution of the two plant populations to the reindeer's carrying capacity. To avoid the effects of extreme weather events which can have cascading effects on the ecosystem and finally on slaughter S, the herders supply artificial feeding F to reindeer (Ballesteros et al., 2013; Horstkotte et al., 2020; Turunen et al., 2016) with β the feeding coefficient. The parameter β represents the effectiveness of the feeding practice, or how susceptible reindeer are to additional feed. This practice is modelled to have a direct additive impact on reindeer intrinsic growth rate $(\alpha_R + \beta F)$. As the supplementary feed is given only under harsh winter conditions in which the animals cannot find enough food, the practice does not alter reindeer carrying capacity nor its grazing limitation, mentioned in the studies of Pekkarinen et al. (2015, 2017, 2021; 2022; 2022). Because of the negative impacts from crowberry K and the feeding effort F on the palatable vegetation V (Bråthen et al., 2018; Gonzalez et al., 2021; Tybirk et al., 2000) , the manager introduces a measure to control the native invasive encroachment. With the removal effort B by burning and the coefficient ε representing the effectiveness of the removal, the manager expects a positive effect on not only the vegetation V but also reindeer population R.

Turning to our management goal, at the final time, T (in years), the manager wants to maintain a discounted value of reindeer described by a salvage term $\theta R(T)$ where $\theta = pe^{-\delta T}$, with p being the current price of one slaughtered reindeer including governmental subsidies, and δ is the societal discount rate. The subsidy is given relative to meat production, and can be seen as a societal willingness to pay for upkeep of Sami culture in Norway, or a cultural value of reindeer and its pasture (Ministry of Agriculture and Food, 2017; Norwegian Government, 2021; Rees et al., 2008). Given the three controls S, F and B, and accounting for the revenues and the costs of reindeer slaughter together with the feeding and burning costs, the decision-maker's objective functional, i.e. the social welfare function, can be described as:

$$max_{S,F,B}\left\{\theta R(T) + V(T) + \int_0^T (pSR - c_0 - c_1 S - c_2 S^2 - c_3 F^2 - c_4 B^2)e^{-\delta t} dt\right\}$$

subject to equations (1), (2), (3) and initial conditions, $V(0) = V_0$; $K(0) = K_0$; $R(0) = R_0$. While c_0, c_1, and c_2 are the fixed costs, linear and quadratic cost coefficients of slaughter, respectively, c_3 is the unit quadratic feeding cost, e.g. of dry feed, and c_4 is the unit cost of the quadratic burning effort. The bounds for the two controls are given by $0 \leq S(t) \leq S_{max}$ and $0 \leq F(t) \leq F_{max}$. We assume that the slaughter cost has both linear and quadratic impact on the profit function, which is in line with the cost functions of other primary industries, such as fisheries (Hanson & Ryan, 1998; Koenig, 1984; Sancho & Mitchell, 1977). Using Pontryagin's Maximum Principle, we introduce the corresponding three adjoint functions, with these final time (transversality) conditions; $\lambda_K(T) = 0$ while $\lambda_V(T) = \frac{\partial V(T)}{\partial V} = 1$ and $\lambda_R(T) = \frac{\partial \theta R(T)}{\partial R} = \theta = pe^{-\delta T}$. While the herding profit (π) results from the gain in slaughtered reindeer, pSR less the total cost from different controls, we assume that at the final time T there exists a vegetation salvage term $V(T)$. The reason for including terminal time value term for vegetation, $V(T)$, also known as the payoff term or scrap value (Lenhart & Workman, 2007), is to acknowledge a type of salvage value of the grazing pasture at the final time T, which has so far not been addressed in the bioeconomic literature of reindeer husbandry. We set the coefficient for $V(T)$ equal to 1 as we could not find any studies about this type of value for the tundra vegetation in Norway. This may be a high value, yet is chosen for illustrative purposes as will be shown later. In the numerical section below, we compute two cases where only one includes the vegetation salvage term, to compare the impact on the optimal solutions.

The current value Hamiltonian then reads:

$$H_1 = pSR - c_0 - c_1S - c_2S^2 - c_3F^2 - c_4B^2 + \lambda_V\left[\alpha_V V\left(1 - \frac{V + \varphi K}{M}\right) - g_V VR\right]$$
$$+\lambda_K\left[\alpha_K K\left(1 - \frac{K}{M - V}\right) - g_K KR - \varepsilon BK\right] + \lambda_R\left[(\alpha_R + F)R\left(1 - \frac{R}{d_V V + d_K K}\right) - SR\right]$$

with the subscript 1 denoting the burning scenario. Concavity conditions for the maximization problem are satisfied as $\frac{\partial^2 H_1}{\partial S^2} = -2c_2$, $\frac{\partial^2 H_1}{\partial F^2} = -2c_3$, and $\frac{\partial^2 H_1}{\partial B^2} = -2c_4$. The first-order conditions (FOC) of the maximization of H_1 w.r.t. two controls are:

$\frac{\partial H_1}{\partial S} = pR - c_1 - \lambda_1 R - 2c_2S = 0$ on the interior of the control set, which then gives

$$S = \frac{(p - \lambda_R)R - c_1}{2c_2} \; or \; \lambda_R = p - \frac{c_1 + 2c_2S}{R} \qquad (4)$$

and $\frac{\partial H_1}{\partial F} = -2c_3F + R\left(1 - \frac{R}{d_VV + d_KK}\right)\beta\lambda_R$ on the interior of the control set, thus

$$F = \frac{R(d_VV + d_KK - R)\beta\lambda_R}{2c_3(d_VV + d_KK)}\ . \tag{5}$$

Equations (4) indicate that the stock size R corresponds linearly with the slaughter rate S and non-linearly with reindeer's shadow price λ_R on the interior of the control set. We expect reindeer's shadow price to be positive, which then leads to

$$p - \frac{c_1 + 2c_2S}{R} > 0 \leftrightarrow R > \frac{c_1}{p} + \frac{2c_2}{p}S \tag{6}$$

Furthermore, solving equation (5) for V and inserting λ_R from (4), we get

$$V = \frac{-2c_3FR}{d_V\big(2c_3F + \beta(c_1 - pR + 2c_2S)\big)} + \frac{R - d_KK}{d_V} \tag{7}$$

The first term of equation (7) shows a negative relationship between V and feeding effort F, given that $2c_3F + \beta(c_1 - pR + 2c_2S) > 0$ since we have $pR - c_1 - 2c_2S > 0$ (inequality condition (6) rearranged). Given this condition is satisfied, supplementary feeding F is therefore beneficial only to the reindeer stock, not to the palatable vegetation. The FOC of the third control is

$$\frac{\partial H_1}{\partial B} = 0 \ \leftrightarrow\ B = -\frac{\varepsilon K\lambda_K}{2c_4}\ \ or\ \lambda_K =\ -\frac{2c_4B}{\varepsilon K} \tag{8}$$

Equation (8) implies that the shadow price of crowberry is negative. Besides, not only will higher burning effort level decrease crowberry's shadow price but also there is a positive correlation between this native invader and its shadow price. This reflects the unfavourability of the invasive species in the objective functional of the manager.

The three adjoint equations read:

$$\dot{\lambda}_V - \delta\lambda_V = -\left[\frac{(\alpha_R+\beta F)d_V\lambda_R R^2}{(d_V V + d_K K)^2} - \frac{\alpha_K K^2\lambda_K}{(M-V)^2} + \lambda_V\left(\alpha_V\left(1-\frac{V+\varphi K}{M}\right) - \frac{\alpha_V V}{M} - g_V R\right)\right] \quad (9)$$

$$\dot{\lambda}_K - \delta\lambda_K = -\left[\frac{(\alpha_R+\beta F)d_K\lambda_R R^2}{(d_V V + d_K K)^2} + \lambda_K\left(\alpha_K\left(1-\frac{K}{M-V}\right) - \frac{\alpha_K K}{M-V} - g_K R - \varepsilon B\right) - \frac{\alpha_V\lambda_V V\varphi}{M}\right] \quad (10)$$

$$\dot{\lambda}_R - \delta\lambda_R = -\left[pS - g_K K\lambda_K - g_V\lambda_V V + \lambda_R\left((\alpha_R+\beta F)\left(1-\frac{R}{d_V V + d_K K}\right) - \frac{(\alpha_R+\beta F)R}{d_V V + d_K K} - S\right)\right] \quad (11)$$

In optimal control with a finite time horizon, equilibrium might not be reached in the short term. However, assuming the system is going to a stable equilibrium, we can calculate the expression of vegetation's shadow price by setting $\dot{\lambda}_V = 0$, substituting λ_R and λ_K from equations (4) and (8) and solving for λ_V:

$$\lambda_V = \frac{\dfrac{d_V R(\alpha_R+\beta F)(pR-c_1-2c_2S)}{(d_V V + d_K K)^2} + \dfrac{2\alpha_K c_4 KB}{\varepsilon(V-M)^2}}{g_V R + \delta + \dfrac{\alpha_V(2V+\varphi K-M)}{M}} \quad (12)$$

All terms in the numerator are positive given inequality condition (6) holds. For the denominator to be positive, and thereby $\lambda_V > 0$, we need $g_V R + \delta > \frac{\alpha_V(2V+\varphi K-M)}{M}$.

We obtain three golden rules at equilibrium from three adjoint equations by setting $\dot{\lambda}_V = \dot{\lambda}_K = \dot{\lambda}_R = 0$, substituting λ_R and λ_K from equations (4) and (8) and solving for δ:

$$\delta = \left[\alpha_V\left(1-\frac{(2V+\varphi K)}{M}\right) - g_V R\right] + \frac{\big((\alpha_R+\beta F)d_V R\big)(pR-c_1-2c_2S)}{\lambda_V(d_V V + d_K K)^2} + \frac{2\alpha_K c_4 BK}{\varepsilon\lambda_V(M-V)^2} \quad (13)$$

$$\delta = \left[\alpha_K\left(1-\frac{2K}{M-V}\right) - g_K R - \varepsilon B\right] + \frac{\varepsilon K}{2c_4 B}\left[\left(\frac{\lambda_V\alpha_V\varphi V}{M} - \frac{\big(d_K R(\alpha_R+\beta F)\big)(pR-c_1-2c_2S)}{(d_V V + d_K K)^2}\right)\right] \quad (14)$$

$$\delta = \left[(\alpha_R+\beta F)\left(1-\frac{2R}{d_V V + d_K K}\right) - S\right] + \frac{\left[pS - (\lambda_V g_V V - \frac{2c_4 B}{\varepsilon}g_K)\right]R}{pR-c_1-2c_2S} \quad (15)$$

The golden rules (also known as rate of return equations) of the three species describe the balance between the required or market rate of return (the left-hand side (LHS)) and the expected rate of return (the right-hand side (RHS)) of these species. The required rate of return, or the discount rate of society, needs to be equal to the marginal growth rate of each species (the square parenthesis in each equation) plus the shadow price adjusted bioeconomic interactions among the three species.

Focusing on the income source from reindeer slaughter, the second term on the RHS of (15), one unit increase in price p enlarges the numerator by SR and λ_V (see (12)), and the denominator by an amount of R. With $S \in [0,1]$, a higher unit price will in general decrease the required rate of return of reindeer as the term pSR in the numerator is always smaller than pR in the denominator, and with an increase in λ_V, the change in the numerator is always smaller than that of the denominator, reducing the RHS. Hence, to keep the constant required rate of return (i.e. equal to the discount rate), an increase in reindeer marginal growth rate is required. The adjustment can, for example, be a decrease in slaughter rate S or an increase in the feeding effort F, *ceteris paribus*. Due to the complexity of the feedback loops between state, control, and adjoint variables, it is difficult to analytically determine how changes in the burning control B leads to changes in other variables.

Carbon scenario

Accounting for carbon sequestration can be expected to change the optimal solution of the maximization problem, as the objective functional now includes an indirect use value from both plant types. Given the carbon price is high enough, the decision-maker might not burn crowberry as this species contains a carbon percentage substantially exceeding that of other palatable plants (Murguzur et al., 2019). We assume that the carbon sequestration capacity in both vegetative populations follows non-linear concave functions (Thomas & Martin, 2012). Thus, we choose the logarithmic function for carbon sequestration of both plants (Thomas & Martin, 2012; Vondolia et al., 2020), in which crowberry sequesters more carbon than the vegetation (Murguzur et al., 2019)[5]. With b_V and b_K being the wood biomass conversion rates of V and K, respectively, and p_2 is the carbon price per unit biomass of the plants, we have the objective functional, or the social welfare function including carbon sequestration, which is desired maximized:

$$max_{S,F,B} \left\{ \theta R(T) + V(T) + \int_0^T (pSR + p_2(b_V \ln(V) + b_K \ln(K)) - c_0 - c_1 S - c_2 S^2 - c_3 F^2 - c_4 B^2) e^{-\delta t} dt \right\}$$

subject to similar initial and first-order conditions of the burning scenario with 3 controls. This then gives the current value Hamiltonian:

$$H_2 = pSR + p_2(b_V \ln(V) + b_K \ln(K)) - c_0 - c_1 S - c_2 S^2 - c_3 F^2 - c_4 B^2 + \lambda_V \left[\alpha_V V \left(1 - \frac{V + \varphi K}{M}\right) - g_V V R \right] + \lambda_K \left[\alpha_K K \left(1 - \frac{K}{M - V}\right) - g_K K R - \varepsilon B K \right] + \lambda_R \left[(\alpha_R + \beta F) R \left(1 - \frac{R}{d_V V + d_K K}\right) - SR \right]$$

with subscript 2 denoting the carbon scenario. The adjoint equation of reindeer is similar to the above scenario, but the two adjoint equations of the vegetation and crowberry change:

$$\dot{\lambda_V} - \delta \lambda_V = -\left[\frac{\boldsymbol{b_V p_2}}{\boldsymbol{V}} + \frac{(\alpha_R + \beta F) d_V \lambda_R R^2}{(d_V V + d_K K)^2} - \frac{\alpha_K K^2 \lambda_K}{(M - V)^2} + \lambda_V \left(\alpha_V \left(1 - \frac{V + \varphi K}{M}\right) - \frac{\alpha_V V}{M} - g_V R \right) \right] \quad (16)$$

$$\dot{\lambda_K} - \delta \lambda_K = -\left[\frac{\boldsymbol{b_K p_2}}{\boldsymbol{K}} + \frac{(\alpha_R + \beta F) d_K \lambda_R R^2}{(d_V V + d_K K)^2} + \lambda_K \left(\alpha_K \left(1 - \frac{K}{M - V}\right) - \frac{\alpha_K K}{M - V} - g_K R - \varepsilon B \right) - \frac{\alpha_V \lambda_V V \varphi}{M} \right] \quad (1$$

with the changes in bold.

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[5] This is the same reasoning as for crowberry having lower nutrition and not being preferred by reindeer, as studies have demonstrated that there is a strong correlation between growth rate and nutritional content of plants.

A stable state is assumed, and the golden rule of reindeer is similar to the burning scenario. Substituting λ_R and λ_K from equations (4) and (8), the golden rules from two adjoint equations of the two plant species read:

$$\delta = \left[\alpha_V\left(1 - \frac{(2V + \varphi K)}{M}\right) - g_V R\right] + \frac{d_V R(\alpha_R + \beta F)(pR - c_1 - 2c_2 S)}{\lambda_V (d_V V + d_K K)^2} + \frac{2c_4 \alpha_K B K}{\lambda_V (M - V)^2} + \frac{\boldsymbol{b_V p_2}}{\boldsymbol{V \lambda_V}} \quad (18)$$

$$\delta = \left[\alpha_K\left(1 - \frac{2K}{M - V}\right) - g_K R - \varepsilon B\right] + \frac{\varepsilon K}{2c_4 B}\left[\left(\frac{\lambda_V \alpha_V \varphi V}{M} - \frac{\big(d_K R(\alpha_R + \beta F)\big)(pR - c_1 - 2c_2 S)}{(d_V V + d_K K)^2}\right) - \boldsymbol{b_K p_2}\right] \quad ($$

Incorporation of carbon sequestration impacts optimal management of both plant species (parts in bold). The optimal vegetation shadow price in this scenario is

$$\lambda_V = \frac{\frac{\boldsymbol{b_V p_2}}{\boldsymbol{V}} + \frac{d_V R(\alpha_R + \beta F)(pR - c_1 - 2c_2 S)}{(d_V V + d_K K)^2} + \frac{2\alpha_K c_4 K B}{\varepsilon (V - M)^2}}{g_V R + \delta + \frac{\alpha_V (2V + \varphi K - M)}{M}} \quad (20)$$

where the term in bold is the increase in shadow price of vegetation due to the carbon sequestration, i.e. a higher carbon price p_2 and biomass conversion rate of vegetation b_V will increase vegetation shadow price.

Regarding crowberry (equation 19), accounting for carbon price will decrease crowberry's expected rate of return by an amount of $\frac{b_K p_2 \varepsilon K}{2c_4 B}$. This implies the decision-maker might optimally decrease the burning effort B or have fewer reindeer R. Decreasing B will increase the marginal production of crowberry (the first square parenthesis of (19)) and increase the term $\frac{\varepsilon K}{2c_4 B}$ while decreasing the vegetation shadow price (see equation (20)). Decreasing R will provide a similar effect on crowberry's marginal production and decrease the term $\frac{\big(d_K R(\alpha_R + \beta F)\big)(pR - c_1 - 2c_2 S)}{(d_V V + d_K K)^2}$. Therefore, the optimal crowberry burning effort in the carbon scenario is smaller than in the burning scenario.

Data

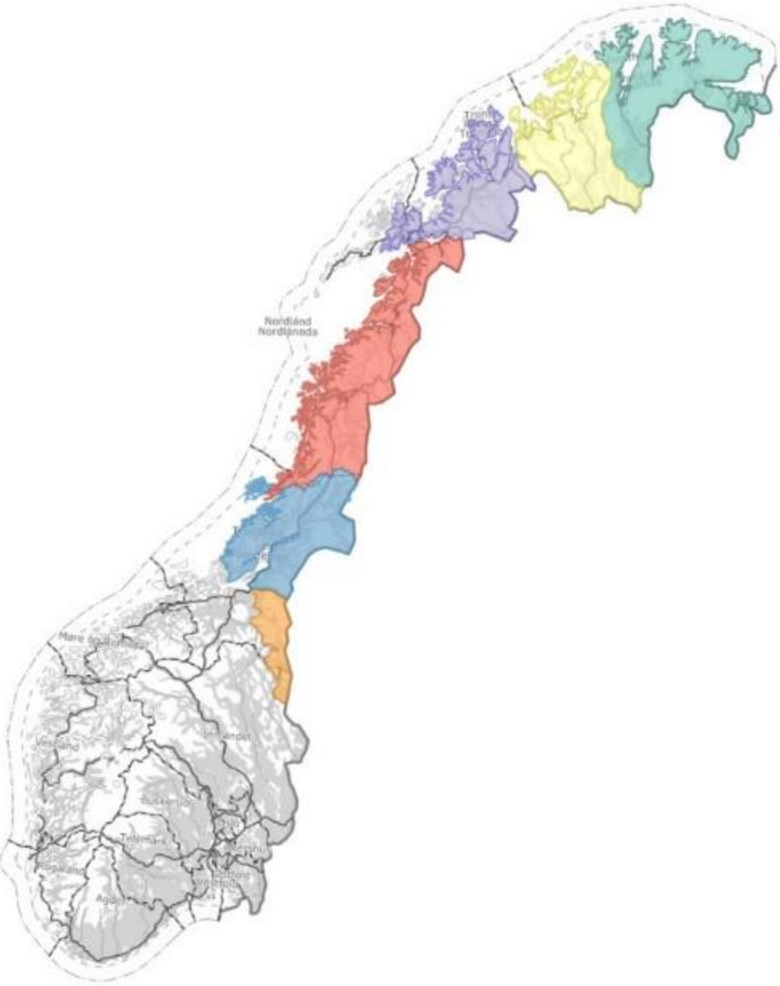

Figure 1: Total defined grazing pasture of the Norwegian reindeer husbandry. Names of the counties from north to south: East Finnmark, West Finnmark, Troms, Nordland, Nord-Trøndelag, and South-Trøndelag and Hedmark. Source:(Agriculture Directorate, 2022b)

Calculated and chosen values for all parameters are listed in Table A.1, Appendix A. The intrinsic growth rates of vegetation and reindeer are adopted from previous studies on the same ecosystem, with growth rate of vegetation α_V equals 0.6 while for reindeer α_3 is 0.7, in all cases. (Moxnes, 1993; Skonhoft et al., 2010). As mentioned, crowberry grows more slowly than the palatable vegetation (Hortipedia, 2022; Wright et al., 2004), hence crowberry intrinsic growth rate α_K is set to one-third of that of vegetation. The carrying capacity of vegetation and crowberry are calculated as 1.2 kg of biomass per square meter (Bråthen & Lortie, 2015), multiplied by the total area of the grazing pasture (Figure 1). In total, the whole carrying capacity of the area M is $8.7 * 10^{10}$ kg biomass[6].

One reindeer consumes 1-10 tonnes of biomass per year (Bakka et al., 2021; White & Trudell, 1980), equivalent to a biomass amount of $g_V V + g_K K$. Due to dietary preferences of reindeer, i.e. they only graze crowberry in the end of winter when other palatable plants have not grown after snowmelt, and also because of the unpalatability of crowberry[7], we choose $g_V = 8 * 10^{-7}$ given the magnitude of V, while $g_K = 1 * 10^{-8}$. Following the same reasoning, the conversion coefficients of vegetation d_V and crowberry d_K into reindeer carrying capacity are also tuned to fit the reindeer population in recent years, with $d_V > d_K$ (Norwegian Government, 2021). The allelopathic rate φ was set to 0,8 after testing the differences in crowberry density in several regions from 2003 to 2020, as described by a dataset in Tuomi et al. (2022). We fit different φ values in the baseline scenario until we got the most realistic increase in crowberry density. Crowberry biomass in 2003 and 2020 are chosen as the initial and final points (Tuomi et al., 2022). The initial number of reindeer $R(t_0)$ was set to 230,000, following governmental data from 2021 (Norwegian Government, 2021), while $V(t_0)$ accounts for only 40% of the total carrying capacity, leaving the rest for crowberry (Tuomi et al., 2022).

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[6] The officially designated grazing area for Norwegian reindeer husbandry, covering roughly 40% of the country or 147,000 km² (Agriculture Directorate, 2022), doesn't account for longstanding environmental and artificial pressures that have reduced this area over the years (Riseth & Tømmervik, 2017; Stoessel et al., 2022; van Rooij et al., 2023). For example, research in the Kvalsund municipality in Finnmark, where reindeer herding is key to the local economy and culture, shows that the true available grazing land is just 54% of the designated pasture (Eira et al., 2020). Given these challenges, we estimate that only about half of the designated area is actually available for grazing.

[7] Total vegetation biomass is quantified in kilograms with the magnitude of 10^{10} (Table 2). Given this scale, we calculate the amount of biomass consumed per reindeer $\frac{\partial(g_V VR + g_K KR)}{\partial R} = g_V V + g_K K$, which satisfies realistic ecological assumptions (Bakka et al., 2021; White & Trudell, 1980)

The price per slaughtered reindeer p was calculated from reported data from 2020, by dividing total revenue, including some government subsidies and compensations, by total slaughtered reindeer numbers (Norwegian Government, 2021). Other subsidies in the shape of economic compensation for lost reindeer were not included. The coefficients for the slaughter costs, c_0, c_1 and c_2 were estimated using the ordinary least squares method on available cost data from the annual reports of the husbandry from 2004 to 2021, provided by the Ministry of Agriculture (Agriculture Directorate, 2023). We use the total cost as the dependent and slaughter share as the independent variable, for fitting the slaughter coefficients[8]. We acknowledge that though the actual slaughter cost of reindeer in itself is minimal compared to other herd maintenance costs such as administration, transportation, etc., we assume that all the costs in this semi-domesticated husbandry contribute to the most important income source – revenue from slaughter. Regression using linear and quadratic cost functions are not statistically significant, so we let $c_1 = 0$ and only regress the quadratic cost function. From Table 1, the results are statistically significant at 1% and 5%; and given the sign of the coefficients, the cost curve is a non-linear convex function. We choose $S_{max} = 0{,}7$, as the actual maximum slaughter rate of a herd is 70% in many areas, while the average slaughter rate is around 40% of the annual herd size (Norwegian Government, 2012, 2021, 2023).

Table 1: Slaughter cost coefficients in quadratic regression (unit: NOK)

Coefficients	Estimate	Standard Error	P-value
c_0	185×10^6 **	$5{,}37 \times 10^7$	0,00387
c_2	$1\,027 \times 10^6$ *	$4{,}73 \times 10^8$	0,04761

** and * significant at 1 and 5% level, respectively.

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[8] We omit two data points in two years, 2018 and 2021, since the total costs are extremely high while the slaughter share is small.

Since there is no literature on the cost of either supplemental feeding or crowberry treatment in Norway, we base our costs on communication with herders. For the feeding cost we apply the input costs of dry feed, on average 6 NOK/ kilogram, making the feeding unit cost c_3 equal to 6 million NOK per thousand tonnes. The number is relatable to other studies of supplementary feeding in Finnish reindeer husbandry where the cost per kilogram dry feed was 0,4 Euro, roughly 4,2 NOK, in 2015 (Pekkarinen et al., 2015). As the practice of burning crowberry is still being tested, there exists no data for the burning cost c_4. Assuming that the unit of controlling effort is number of burning days per year, we use an estimate of $c_4 = 3500$ NOK as the labour cost for a 12-hour working day. Thus, we choose $F_{max} = 10$ (thousand tonnes dry feed) and $B_{max} = 365$ (days, with only one person working per day). The value for B_{max} can be increased more days or more than one person to burn crowberry efficiently yearly, if it is necessary. For this study, we calibrate the values for ε and β, in which $\varepsilon = 0$ is chosen for the baseline scenario (no burning) and $\varepsilon = 10^{-3}$ is chosen for other scenarios, while $\beta = 10^{-1}$ for all scenarios.

Regarding carbon sequestration parameters, we tune the b_V and b_K coefficients following a recent study of carbon percentage in vegetation and crowberry (Murguzur et al., 2019). For the carbon storage function we choose $b_V = 1{,}6 * 10^9$ and $b_K = 2 * 10^9$ so that the carbon biomass for both plant species follows the study of Murguzur et al. (2019). The carbon price p_2 is set to 0,4 NOK/ kilogram carbon after adjustment of inflation on the data of Vondolia et al. (2020).

Dynamic numerical solutions are solved using the Runge-Kutta Four method in MATLAB, while numerical results for equilibria of different scenarios are calculated in Mathematica. Among the three scenarios (baseline, burning, and carbon), the latter two are computed with two cases, one with and one without the vegetation salvage value term.

Numerical results

We demonstrate 5 scenarios, including the baseline scenario (no crowberry burning control), and the burning and carbon scenarios, each divided into two cases, with or without the vegetation salvage term $V(T)$. The baseline scenario is included to test whether the crowberry burning control is effective. The question of whether burning crowberry is necessary for sustainable grazing, and if so, what level of burning effort is optimal, is answered after comparing the baseline and two cases of the burning scenario (with and without vegetation salvage term $V(T)$).

To burn or not to burn – comparing the baseline and burning scenario

Due to the additional burning cost and the complex dynamics of the modelled socio-ecological system, it could be beneficial to know whether it is profitable to burn crowberry in the short run (5-year period), or whether the burning measure is only optimal in the longer run, in order to achieve a sustainable pasture development (for example in a 30-year period).

Comparing the baseline and the burning scenario in the short run (5 years), without vegetation salvage value $V(T)$ (Figure 2), crowberry decreases approximately 20% but then increases again in the latter half of the time period. In the beginning, some effort is required to control the native invader, yet the control diminishes through time. Although slaughtering reaches its maximum 70% level of the herd in both scenarios, the positive impact of burning on the optimal reindeer herd size and vegetation stock is shown already after 3 years. There is no substantial difference in the dynamic of feeding or the discounted herding profit in the baseline scenario and the burning scenario without $V(T)$ (Table 2)[9].

Incorporating a vegetation salvage term $V(T)$ in the objective functional illustrates the difference between the baseline and burning scenario. In the short run (Figure 2), a maximum level of burning effort is required such that the crowberry stock decreases severely. Presumably, this is due to the vegetation salvage term $V(T)$ dominating the optimal slaughter control S^*, decreasing the slaughter and thereby the herding profit, in the burning scenario. This decline in optimal slaughter leads to a much larger reindeer herd size, which dampens the optimal vegetation stock. The social welfare in the burning scenario with $V(T)$ is higher than that of either the scenarios of no $V(T)$ or no burning (baseline scenario) (as the total social welfare of the burning scenario with $V(T)$ equals $-8{,}72 + 24\,175 = 24\,166{,}28$ million NOK[10]). Nonetheless, comparing solely the herding profit in the short run, although crowberry can be controlled either slightly or strictly, the pasture crisis still remains while the profit gain is minimal, or even decreasing.

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[9] Low discounted herding profit in the short run reflects the current economic structure of reindeer husbandry in Norway, where substantial governmental subsidies are critical for the sector's viability. The annual reports reveal that, absent these subsidies, the husbandry industry would incur significant losses (Agriculture Directorate, 2022). This economic reality is primarily due to the substantial labor costs associated with reindeer husbandry, which significantly outweigh the revenue derived from meat sales.

[10] The reason for a negative discounted herding profit is due to the short run impact of a large $V(T)$.

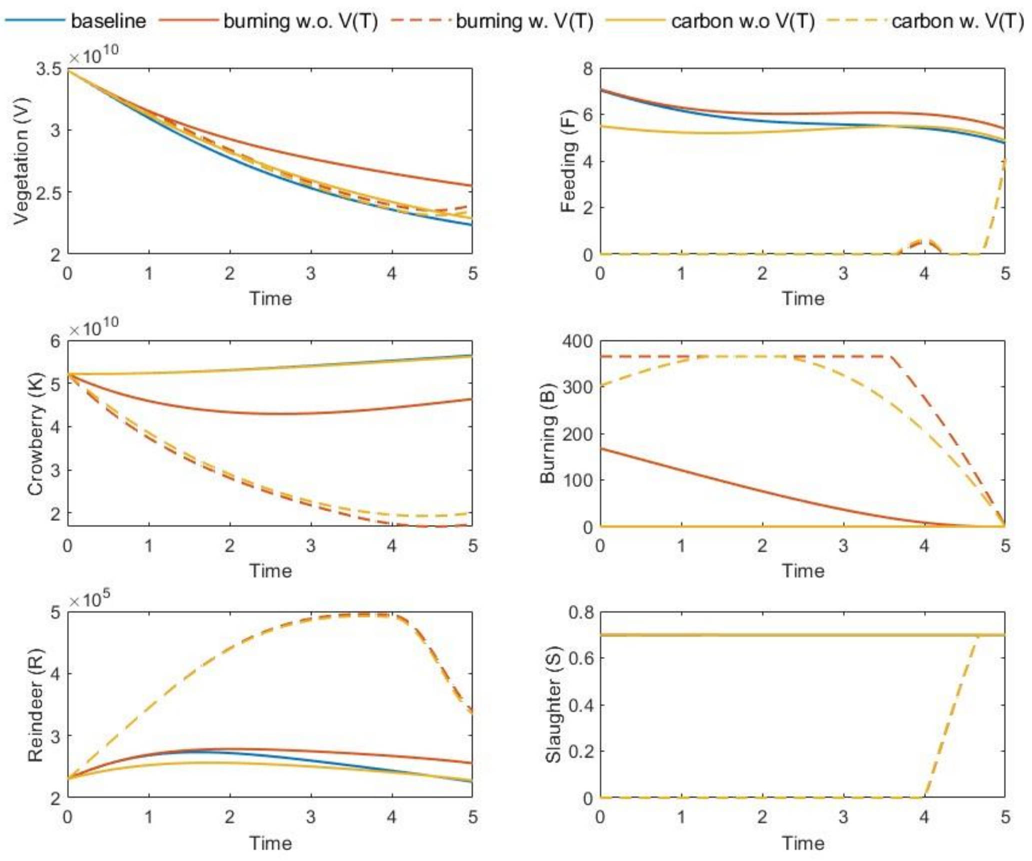

Figure 2: Optimal dynamics of all scenarios in 5 years

To assess the long-run effects, we turn to the 30-year simulation, and comparing between the baseline scenario and the burning scenarios without $V(T)$, the difference in the herding profits is substantial, as now the profit in the baseline scenario is much smaller than for the other scenarios. The long-run slaughter and burning trajectories are, nevertheless, similar to the dynamics in the short run, though the slaughter percentage of the baseline scenario decreases non-linearly; which is as expected since without burning, both optimal vegetation stock and reindeer herd shrinks.

Regarding the long run burning scenario with $V(T)$, only trajectories of the reindeer herd and slaughter effort are different from those in the short run. The peaks in many trajectories at the end-time are caused by the vegetation salvage value, as higher λ_V at the end $(\lambda_V(T) = 1)$ forces the slaughter effort to decrease abruptly, thus sharply increase R and decrease V from year 25 (Figure 3). Nonetheless, in practice this sharp jump in the end can be ignored as the husbandry is expected to continue in many centuries to come.

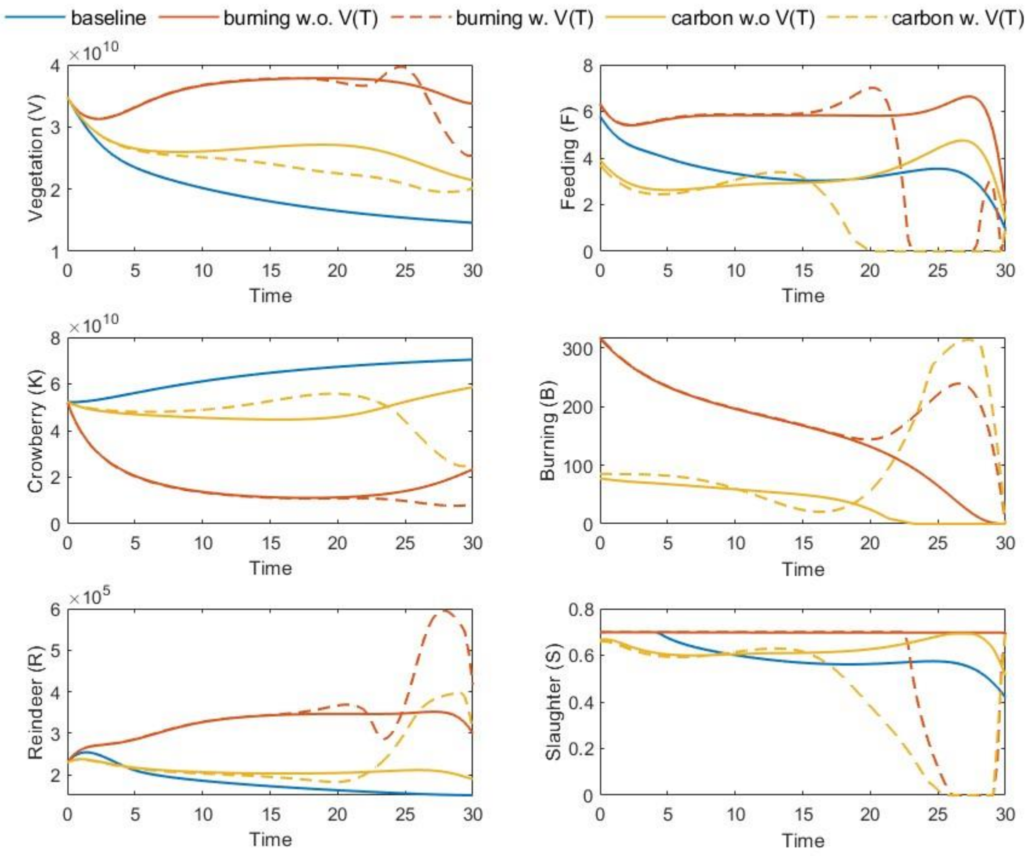

Figure 3: Optimal dynamics of all scenarios in 30 years

Comparing the discounted herding profits between three scenarios (baseline, burning with, and burning without $V(T)$), in the short run the decision-maker should not consider burning crowberry as it yields too little profit. In other words, 5 years are not enough for the burning practice to become profitable. Nevertheless, if the decision-maker does not control the native invader early, in long-run the reindeer stock will decline. Additionally, for a sustainable development of the husbandry, the decision-maker should burn crowberry in the long run if including the pasture's salvage value as not only the pasture can provide future optinal and bequest values but the total social welfare is also equal to $124{,}89 + 25\,307 = 24\,431{,}89$ million NOK (Table 2). Furthermore, regarding the dynamics of crowberry biomass in the burning scenario without $V(T)$, at the final time in both the short and long run, the uplifting tail of the trajectory can easily be noticed. This signals that after ceasing the burning process, crowberry might regrow and bring back the pasture crisis after the terminal time. Thus, accounting for $V(T)$ at final time re-emphasizes the necessity of the burning measure (reflecting by the big jump in burning at the tail-end), preventing the re-encroachment of the native invader.

Table 2: Discounted profit and other values in different scenarios

Scenarios		**Profit (π) and vegetation's salvage value**		**Crowberry's carbon sequestration value**	
		5 years Mil. NOK	**30 years** Mil. NOK	**5 years** Mil. NOK	**30 years** Mil. NOK
Baseline scenario		$\pi = 5{,}66$	$\pi = 14{,}77$		
Burning scenario	No $V(T)$	$\pi = 5{,}68$	$\pi = 164{,}94$		
	With $V(T)$	$\pi = -8{,}72$ $V(5) = 24\ 175$	$\pi = 124{,}89$ $V(30) = 25\ 307$		
Carbon scenario	No $V(T)$	$\pi = 5{,}48$	$\pi = 86{,}13$	437	9 073
	With $V(T)$	$\pi = -7{,}35$ $V(5) = 23\ 688$	$\pi = 50{,}73$ $V(30) = 20\ 584$	426	9 167

To burn or not to burn with carbon (comparing all scenarios)

In the short run without $V(T)$ (Figure 4), carbon price dominates the burning effort in the carbon scenario, as it switches the sign of crowberry's shadow price from negative to positive, thus implying the importance of the native invader in the social welfare function. Trajectories of the two plant species follow similarly those of the baseline scenario (no burning), while the reindeer population is lowest among three scenarios. The reason being that as both plant species, especially crowberry, provide significant carbon sequestration value for society, causing the decision-maker to decrease supplementary feeding for reindeer. This is reflected further in the dynamics of three species. Our hypothesis of how carbon sequestration incorporation decreases crowberry burning and impacts on the dynamics of the other variables is not reflected clearly in 5 year's time, though in 30 years the hypothesis is confirmed (Figure 3). Furthermore, with the carbon sequestration value, it is optimal not to burn crowberry in the short run without $V(T)$ as the total social welfare is $5,48 + 437 = 442,48\, million\, NOK$, though the herding profit is smaller than that of the baseline scenario.

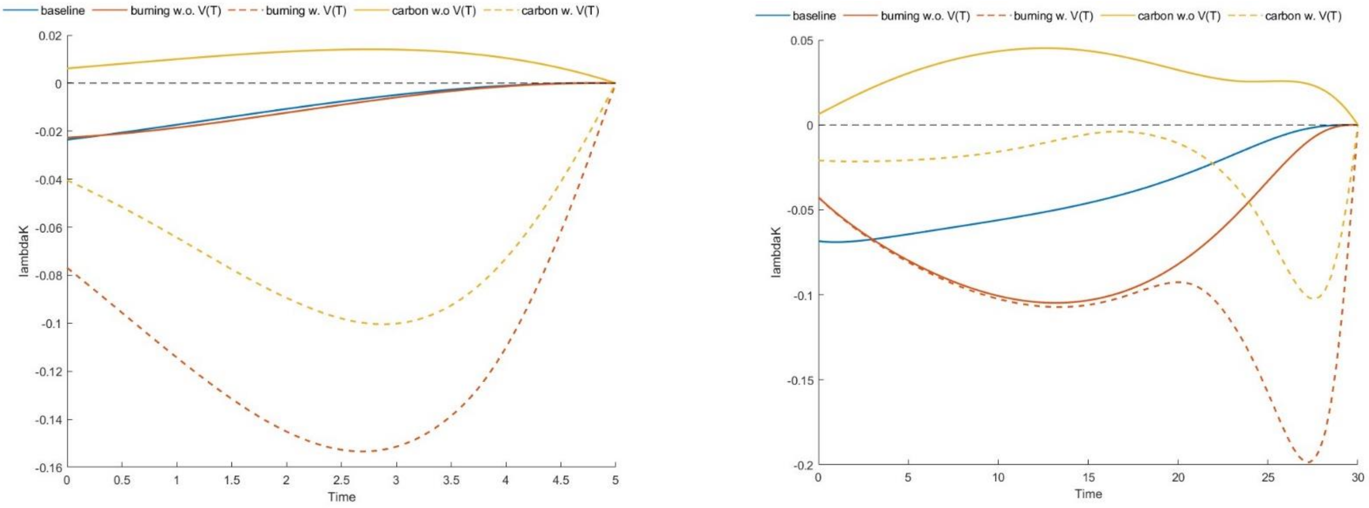

Figure 4: Optimal dynamics of crowberry's shadow price in all scenarios in 5 and 30 years. The horizontal black dashed line at $\lambda_K = 0$ denotes the zero level, indicating points where the shadow price switches from negative to positive values in the carbon scenario without $V(T)$.

In the long run, the trajectories of the state variables of the carbon scenario lie between the trajectories of the baseline and burning scenarios. This indicates that as crowberry has high carbon biomass conversion rate and despite the carbon market price, it is still optimal to burn crowberry, though using less effort than in the burning scenario. The dynamics of the crowberry shadow price follow to a large extent those in short-run (Figure 4). Though in the two former scenarios, crowberry's shadow price is always negative, while in the carbon scenario without $V(T)$, λ_K is positive. Incorporating carbon sequestration brings higher social welfare than the burning scenario $(86{,}13 + 9\,073 = 9\,159{,}13\ million\ NOK)$ (Table 2).

Studying 5 and 30 years separately, with or without the vegetation salvage value $V(T)$, the dynamics of all variables in the burning and carbon scenarios are somewhat similar, and the social welfare from carbon is nearly equal. One exception is the negative sign of λ_K in the carbon scenario in the long run, showing that if the vegetation's salvage value term is included, then the shadow price of the native invader is less than zero. It is, furthermore, interesting that in the last 10 years, the optimal burning effort of the carbon scenario with $V(T)$ is higher than that of the burning scenario. Carbon sequestration increases the value of both plant species, especially crowberry, leading to less reindeer slaughter and feeding effort. The discounted profit and social welfare results clearly indicate that in the short run, it is nevertheless profitable to control the native invader. Total social welfare from reindeer herding when $V(T)$ is acknowledged in the carbon scenario equals to $-7{,}35 + 23\,688 = 23\,680{,}65$ million NOK. The final-time value of vegetation and the welfare from carbon sequestration are much larger than the herding profits from slaughtering reindeer, especially in the long run. The discounted welfare results from carbon sequestration are nearly the same in the short and long run, with or without $V(T)$.

Overall, the results point out that regardless of vegetation scrap value, it is profitable to burn crowberry even when carbon is accounted for. Comparing to the two cases of the burning scenario, the reason why the herding profit in the carbon scenarios is higher than without carbon is because the carbon sequestration value dampens optimal burning effort, leading to smaller total burning costs.

Sensitivity analysis at the terminal point is conducted and shown in the Appendix. Overall, the model is largely robust to 10% changes in parameters.

Discussion

The perspective of the decision-maker plays a critical role in natural resource management, particularly in the decision of whether or not both disservices and services of a resource should be evaluated comprehensively. Including vegetation salvage value in the social welfare function leads to greater crowberry burning, which proves to be profitable for reindeer herders only in the long run. When the perspective is shifted to additionally including carbon sequestration value, crowberry is treated differently. Initially viewed as a native invasive species ($\lambda_K < 0$), crowberry is then recognized as a beneficial native species ($\lambda_K > 0$), that nonetheless requires some control. This shift underscores the dual role of crowberry as both a contributor to carbon sequestration and a challenge to pasture quality, thus asking for a comprehensive and balanced approach to its management. Given the services and disservices provided by crowberry, societal preferences and values will influence the optimal management strategy. Different societies may prioritize these values differently, leading to different context-specific optimal management strategies.

Furthermore, our study argues for a more comprehensive approach in the Norwegian reindeer management, which needs to take into account the pasture's quality, not only quantity. We provide further insight for the current management strategy of the Norwegian husbandry, which is struggling to manage the grazing pasture sustainably (Ministry of Local Government and Modernisation, 2023; Tuomi et al., 2022). To achieve a sustainable pasture and husbandry development, controlling the native invasive crowberry seems essential and beneficial.

One critical issue highlighted by our study is the negative herding profit associated with crowberry burning in the short run due to significant additional burning cost. This presents a challenge for the herders who may not have the financial resilience to endure short-term losses. The societal incentive to carry out crowberry burning suggests that this initial burning cost should be viewed as a societal burden rather than a private one. Additional government subsidies or other forms of financial support are necessary to bridge this gap, ensuring that the husbandry is not disproportionately affected by the initial economic downturn. This approach would align short-term economic impacts with long-term ecological and economic benefits, ultimately contributing to sustainable pasture management and reindeer husbandry.

The concept of salvage value plays a pivotal role in our model as it changes the optimal management strategies among the scenarios. Though some studies mention or apply salvage value (Lenhart & Workman, 2007; Salau & Fenichel, 2015; Sanchirico & Springborn, 2011), most have not identified its meaning within the total economic value framework. In our study, we see the vegetation salvage value acts as an option value in the short run, while in the long run it can be considered as both option value, existence value, and bequest value. By incorporating these values into the social welfare function, we acknowledge potential future use and the preservation of the grazing pasture for future generations. Our findings suggest that a comprehensive management strategy that includes the habitat salvage value can better align management strategies with long-term sustainability goals, ultimately enhancing the overall welfare of the society.

Although our models show that it is optimal to burn crowberry in most of the cases, accounting for the carbon sequestration value alters the optimal burning effort significantly. At a specific carbon price, approximately 3 NOK/ kilogram carbon (see Appendix B for the detailed analysis), it is no longer optimal to burn crowberry, even when the vegetation salvage term is included in the social welfare function. Although this price is nearly 8 times higher than the carbon price we used for our model, carbon pricing plays a crucial role in determining whether and until when it is optimal to burn crowberry. As carbon has increasingly become a critical indicator for decision-making (Directorate, 2023; West et al., 2018), if the reindeer meat price does not increase in line with the carbon price, or the slaughter cost, feeding cost, or burning cost decreases (for instance by governmental subsidies), there would be a point in the future when it is no longer optimal to burn crowberry.

Conclusion

Using bioecononomic modelling and applying optimal control theory, we emulate the current ecological problem of crowberry encroachment in the Norwegian tundra biome and simulate the changes in the biomasses of crowberry, vegetation, and reindeer through time. We incorporate further the burning effort, vegetation salvage value, and the two plants' carbon sequestration service to scrutinize the optimal burning and how different ecological and economic factors alter the optimal management of the decision-maker. Overall, our five contributions include 1) calculating the optimal burning effort under different scenarios to find the optimal management strategy, 2) emphasizing the crucial importance of the high biodiversity nutrient-rich grazing pasture, especially its non-use value, hence supporting the sustainable development of the grazing pasture, 3) incorporating the practical role of carbon sinks in decision-making, 4) studying the trade-offs of both ecosystem services and disservices of crowberry on management of the reindeer husbandry, and 5) showing analytically and numerically the negative indirect impact of supplementary feeding on the pasture. Our models can be applied for the reindeer husbandry of other Nordic countries, or other similar ecological settings of pasture management for the semi-domesticated-herbivore husbandries.

We acknowledge that there are several limitations in our model, which can be improved by further studies. First, we did not adopt spatial modelling that could incorporate heterogeneity in different types of grazing pastures. Solving an optimal spatial-temporal control problem may reveal more insight both when and where the decision-maker should burn crowberry. Second, to avoid the final jump at the tail-end of the trajectories in several variables, future studies may calculate the numerical equilibrium and then potentially use the result of the vegetation shadow price to determine the coefficient for the scrap value term. Third, when assessing carbon, we did not include the carbon footprint of the husbandry. Several papers have studied the carbon footprint of reindeer, though most of the studies were experimental and provided conflicting results (Fritze et al., 2021; Köster et al., 2018; Laiho et al., 2017). Inclusion of reindeer's carbon footprint may increase the slaughter rate so as to keep the herd smaller, something which could beneficially be included in future studies. Besides, as reindeer husbandry is a symbolic industry of the Sami people, further analyses could also incorporate social and cultural values of the husbandry to scrutinize better the optimal feeding and slaughtering controls.

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Appendix

Appendix A – Data summary

Table A.1: Parameters for numerical application

Parameters	Indicators	Unit	Value	Sources
α_V	Vegetation intrinsic growth coefficient		0,6	Moxnes., 1993; Skonhoft et al., 2010, Myers-Smith et al., 2020
α_K	Crowberry intrinsic growth coefficient		0,2	
α_R	Reindeer intrinsic growth coefficient		0,7	Moxnes., 1993; Skonhoft et al., 2010
M	Pasture carrying capacity	kilogram biomass	8,7 x 10^{10}	Calculated from Bråthen and Lortie., 2015
g_V	Grazing coefficient on vegetation		8 x 10^{-7}	Bakka et al., 2021; White & Trudell., 1980
g_K	Grazing coefficient on crowberry		1 x 10^{-8}	Guesstimate
d_V	Conversion coefficient of vegetation biomass into reindeer carrying capacity		2,5 x 10^{-5}	Guesstimate from Regjeringen., 2021
d_K	Coonversion coefficient of crowberry biomass into reindeer carrying capacity		5 x 10^{-7}	Guesstimate from Regjeringen., 2021
φ	Climate change impact coefficient		0,8	Calculated from Tuomi et al., 2022
$V(t_0)$	Initial condition of vegetation	kilogram biomass	3,48 x 10^{10}	Bråthen et al., 2018, Tuomi et al., 2022

$K(t_0)$	Initial condition of crowberry	kilogram biomass	5,22 x 10^{10}	Bråthen et al., 2018, Tuomi et al., 2022
$R(t_0)$	Initial condition of reindeer	reindeer	230.000	Regjeringen, 2021
S_{max}	Upper bound of slaughter control	Percentage slaughtered of the herd	0.7	Calculated from Regjeringen., 2021
F_{max}	Upper bound of feeding control	Thousand tonne dry feed	10	From discussion with the herders
B_{max}	Upper bound of burning control	Days in a year	365	Guesstimate
ε	Burning coefficient		10^{-3}	Guesstimate
β	Feeding coefficient		10^{-1}	Guesstimate
b_V	Biomass conversion rate of vegetation		1,6 x 10^{9}	Murguzur et al., 2019
b_K	Biomass conversion rate of crowberry		2 x 10^{9}	Murguzur et al., 2019
c_0	Fixed cost	NOK	185 x 10^{6}	Estimated from data from 2004 – 2021
c_2	Quadratic slaughter cost coefficient	NOK/ quadratic percentage slaughtered reindeer	1 027 x 10^{6}	Estimated from data from 2004 – 2021
c_3	Feeding cost	NOK/ thousand tonne dry feed	6.000.000	Calculated from discussion with herders
c_4	Burning cost	NOK/ labour day	3500	Guesstimate
p	Price per reindeer	NOK/ reindeer	6300	Calculated from Regjeringen, 2021
p_2	Carbon price	NOK/ kilogram carbon	0,4	Vondolia et al., 2020
δ	Discount rate		0,05	Regjeringen, 2012

Appendix B - Sensitivity analysis

We choose the last scenario with vegetation salvage value term, in the long run, as the case to conduct sensitivity test. We use the final-time point as the point of reference for sensitivity testing. Sensitivity analysis results indicate that within 10% change of parameters, many variables are insensitive to these changes, thus supporting, to a large extent, the robustness of the model (Table B.1). 10% increase in the price per slaughtered reindeer p increases all five optimal state and control variables, while decreases the optimal feeding control. Yet increasing 10% of the carbon price p_2 shows a different dynamics, as it decreases the optimal slaughter and burning controls and crowberry population, while increases the other variables. The signs of changes of variables given 10% increases in both price parameters are not as expected, although higher quadratic slaughter cost c_2, feeding cost c_3, and burning cost c_4 show the expected changes of signs of the variables. Since we used the final-time point as reference for calculating the sensitivity results, the sensitivity analysis may not reveal the changes in dynamics of the whole system.

Table B.1: Sensitivity analysis of the carbon scenario with $V(T)$ in the long run

Parameters	**Carbon scenario with $V(30)$**							
	ΔV^*	ΔR^*	ΔS^*	ΔK^*	ΔF^*	ΔB^*	**Profit**	**Welfare**
α_V	10,7	9,7	**19**	-7,8	10,5	**17**	-0,9	0,04
α_K	-0,03	-0,4	-3,2	0,3	0,7	1,5	1,5	0,01
α_R	-0,9	1	**20,4**	3,9	-4,7	2,8	**11,5**	0,06
M	3,2	4,2	7,2	10	1,2	4,2	6,2	0,3
g_V	**-15,8**	-6,1	-7,2	10,5	-7,2	-8,7	**15,5**	-0,01
g_K	0,03	0,03	0,05	-0,2	0,02	-0,2	0,06	0
d_V	-7,6	3	7,9	6,6	-0,8	-2,6	5,6	-0,02
d_K	-0,2	0,2	0,2	0,1	-0,1	-0,1	0,2	-0,002
φ	-2,7	2	10,8	9,5	-7,5	9,3	7	-0,1
b_V	-0,07	0,9	-1,4	1,4	-1,8	0,6	5,2	4,4
b_K	10,4	8,5	-1	**-33,2**	5	**-17,9**	**24,9**	5,55
β	-0,3	0,04	3,3	1,7	9,2	1	5,5	0,01
ε	0,4	0,7	4	-1,1	0,3	4,4	-1,7	-0,02
p	0,2	3	**31,9**	6,3	-5,9	5	**18,7**	0,1
p_2	10,9	9,7	-0,6	**-34,9**	3,3	**-18,7**	**31,5**	9,9
c_1	0,1	0,5	2,9	0,3	-0,7	0,3	3,5	0,03
c_2	-0,8	-0,9	-8,8	1,5	-0,3	0,3	10	0,03
c_3	0,2	0,2	-1,4	-0,9	-8,8	-0,6	-2,1	-0,002
c_4	-0,6	-0,4	-1,5	2,2	-0,7	-6,3	1,5	0,02
δ	-0,1	-0,3	-0,3	0,1	0,4	-0,2	0,5	0,008

As the model is sensitive with the two price parameters, we conduct several tests to investigate deeper the changes in optimal results. Regarding different reindeer price p, we compare the baseline with the burning scenarios with two different slaughtered reindeer prices. 20% higher price per slaughtered reindeer p, with vegetation salvage value, will increase burning and feeding efforts, leading to much higher reindeer stock level, slightly higher in vegetation stock, and lower crowberry population (Figure B.1). Hence, it takes shorter time to gain profit from burning crowberry than the case with original price parameter.

Regarding different carbon prices p_2, we choose the other higher prices as 5 and 10 times higher than the current used price to see the dynamics of the system and to find at which carbon price the burning effort is totally discouraged. In case of no vegetation salvage value $V(T)$, higher carbon prices put an end to the burning question and drive down vegetation stock, yet increases crowberry and reindeer populations (reindeer increases since it still grazes on crwberry though very little) (Figure B.2). Higher p_2 also discourages feeding and slaughtering, thus decreasing λ_R but increasing λ_V and λ_K. With the vegetation salvage value $V(T)$, burning activity is, nevertheless, encouraged even the carbon price is five times higher, yet with much lower effort (Figure B.3). One difference is with vegetation salvage value, it requires more supplementary feeding for reindeer when carbon price increases. At the carbon price of around 3 NOK/ kg carbon biomass, burning effort may be shut down totally, i.e. $B = 0$, regardless of whether the vegetation salvage value is accounted for or not.

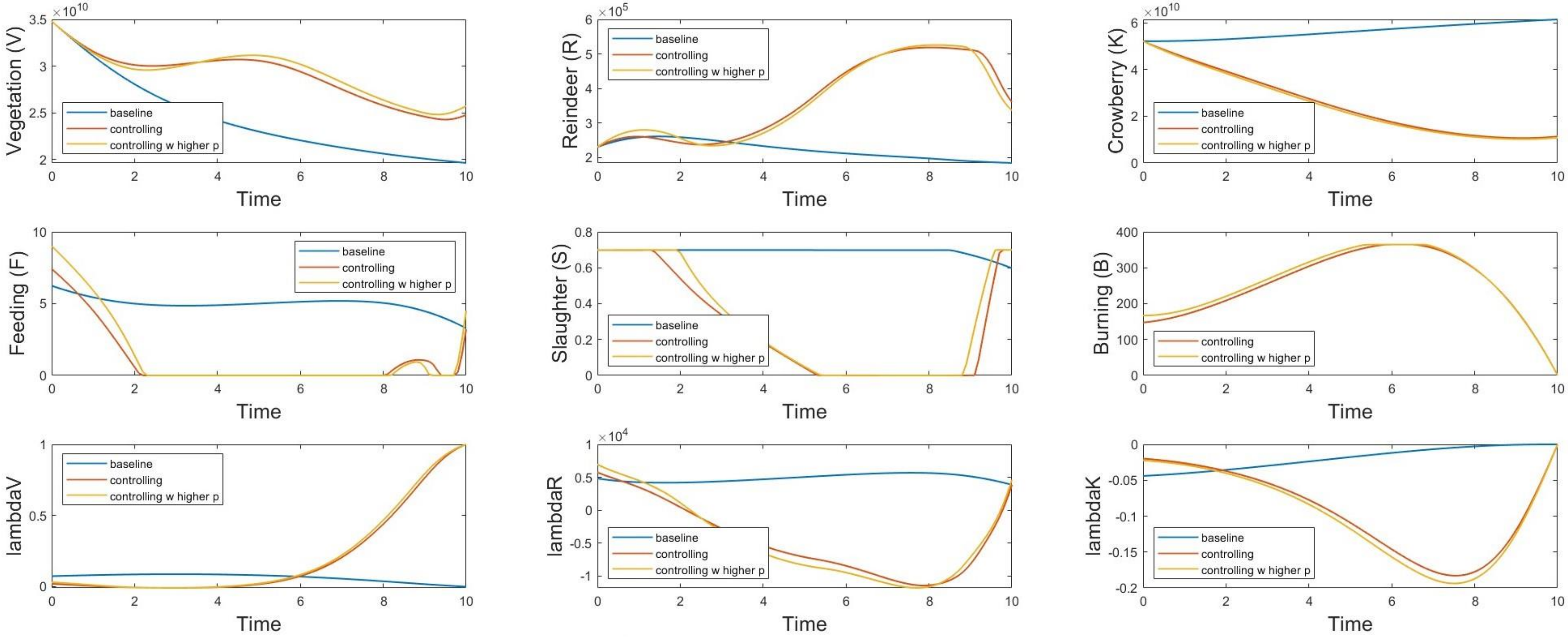

Figure B.1: Optimal dynamics in the baseline and burning scenarios with 20% higher reindeer prices (p) with vegetation salvage value term

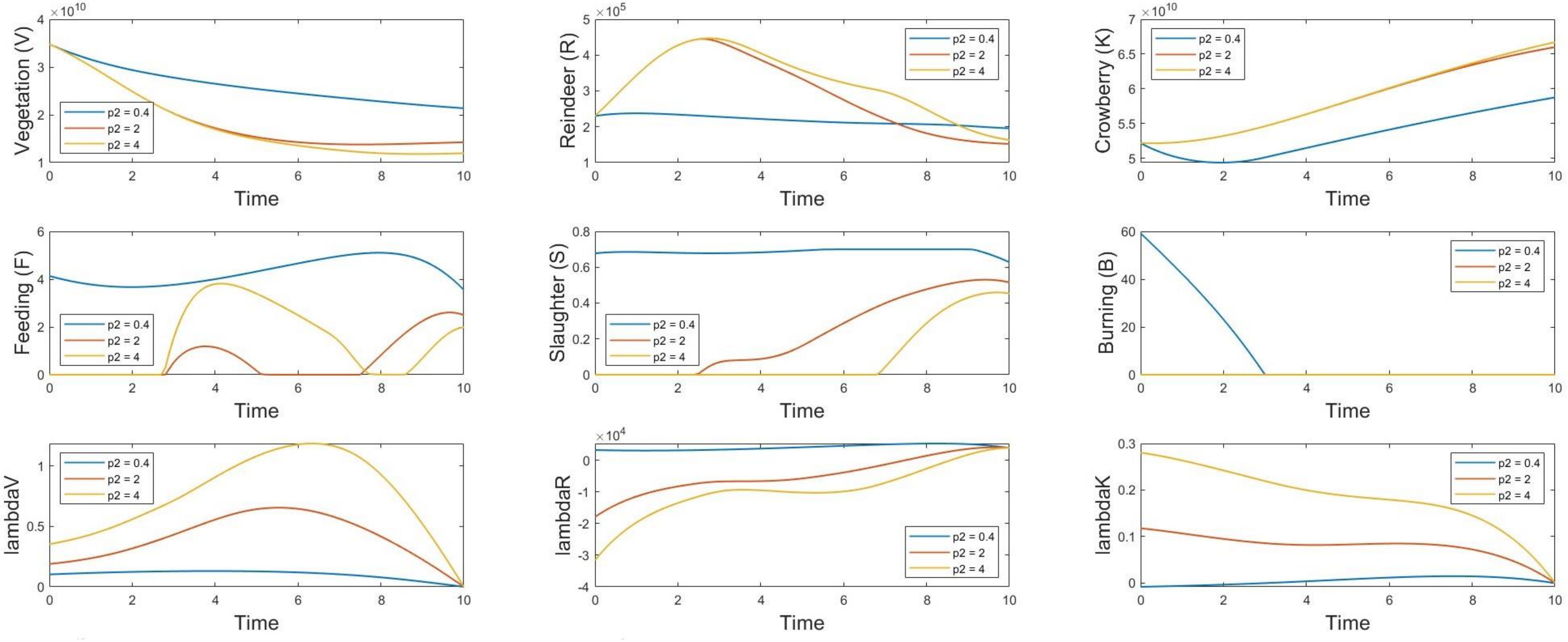

Figure B.2: Optimal dynamics in the carbon scenario with 20% higher carbon prices (p_2) without vegetation salvage value term.

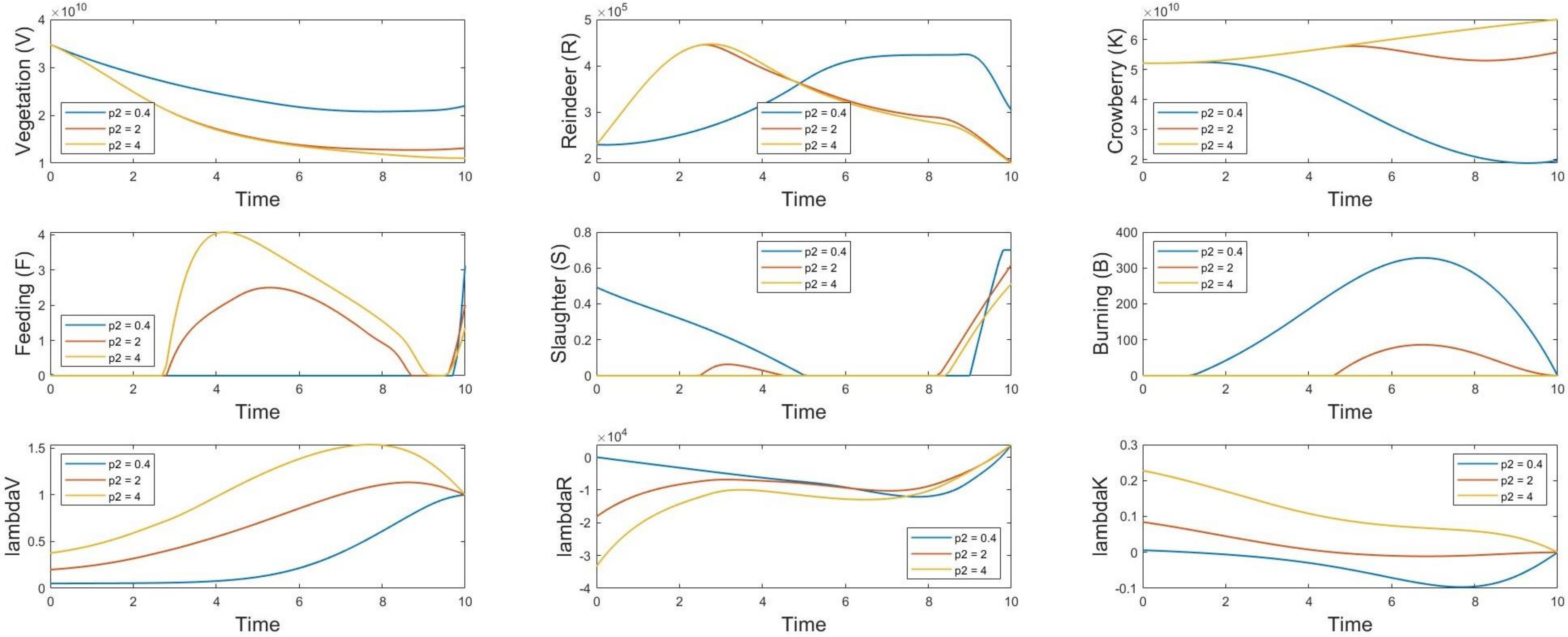

Figure B.3: Optimal dynamics in the carbon scenario with 20% higher carbon prices (p_2) with vegetation salvage value term

Appendix C – Stability and Equilibrium Solutions

In 30 years, the stability equilibria in are not clearly reached in several cases. However, setting the time to 100 years, stable trajectories are shown in Figure C.1. To investigate the long-run stability, we calculate the equilibrium solution in all three scenarios (Table C.1). Without burning the native invader, vegetation stock decreases critically due to both reindeer grazing and crowberry encroachment. Controlling crowberry encroachment supports increases in the optimal stocks of vegetation, reindeer, and slaughter percentage. The result also shows a clear negative sign of crowberry's shadow price, implying the negative impact of the native invader on the profit functions. As the reindeer population correlates positively with its shadow price, burning crowberry also increases λ_R.

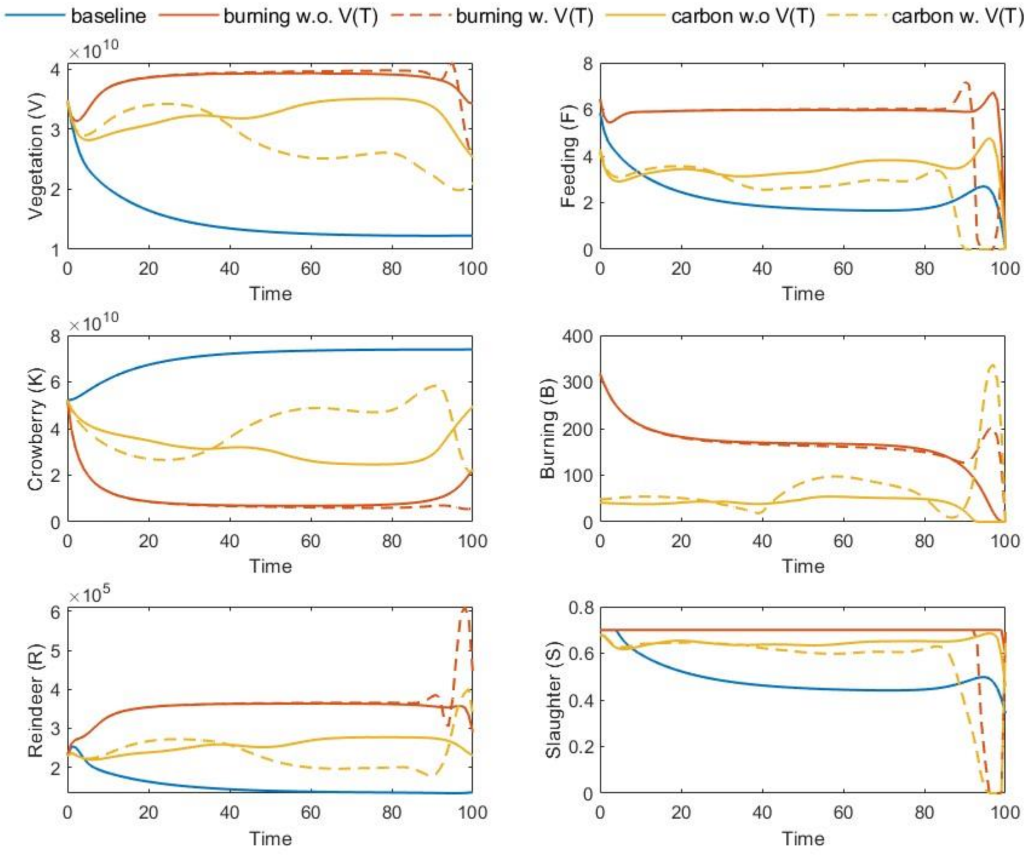

Figure C.1: Optimal dynamics of all scenarios in 100 years

As can be seen in table C.1, less than 6 months is spent burning crowberry, while the required amount of dry feed for reindeer is 3600 tonnes. As expected from our hypothesis, incorporating carbon sequestration of crowberry will decrease the optimal burning effort, thus decreasing the herding profit at equilibrium. However, the additional indirect use value from carbon sequestration of the pasture exceeds the monetary profits from slaughtering reindeer. Stability tests of three equilibria show that all three points are stable (Table C.2).

Table C.1: Equilibrium solutions of three scenarios

Scenario	V^*	R^*	S^*	K^*	F^*	B^*	λ_R^*	λ_V^*	λ_K^*	**Profit from slaughtering reindeer (mil NOK)**	**Social Welfare from crowberry's carbon sequestration (mil NOK)**
Baseline	1×10^{10}	138 671	0,31	$7{,}62 \times 10^{10}$	0,8		1 782,19	0,13	- 0,029	169,5	
Burning	$3{,}76 \times 10^{10}$	373 577	0,6	$7{,}65 \times 10^{9}$	4,83	163,1	3072,31	0,06	- 0,15	623	
Carbon	$2{,}53 \times 10^{10}$	207 765	0,51	$4{,}7 \times 10^{10}$	1,43	44,73	1 364,12	0,13	- 0,007	199,6	19 658,4

Table C.2: Stability results of three equilibria

Scenario	**Eigenvalues**	**Stability**
Baseline	$-0.406 + 0.142\, i$ $-0.406 - 0.142\, i$ $-0.064 + 0.\, i$	Stable point
Burning	$-0.443 + 0.21\, i$ $-0.443 - 0.21\, i$ $-0.077 + 0.\, i$	Stable point
Carbon	$-0.267 + 0.19\, i$ $-0.267 - 0.19\, i$ $-0.1 + 0.\, i$	Stable point