# Arctic evergreening - encroaching allelopathy in a management blind spot

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*Abstract*

Management blind spots, i.e., influential processes not included in management models, may undermine management objectives and reduce system resilience. Here we address one such blind spot in the management of *Rangifer* in Norway. The current model is based on regulation of pastures and population vital rates through reindeer density, but lacks validation of the underlying assumption of forage stability, which is a critical blind spot. We report pasture changes over 18 growing seasons, under variable reindeer densities and a changing climate. We show a strong increase of the native evergreen, allelopathic crowberry, contrasted by smaller increases of deciduous dwarf-shrubs and stagnation in herbaceous species. We found no evidence of reindeer density influencing these vegetation changes. Our results unveil a trajectory of Arctic evergreening and increasing allelopathy, and a shift towards lower biodiversity and ecosystem functioning. It exemplifies an ongoing change in a management blind spot that greatly impacts social-ecological systems.

## *Introduction*

Sustainable management of ecosystems and social-ecological systems (SES) is contingent on models that are representative of the managed system and its uncertainties (Milner-Gulland and Shea 2017; Regan, Colyvan, and Burgman 2002; Latombe et al. 2019). Management blind spots, i.e. *influential variables or processes not included in a management model*, may severely undermine management objectives (Madden and McQuinn 2014), lead to misguided management efforts, and reduce the capacity of the system to adapt and maintain system resilience against undesirable states (Dudney et al. 2018). Particularly challenging are slow and poorly detectable changes in external or internal drivers of the system (Schneider, Leifeld, and Malang 2013) that, if overlooked through being a management blind spot, may develop unnoticed and potentially push the system towards a less favorable state. Hence, sustainable SES-management under climate change is contingent on assessment and revision of management models to identify potential critical blind spots.

In the Arctic, climate change brings novel threats (Post et al. 2009; Mallory and Boyce 2017), and opportunities (Mallory and Boyce 2017; Henden et al. 2020) for caribou and reindeer (*Rangifer* sp.) populations and associated indigenous pastoral systems (Horstkotte et al. 2017). The anticipated warming-induced vegetation trends in summer pastures include increased productivity, biomass and leaf area, which contribute to Arctic greening (Myers-Smith et al. 2020), and shifts towards more resource acquisitive species (Bjorkman et al. 2018; Elina Kaarlejärvi, Eskelinen, and Olofsson 2013). Such changes are expected to manifest through biomass increases of plants with taller growth and higher nitrogen (N) concentrations, such as willows, graminoids and forbs (Bråthen, Gonzalez, and Yoccoz 2018; Bjorkman et al. 2018; Myers-Smith et al. 2019). Increased productivity of these palatable species should translate into higher population growth rates of ungulates through positive bottom-up effects (Henden et al. 2020; Tveraa et al. 2013). By foraging, ungulates can even counteract shrubification (Christie et al. 2015), keeping willows in a “browse-trap” (Bråthen et al. 2017), thereby preventing the most nutritious forbs and graminoids from being overgrown (Bret-Harte et al. 2001; Mod and Luoto 2016).

However, although rapid changes in climate in the Arctic (IPCC 2021) are altering primary productivity, biodiversity and ecosystem functions (Myers-Smith et al. 2020; Barry, Berteaux, and Bültmann 2013; Post et al. 2019; Taylor et al. 2020), recent observations

indicate that ongoing Arctic greening may conceal qualitatively and functionally contrasting trends. The satellite-derived greening signal in North-America is negatively related to caribou population growth rates, and this has been attributed to expansion of deciduous shrubs with high levels of anti-browsing defenses (Fauchald et al. 2017). Contradicting satellite-derived inference, field-derived observations show increments in especially evergreen dwarf-shrubs across the circumpolar Arctic (Wilson and Nilsson 2009; Elmendorf et al. 2012; Maliniemi et al. 2018; Vowles et al. 2017). These plants often have high phenolics and low N content, and can contribute to lowering ecosystem productivity (Vowles and Björk 2019; Tuomi et al. 2018). These observations suggest a decline of pasture quality, an "evergreening" trend that is functionally distinct from that of greening. In Arctic pastoral SES, already under pressure from a multitude of anthropogenic pressures (Horstkotte et al. 2017; Hausner et al. 2020), ecosystem bottom-up effects that erode pasture quality could pose a significant management risk, and undermine system resilience if left unchecked.

In this context, of particular interest is the niche-constructing, native, allelopathic evergreen dwarf-shrub, black crowberry (*Empetrum nigrum*) (Bråthen, Gonzalez, and Yoccoz 2018; Wardle et al. 1998) (Table S1). In Fennoscandia, crowberry is already abundant and commonly dominant, and as a boreal-Arctic species it appears to thrive under climate change and tolerates various environmental stressors (Tybirk et al. 2000; Aerts 2010; Preece and Phoenix 2014). Owing to its low foliar nutrient concentrations, high levels of allelochemical polyphenolic compounds in its leaves and a dense, clonal growth, crowberry is highly unpalatable, and can significantly retard ecosystem processes such as litter decomposition, soil nutrient fluxes and seedling establishment (Bråthen, Fodstad, and Gallet 2010; González et al. 2021; Tybirk et al. 2000; Wardle et al. 1998; Nilsson and Wardle 2005). It can also suppress biodiversity and herbaceous plant growth in summer pastures (Bråthen, Gonzalez, and Yoccoz 2018) (Table S1). While herbivores can suppress growth of palatable deciduous shrubs (Bråthen et al. 2017; Olofsson et al. 2009), their effect on crowberry growth is less clear (Maliniemi et al. 2018; Vowles et al. 2017), as reindeer avoid crowberry-dominated areas for most of the growing season (Iversen et al. 2014). This indicates that ecosystem evergreening may severely undermine a management system based on an assumption of density-dependent population regulation derived from stable-state conditions (Krebs 2002).

In the present paper, our focus is on tundra pastures used for reindeer husbandry, which are core to the indigenous Sámi livelihood and culture (James 2020). *Rangifer* (reindeer

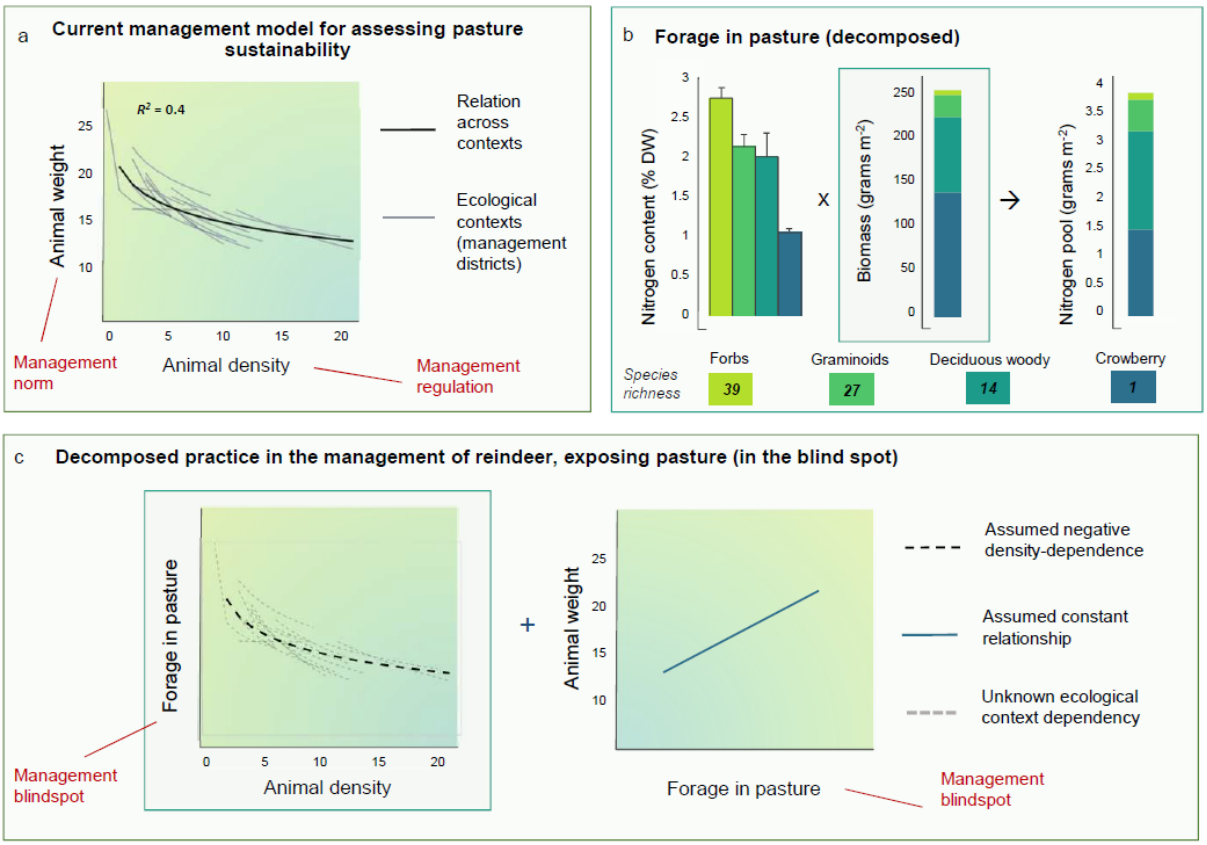


**Figure 1.** Pastures as a blind spot of a reindeer management system. **The current management of reindeer in Norway applies reindeer density as the regulatory mechanism of sustainable pastures** (*Reindeer Husbandry Act*). The central norm for assessing sustainability of the summer pastures is the autumn slaughter weight of animals, as a proxy for body condition, and no measures pertaining to the pastures themselves. **a) Empirical density-dependence between reindeer densities and weights within and across herding districts**. Over the time-period of 2000-2019 and among the management districts of the current study, weights declined with increasing reindeer density both within districts representing different ecological contexts and across all districts, here exemplified with calf weights (*Ministry of Agriculture*). **b) Available forage quality and quantity in summer pastures in northern Fennoscandia in 2003.** Pasture forage consists of plant groups of varying species richness (Bråthen et al 2007), quality (nitrogen content (Murguzur et al 2019)) and abundance (biomass (Bråthen et al 2007)). Forbs, the most nutritious and species-rich group, make up the least biomass in pastures. Conversely, the least nutritious and evergreen dwarf-shrub crowberry makes up the most biomass. **c) Exposing pastures as a blind spot in the current reindeer management model.** The link between reindeer densities and weights is indirect, assumed to be mediated through pasture carrying capacity in an equilibrium system, i.e. forage (*Reindeer Husbandry Act*; *White Paper 32 (2016-2017)*). The decomposed model shows the assumed negative top-down relationship between animal density and forage in an equilibrium system (left panel), and an empirical positive bottom-up relationship between forage and weights (right panel, see Tveraa et al. 2013). However, negative density-dependence in animal populations can operate independent of pasture development (Krebs 2002). Framed graphs in panels b) and c) indicate patterns and relationships that are empirically addressed here.

and caribou) grazing systems span the circumpolar area (Mallory and Boyce 2017) and, akin all extensive pastoral or grazing systems, rely on high-quality plant resources in pastures as forage for the animals (Sinclair and Krebs 2002). Changes in pastures are therefore focal to understanding mismanagement and adaptation risks in pastoral systems, as exemplified in our study system: the Norwegian reindeer herding SES. The current Norwegian reindeer management model (Fig 1a), set by the reindeer herding law of 1978 and 2007 (*Reindeer Husbandry Act*, lovdata.no/dokument/NL/lov/2007-06-15-40), operates based on an empirically supported negative density-dependent relationship between reindeer numbers

and body mass (Henden et al. 2020; Stien et al. 2021), and an implicit assumption of a stable-state population dynamics, suggesting that population vital rates can be predictably managed via animal density (Krebs 2002) (Fig 1a, Supplementary Figure S1). Whenever animal weights fall below a threshold, husbandry sustainability is, according to this model, attained via lowering animal densities. A key implicit mediator of this relationship are summer pastures and their quality, assumed to be in an equilibrium state (Krebs 2002), but this is a blind spot in the management model (Fig 1c). In 2003, crowberry made up the majority of plant biomass across the northern Norwegian tundra, resulting in pastures that are abundant in forage of low nitrogen content (Fig 1b). Monitoring the change in crowberry abundance over time relative to that of the more nutritious shrubs, forbs and graminoids, is vital to understanding the development of these tundra ecosystems and their pastoral SES.

Specifically, we ask 1) to what extent crowberry and other forage plant groups are changing their abundance in tundra pastures, 2) whether the densities of reindeer, which are the primary regulating factor in reindeer management, are linked to these changes, and 3) what are the implications of the observed changes in forage quantity for sustainability of the reindeer management system. To answer these questions, we present results from a unique, large-scale resurvey of 292 plant communities within 56 landscape areas sampled across 20 reindeer summer pastures, or management districts, in northern Norway over 18 growing seasons from 2003 to 2020 (Figure S2). Finally, we use these empirical findings to support a revision to the reindeer management model.

Located at the transition from subarctic to the low-Arctic, Northern Fennoscandia is a bellwether for changes in tundra vegetation (Vuorinen et al. 2017; Elmendorf et al. 2012) and ecosystem functioning (Parker et al. 2021). The region has experienced lengthening of the growing season as spring and autumn have become warmer over the past century

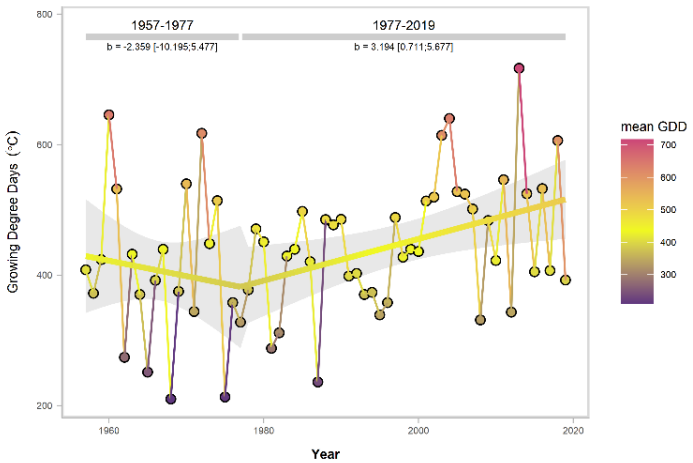


**Figure 2.** Growing degree days (GDD), as annual sums of daily temperatures above 5°C during May-October 1957-2019, averaged across the studied reindeer summer pastures (Pedersen et al. 2020/met.no). Solid thick line and shaded areas represent mean ± 95% confidence intervals from segmented linear regression with a breakpoint at year 1977. Parameter estimates are provided at the top of the figure.

(Kivinen et al. 2017). With an approximate increase of 100 growing degree days in the studied summer pastures since the late 70's (Fig. 2), the pastures have been subject to a growing season prolongation, which is a key driver behind increased shrub growth in the Arctic (Post et al. 2019; Weijers et al. 2018; Myers-Smith et al. 2019). We used identical georeferenced plant communities and sampling methods within each community in both 2003 and 2020. Each plant community was represented by a 50m long transect with 11 equidistant, triangular measurement plots with 40cm sides (Bråthen et al. 2007). We used Bayesian generalized linear mixed models (Bürkner 2017) to test if 1) community-level standing biomass of forbs, graminoids, deciduous woody plants (shrubs and dwarf-shrubs) and crowberry, and the area covered by these groups, changed over the study period, and if 2) the standing biomass of these forage groups was associated with reindeer density. For the latter, we linked the plant biomass estimated for each of the survey-years with their averaged reindeer densities from the previous two decades (*Ministry of Agriculture,* https://www.landbruksdirektoratet.no/nb/nyhetsrom/rapporter/ressursregnskapet-for-reindriftsnaeringen, accessed via reinbase.no). We report results as posterior mean effect sizes (pmes) and their 95% credible intervals (CI), unless stated otherwise.

## Results

### *Vegetation changes in tundra pastures*

Over the 18 growing season interval of our surveys, crowberry standing biomass increased by 60% (Figure 3, Table S2), and by 14% in cover (Supplementary Table S3). The increase in crowberry is in sharp contrast with a complete stagnation in the standing biomass and cover of the more nutrient rich and faster growing forbs and graminoids over this period (Figure 3a, Table 1, S2 and S3). Crowberry's increase is nearly an order of magnitude larger than the increase of deciduous dwarf-shrubs and shrubs (Figure 3a, Table 1, S3). The frequency of communities for which more than 25% of total vascular biomass was crowberry rose significantly over this period [pmes 0.57; 95%CI 0.10-1.05], from an already high 0.76 to 0.83, suggesting that an increasing number of communities is subject to allelopathic effects from crowberry.

In contrast, we found little evidence of reindeer densities correlating with abundances of any of the plant forage groups either in 2003 or 2020 across the different management districts (Figure 3b), with small effect sizes and 95% credible intervals for all parameter estimates overlapping zero (Table 1). While crowberry biomass did not vary with reindeer density, it varied substantially among landscape areas within management districts (Fig 3b, Table S3), suggesting strong ecological context-dependence in its abundance. Deciduous shrubs and graminoids varied m arkedly between districts and in landscape areas, while variation in forb biomass was largest between districts (Fig 3b, Tables S3, S4).

**Table 1.** Parameter estimates for plant biomass change from 2003 to 2020 and plant biomass variation with animal density in 2003 and 2020. For full population-level estimates (fixed effects) and estimates of group-level standard deviation (random effects), see Supplementary Table S2. Error terms Q2.5 and Q97.5 represent the 95% credible interval, within which the true estimate lies with a 95% probability. Bold font indicates strong support for the effect, and italic indicates relatively strong support for the effect, given the data.

| response | parameter | estimate | Q2.5 | Q97.5 |
|---|---|---|---|---|
| Forbs | Density 2003 | -0.089 | -0.190 | 0.013 |
| | Biomass 2020 | -0.306 | -0.846 | 0.240 |
| | Density 2020 | 0.032 | -0.043 | 0.107 |
| Graminoids | Density 2003 | -0.0004 | -0.067 | 0.066 |
| | Biomass 2020 | -0.115 | -0.514 | 0.289 |
| | Density 2020 | 0.009 | -0.047 | 0.067 |
| Deciduous woody | Density 2003 | -0.015 | -0.067 | 0.037 |
| | *Biomass 2020* | *0.283* | *-0.001* | *0.575* |
| | Density 2020 | 0.004 | -0.039 | 0.045 |
| Crowberry | Density 2003 | 0.026 | -0.019 | 0.072 |
| | **Biomass 2020** | **0.601** | **0.301** | **0.905** |
| | Density 2020 | -0.019 | -0.062 | 0.025 |

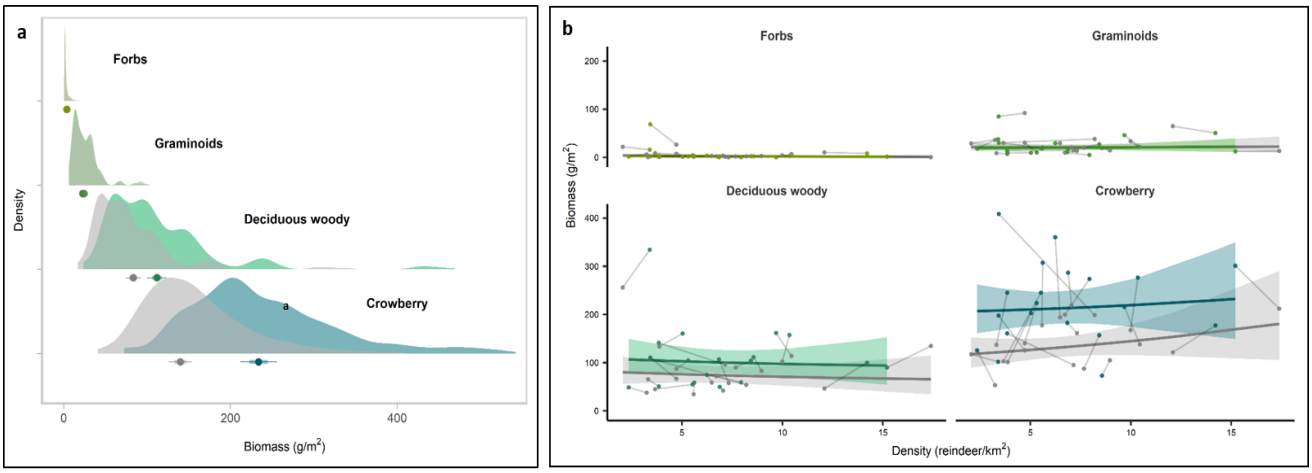


**Figure 3.** Changes in the abundance of plant groups of pasture forage in the management blind spot. **a)** Modelled posterior predictions of biomass of forbs, graminoids, deciduous woody plants and crowberry, separately for each plant group in 2003 (grey) and in 2020 (greens). Means and 95% confidence intervals from observed data for each year are provided as point intervals below each biomass density plot. **b)** Modelled association with confidence bands (model-derived 95% credible intervals of the posterior mean estimate) between plant groups of pasture forage (forbs, graminoids, deciduous shrubs and dwarf-shrubs and crowberry), and reindeer densities across management districts, separately for 2003 (grey) and 2020 (greens). Observed associations within each district and year (points) are linked per district to display the trajectory of change in forage group biomass with changing reindeer densities over time.

## Discussion

We show that tundra pastures over the last two decades have been subject to a strong evergreening forcing, attributable to the increased abundance of the native, allelopathic evergreen dwarf-shrub crowberry (Fig. 4a), and a weaker greening forcing. The process of pasture evergreening (Maliniemi et al. 2018; Vuorinen et al. 2017; Vowles et al. 2017) far outpaces that of the deciduous shrubs – species typically linked to the process of greening (Post et al. 2019; Weijers et al. 2018; Myers-Smith et al. 2019). Moreover, we show this process juxtaposed with no increase of the already scarce yet most species-rich and productive plant groups, the forbs and graminoids, likely resulting in an important biodiversity loss through reduced species evenness.

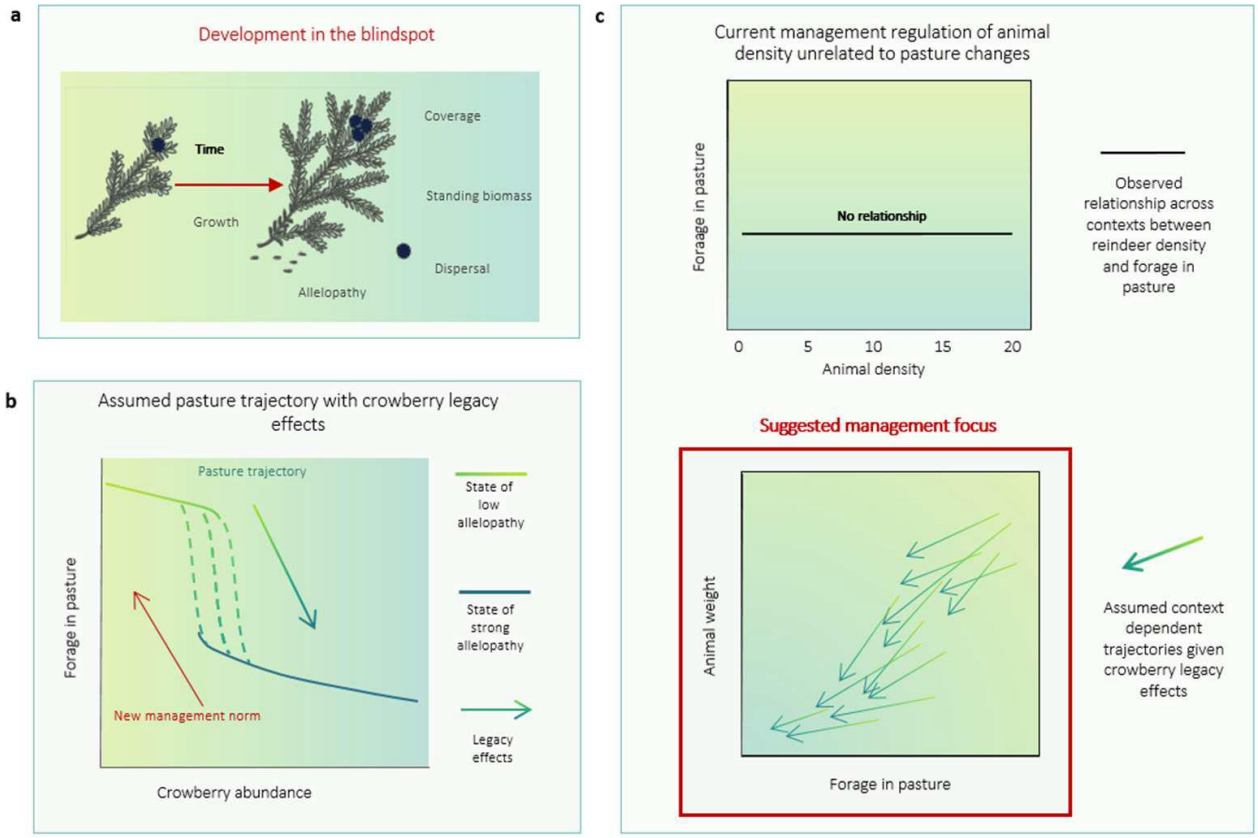


**Figure 4. a)** Mechanisms of crowberry encroachment and increased allelopathy over time. Growth of established plants results in infilling and increased biomass, leading to stronger allelopathic litter effects. Dispersal via seeds and clonal reproduction are means of lateral encroachment. Already an abundant and long-lived species, slow growth may still cause substantial increments in abundance. **b)** Conceptual model of the pasture state transition based on bottom-up effects. Increasing crowberry abundance may push the system towards higher allelopathy and induce legacy effects (green arrow) that over time will reduce new plant establishment (Gonzalez et al 2021) at levels as low as 25% crowberry out of total community standing biomass (Bråthen et al 2018). The average proportion of crowberry in community standing biomass in Fennoscandia was above 25% in 2003 (upper panel) and even higher in 2020. A new management norm of *pastures in a state of low allelopathy* (red arrow) could push the system back. **c)** Conceptual model of a revision to the management model based on results from the current study. Weak or no relationship between the abundance of pasture forage and reindeer densities decouples the regulatory mechanism and the norm in the current management model, suggesting primacy of bottom-up regulatory effects in reindeer summer pastures, prompting the inclusion of a new management focus: pasture forage.

Across management districts, representing a range of different ecological contexts, reindeer densities were not related to abundance patterns of any forage group (Fig 3b). Our results therefore point at evergreening by crowberry encroachment as a bottom-up forcing on the pastures (Fig 4) (cf. le Roux et al. 2013), an ever stronger process in the management blind spot of the reindeer herding SES with potentially adverse long-term consequences for the diversity and productivity of this critical indigenous Arctic pastoral system. Furthermore, our results suggest crowberry encroachment delimits areas available for pastures (Skarin et al. 2020; Iversen et al. 2014), adding to ongoing loss of land with productive pastures due to human disturbance (Hausner et al. 2020) and other stressors (Vaas et al. 2021; Horstkotte et al. 2017). Such loss may even amplify other stressors, further eroding resilience of the system.

*Evergreening: tundra pastures in transition*

As a strong niche-constructing species, crowberry can modify the environment once established (González et al. 2021; Bråthen, Gonzalez, and Yoccoz 2018; Wardle et al. 1998) and through legacy effects and reinforcing feed-backs, push the system towards a state of strong allelopathy (Supplementary Table S4, Fig 4a-b). Consequently, we suspect that the legacy effects at the community- and ecosystem-level from crowberry allelopathy may represent an ongoing shift with potential context-specific thresholds (Hughes et al. 2013) (Fig 4bc). Diminishing diversity may happen gradually through reduced seedling recruitment (González et al. 2015; 2021), and over time induce an extinction debt on the plant communities (Kuussaari et al. 2009, Gilbert & Levine 2013). As a consequence of such reinforcing feedbacks, along with the potential longevity, dense growth and poorly palatable leaves of crowberry (Aerts 2010), crowberry-dominance of communities is likely to be a highly resilient state (E.a Kaarlejärvi, Hoset, and Olofsson 2015; González et al. 2021; Wardle et al. 1998; Nilsson and Wardle 2005), and once established, may require strong external disturbances to reverse (Fig 4a-b).

While we show that crowberry encroachment occurs in landscapes across northern Fennoscandia, we also find large spatial variability in this encroachment, indicating there are landscape areas and ecological contexts in which the shift seems weaker or absent (Fig. 3b, Supplementary Table S3). Tundra vegetation changes are repeatedly found to be spatially heterogeneous across scales (Björkman et al 2020, van Wijk et al. 2004) and can be linked to e.g., variation in microclimate or herbivory. For instance, cyclic small rodent outbreaks across

the resurveyed region can decimate dwarf-shrubs and especially crowberry in patches across landscapes (Tuomi et al. 2018; Hoset et al. 2017) (Fig. S3) - a temporary reduction even detectable from space (Olofsson, Tømmervik, and Callaghan 2012). However, strong localized rodent impact has not limited the overall high-magnitude encroachment of crowberry documented here.

While neither small nor large herbivores may halt the trend of allelopathic encroachment across tundra pastures, they are likely adversely affected by the observed, extremely low abundance of forbs and diminishing prevalence of communities with little crowberry (Oksanen et al. 2020; Iversen et al. 2014). Apart from reindeer, other endotherm herbivores, such as small rodents, ptarmigans, domesticated sheep and musk-ox also rely on N-rich forage (Schmidt et al. 2018), and seek pastures with high-quality food (Iversen et al. 2014; Jenkins et al. 2020; Skarin et al. 2020). Furthermore, crowberry being a wind-pollinated plant (Bell and Tallis 1973), its encroachment over forbs may over time also affect insect pollinators. In summary, crowberry encroachment of the magnitude documented here raises significant concerns of cascading effects onto the tundra ecosystem and human beneficiaries relying on them – including pastoralists, sheep farmers and game hunters.

*Encroaching allelopathy in a management blind spot*

A trajectory towards stronger allelopathy (Fig 4b) – resulting in lowered pasture process rates, forage availability and carrying capacity – induces a risk of mismanagement and loss of resilience of the SES (Valéry, Fritz, and Lefeuvre 2013; Carey et al. 2012; Shackleton, Shackleton, and Kull 2019). Therefore our results call for explicit inclusion of norms relating to pasture plant diversity and productivity, especially that of forbs (Bråthen, Pugnaire, and Bardgett 2021), in the management model (Fig 4c), in line with intentions for sustainable reindeer husbandry (lovdata.no) and the urgency of translating the IPBES Global Assessment to policy (Ruckelshaus et al. 2020).

Presently, however, crowberry encroachment, and its ecological and socio-economic impacts, remain largely unobserved and subject to high epistemic uncertainty (cf. Shackleton, Shackleton, and Kull 2019; van der Wal et al. 2015) that can impede development of management norms and objectives (Vaas et al. 2021; Davis et al. 2019). Validation and monitoring of Arctic vegetation change has relied heavily on remote sensing indices (Myers-Smith et al. 2020; Henden et al. 2020), which may not necessarily capture changes in

functional composition (Wang et al. 2021), or indeed, distinguish greening and evergreening as functionally different processes (Vowles and Björk 2019). Adaptive and long-term ecosystem and pasture monitoring programmes are key to mitigating uncertainty about climate-driven vegetation change (Post et al. 2009; Myers-Smith et al. 2019; Lindenmayer and Likens 2009). Such programmes have recently been implemented, for example, in Iceland (Marteinsdóttir et al. 2021), and in the Varanger peninsula and Svalbard, in Norway (Ims and Yoccoz 2017).

Management interventions or norms that promote diversity, productivity and spatial heterogeneity of pastoral landscapes have centennial or even millennial roots in extensive management practices of European coastal heathlands (Webb 2008; Vandvik et al. 2005) and in European agri-environmental policy focused on preventing loss of open semi-natural grasslands (Critchley, Burke, and Stevens 2004). Especially fire has the capacity to ameliorate soil conditions against crowberry's allelopathic effects (Bråthen, Fodstad, and Gallet 2010; Keech, Carcaillet, and Nilsson 2005), suggesting management through burning as a way to control ecosystem state shifts similar to that of coastal heathlands (Vandvik et al. 2005) or boreal *Pinus*-dominated forests (Wardle et al. 1998; Nilsson and Wardle 2005). Here, the challenge lies in the already scarce and diminishing herbaceous resource, the forbs (Bråthen, Pugnaire, and Bardgett 2021), for adaptive monitoring and as a basis for management, emphasising the need to see SES and their management in light of constantly changing biodiversity.

*System-wide consequences of native encroachment*

Encroachment puts an increasing pressure on sustainable land-use planning and prioritization, in particular to preserve remaining forb-rich pastures and enhance productive and diverse tundra landscapes. Evergreening through crowberry encroachment exemplifies emergence of super-dominance among native species, a phenomenon linked with anthropogenic pressures or novel climates across biomes (Pivello et al. 2018; Shackelford et al. 2013; Valéry et al. 2009). We show how the lack of monitoring or management norms for a native species with niche constructing potential can cause an unnoticed development of biotic, bottom-up forcing of a pastoral management system. This also demonstrates how a native species can cause ecosystem effects similar to non-native invasive species, and can

occur in the blind spot of any management system focusing on potential harm from invasive species or changed top-down forcing, only.

Ignoring the capacity of native species to be internal drivers of change is a critical blind spot that threatens the biodiversity and sustainability of ecosystems. We recommend that norms and objectives constantly informed by ecosystem-based monitoring will enhance sustainable management of diversity, and complex social-ecological systems. For the Arctic pastoral system studied here, the management of tundra ecosystems and SES post-2020 should align targets of reindeer and biodiversity management, and ensure resilience through explicit norms related to its resource base; the biodiversity of forage.

*Materials and Methods*

**Study area and resurvey design.** We conducted a vegetation survey of 292 remote, georeferenced vegetation communities in summer pastures across Northern Norway (lat N69° 25.806'- N70° 58.471', lon E20° 47.186'- E27° 31.099') during peak growing season in 2003 and again in 2020. The study area includes strong climatic gradients from west to east and from coast to inland, altitudinal variation from 60 to 600 m asl, as well as variation in bedrock types. Sampling included the most common vegetation types in the region: heaths, mires, snow beds, meadows, and windblown ridges. The survey design (Supplementary Figure S2) incorporates summer pasture areas of 20 reindeer districts, where adjacent districts of similar climatic conditions were organized into 10 district pairs of contrasting reindeer densities, based on average reindeer density from 1980 to 2003. Within each district, a 2x2 km vegetated grid was assigned out of which a random subset was chosen as landscape areas for sampling. Within each landscape area, a random set of 25 of the 100, 200 x 200m squares that constitute the vegetated grid were assigned for plant community sampling. Squares were then sampled by the transect method (each transect representing a plant community), whereby a 50m transect was placed from the midpoint towards a random GPS-position along a circle with a 50m radius. We used the point-frequency method in 11 plots every 5m along the transect to sample each community (Supplementary Figure S2). Each plot was measured by placing a triangular frame with sides of 40cm and one pin in each corner, counting all intercepts with the vegetation. The *a priori* stratification of the original 2003 design, inclusion rules of transects and sampling method are described in more detail in Bråthen et al. (2007; 2018). In 2020, we resurveyed a subset of 292 (of the original 1450) communities in 56 (of if the original 151) landscape areas. The re-sampling retained the

geographic extent as well as most of climatic and abiotic variability. *A priori*, we also set a higher priority to resample communities where crowberry occurrence was lower in 2003, i.e., in transects where crowberry did not occur along the entire transect, to allow for detection of changes in crowberry extent. This was accomplished by limiting sampling to transects where crowberry *occurrence* was in lower 70% quantiles of the entire 2003 dataset. We were only partially able to follow this prioritization due to limited accessibility to sites, and hence also transects with higher than 70% crowberry occurrence in 2003 were included in the sample. Based on transect descriptions from 2003 (e.g., "transect was moved 10m backwards due to a lake") we accurately relocated all resampled communities that were measured in 2003.

**Environmental data.** We estimated climatic trends between 1957 and 2019 in the studied summer pastures for growing degree days (GDD), using data described in Pedersen (2021). We applied segmented linear regression models using the R-package segmented (Muggeo 2017) to explore trends and breakpoints in the mean estimates for the regional climate.

We retrieved data on reindeer numbers from the onset of the reindeer herding year (cf. Stien et al. 2021) for each studied reindeer herding district (Ministry of Agriculture, accessed via reinbase.no), which we then divided by summer pasture area ($km^2$) to obtain reindeer density for each district (individuals/$km^2$). We used the average density from 1980 to 2003 as a predictor for the 2003 vegetation data, and average density from 2003 to 2019 as a predictor for the 2020 vegetation data.

**Vegetation sampling.** We used the point-intercept method (Bråthen and Hagberg 2004) with a triangular 3-pin frame to obtain a measure of vascular plant abundance. We counted all hits of all vascular species in 11 0.08$m^2$ plots spaced along each 50m transect. Prior to further analysis, we converted point-frequency hits per species per plot to biomass estimates (g/$m^2$) using established calibration equations (Tuomi et al. 2018; Ravolainen et al. 2010). For analyzing biomass data, we first pooled species-specific biomass estimates based on functional grouping to forbs, graminoids, deciduous woody shrubs and dwarf-shrubs (deciduous woody), and crowberry. Other groups not included in the analysis (Supplementary table S2) were other evergreen woody dwarf-shrubs, non-woody evergreen plants and vascular cryptogams. We then averaged biomass of all 11 plots along each transect to reach a community-averaged estimate of g/$m^2$ for forbs (non-zero sample size $N_{year}$: $N_{2003}$ = 136, $N_{2020}$ = 136), graminoids ($N_{2003}$ = 257, $N_{2020}$ = 252), deciduous woody ($N_{2003}$ = 282, $N_{2020}$ = 279), and crowberry ($N_{2003}$ = 261, $N_{2020}$ = 269). We also calculated and analyzed the cover of crowberry within each community, using plot-level presence-absence data and summarized numbers of plots with crowberry present in each transect (results in Supplementary table S4).

**Statistical analyses.** To test our first two hypothesis, we used Bayesian linear multilevel models fitted with the package *brms* (Bürkner 2017) in the R statistical environment (version 4.0.4 / 15.02.2021).

We modeled biomass of each plant group and crowberry cover separately, with year (2003 vs. 2020) and reindeer density and their interaction as population-level predictors. Landscape areas nested within reindeer districts were set as the group-level predictors of the intercept. We fitted gamma-hurdle models for biomass data and zero-inflated beta models for crowberry extent data. We used package default weakly informative priors for population and group-level predictors and family parameters (Bürkner 2017), and evaluated convergence and independence of HMC chains based on the ^R statistics (< 1.1) and effective sample size (> 1000) (Muth, Oravecz, and Gabry 2018). We confirmed model fit visually through posterior predictive checks as well as comparing model-simulated data to observed data (Muth, Oravecz, and Gabry 2018). Data visualization was done with packages ggplot2 (Wickham 2009) and ggdist (Kay 2021).

## Data availability

The datasets collected and analyzed in this study as well as R scripts for analysis are available in UiT repository at ---.


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## Author contributions

K.A.B. conceived the idea, M.T., K.A.B. and N.Y. planned the re-sampling design. K.A.B. designed conceptual figures, based on discussions with all authors. M.T., K.A.B., T.Aa.U., N.Y. and S.Z. collected the data. M.T., K.A.B. and N.Y. planned data analysis. M.T. analyzed the data and extracted the results. M.T. and K.A.B. led data interpretation, with all authors contributing to interpreting the results. M.T. wrote the manuscript with frequent advice and support from K.A.B. All authors contributed substantially to editing the manuscript.

## Additional information

**Extended data: Extended discussion**

**Supplementary Material:**

**Supplementary Table S1.** Literature synthesis of key characteristics of crowberry (*Empetum nigrum* ssp. *nigrum* / *hermaphroditum*).

**Supplementary Table S2.** Observed biomass and species richness of all functional groups.

**Supplementary Table S3.** Parameter estimates for plant biomass change from 2003 to 2020 and plant biomass variation with animal density in 2003 and 2020.

**Supplementary Table S4.** Parameter estimates for plant extent change from 2003 to 2020 and plant biomass variation with animal density in 2003 and 2020.

**Supplementary Figure S1.** Map of the study area and illustration of the sampling design.

**Supplementary Figure S2.** Small rodent outbreak impacts on dwarf-shrub vegetation during 2020 re-sampling.

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