Arctic evergreening - encroaching allelopathy in a management blind spot

Tuomi M.W.[1*†], Utsi T.Aa.[2], Yoccoz N.[1], Armstrong C.W.[3], Gonzalez V.[4], Hagen S.B.[4], Jónsdóttir I.S.[5], Pugnaire F.I.[6], Shea K.[7], Wardle D.A.[8], Zielosko S.[1], Bråthen K.A.[1*†]

Affiliations

[1] Department of Arctic and Marine Biology, UiT – Arctic University of Norway, Tromsø, Norway

[2] Department of Arctic and Marine Biology, UiT – Arctic University of Norway, Alta, Norway

[3] The Norwegian College of Fishery Science, UiT – Arctic University of Norway, Tromsø, Norway

[4] Department of Ecosystems in the Barents region, Norwegian institute of Bioeconomy Research-NIBIO, Svanvik, Norway

[5] Institute of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

[6] Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas (EEZA-CSIC), Almería, Spain

[7] Department of Biology and IGDP in Ecology, The Pennsylvania State University, University Park, Pennsylvania, 16802 USA

[8] Asian School of the Environment, Nanyang Technological University, Singapore

* corresponding authors

maria.w.tuomi@uit.no, kari.brathen@uit.no

†These authors contributed equally to this work

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[1–3]. Management blind spots, i.e. *influential variables or processes not included in a management model*, may severely undermine management objectives[4], lead to misguided management efforts, and reduce the capacity of the system to adapt and maintain system resilience against undesirable states[5]. Particularly challenging are slow and poorly detectable changes in external or internal drivers of the system[6] 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[7,8], and opportunities[8,9] for caribou and reindeer (*Rangifer* sp.) populations and associated indigenous pastoral systems[10]. The anticipated warming-induced vegetation trends in summer pastures include increased productivity, biomass and leaf area, which contribute to Arctic greening[11], and shifts towards more resource acquisitive species[12,13]. 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[12,14,15]. Increased productivity of these palatable species should translate into higher population growth rates of ungulates through positive bottom-up effects[9,16]. By foraging, ungulates can even counteract shrubification[17], keeping willows in a "browse-trap"[18], thereby preventing the most nutritious forbs and graminoids from being overgrown[19,20].

However, although rapid changes in climate in the Arctic[21] are altering primary productivity, biodiversity and ecosystem functions[11,22–24], 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[25]. Contradicting satellite-derived inference, field-derived observations show increments in especially evergreen dwarf-shrubs across the circumpolar Arctic[26–29]. These plants often have high phenolics and low N content, and can contribute to lowering ecosystem productivity[30,31]. 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[10,32], 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*)[14,33] (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[34–36]. 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[33,34,37–39]. It can also suppress biodiversity and herbaceous plant growth in summer pastures[14] (Table S1). While herbivores can suppress growth of palatable deciduous shrubs[18,40], their effect on crowberry growth is less clear[28,29], as reindeer avoid crowberry-dominated areas for most of the growing season[41]. 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[42].

In the present paper, our focus is on tundra pastures used for reindeer husbandry, which are core to the indigenous Sámi livelihood and culture[43]. *Rangifer* (reindeer and caribou) grazing systems span the circumpolar area[8] and, akin all extensive pastoral or grazing systems, rely on high-quality plant resources in pastures as forage for the animals[44]. 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[9,45], and an implicit assumption of a stable-state population dynamics, suggesting that population vital rates can be predictably managed via animal density[42] (Fig 1a, Fig 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[42], but this is a blind spot in the management model (Fig 1c). In 2003,

103 crowberry made up the majority of plant biomass across the northern Norwegian tundra,
104 resulting in pastures that are abundant in forage of low nitrogen content (Fig 1b). Monitoring
105 the change in crowberry abundance over time relative to that of the more nutritious shrubs,
106 forbs and graminoids, is vital to understanding the development of these tundra ecosystems
107 and their pastoral SES.
108

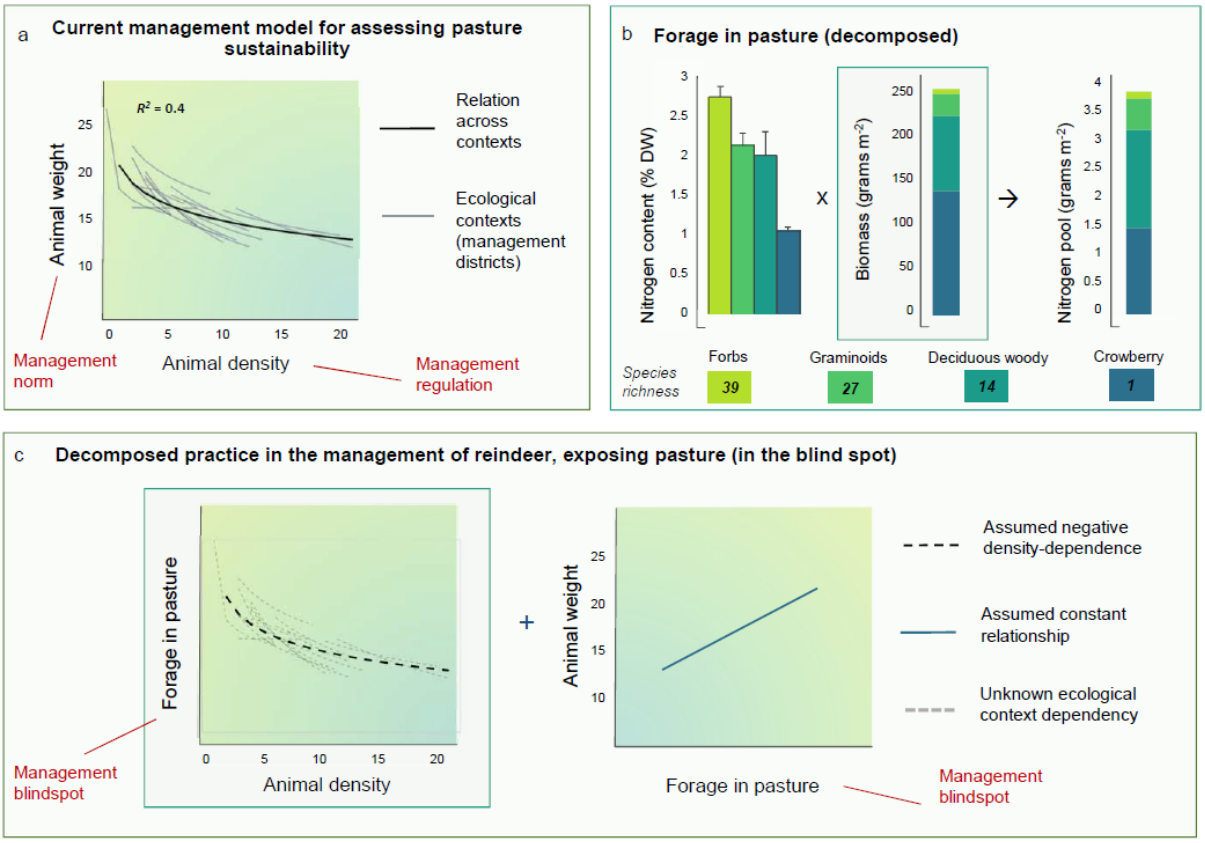

Figure 1. Pastures as a blind spot of a reindeer management system. **The current management of reindeer in Norway applies reindeer density as the regulatory mechanism of sustainable pastures** (*Reindeer Husbandry Act*). The central norm for assessing sustainability of the summer pastures is the autumn 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.

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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 (Fig 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[27,46] and ecosystem functioning[47]. The region has experienced lengthening of the growing season as spring and autumn have become warmer over the past century[48]. 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[15,23,49]. 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[50]. We used Bayesian generalized linear mixed models[51] 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,*

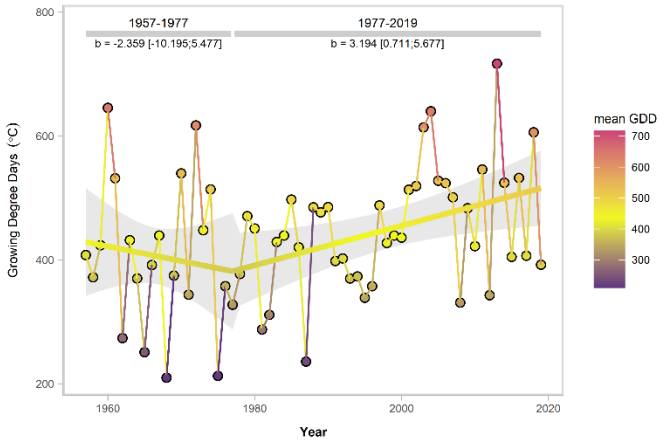

Figure 2. Growing degree days (GDD), as annual sums of daily temperatures above 5°C during May-October 1957-2019, averaged across the studied reindeer summer pastures (Pedersen et al. 2020/met.no). Solid thick line and shaded areas represent mean ± 95% confidence intervals from segmented linear regression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

142 https://www.landbruksdirektoratet.no/nb/nyhetsrom/rapporter/ressursregnskapet-for-
143 reindriftsnaeringen, accessed via reinbase.no). We report results as posterior mean effect
144 sizes (pmes) and their 95% credible intervals (CI), unless stated otherwise.
145
146 Results
147 *Vegetation changes in tundra pastures*
148 Over the 18 growing season interval of our surveys, crowberry standing biomass
149 increased by 60% (Fig 3, Table S2), and by 14% in cover (Table S3). The increase in crowberry
150 is in sharp contrast with a complete stagnation in the standing biomass and cover of the more
151 nutrient rich and faster growing forbs and graminoids over this period (Fig 3a, Table 1, Tables
152 S2 and S3). Crowberry's increase is
153 nearly an order of magnitude larger
154 than the increase of deciduous dwarf-
155 shrubs and shrubs (Fig 3a, Table 1, Table
156 S3). The frequency of communities for
157 which more than 25% of total vascular
158 biomass was crowberry rose significantly
159 over this period [pmes 0.57; 95%CI 0.10-
160 1.05], from an already high 0.76 to 0.83,
161 suggesting that an increasing number of
162 communities is subject to allelopathic
163 effects from crowberry.

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

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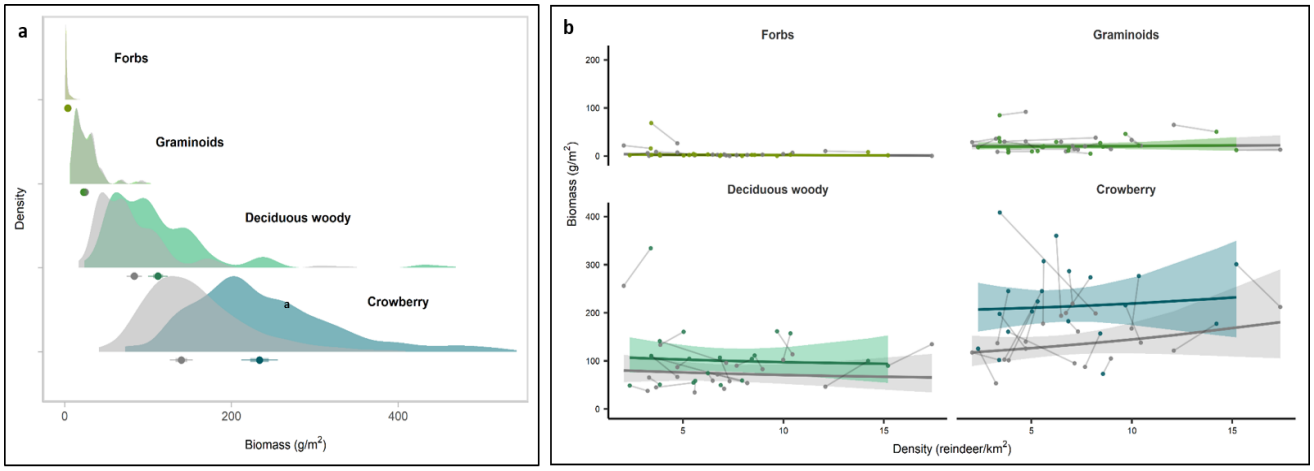

Figure 3. Changes in the abundance of plant groups of pasture forage in the management blind spot. **a)** Modelled posterior predictions of biomass of forbs, graminoids, deciduous woody plants and crowberry, separately for each plant group in 2003 (grey) and in 2020 (greens). Means and 95% confidence 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[28,29,46] far outpaces that of the deciduous shrubs – species typically linked to the process of greening[15,23,49]. 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.

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. 52], 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[41,53], adding to ongoing loss of land with productive pastures due to human disturbance[32] and other stressors[10,54]. Such loss may even amplify other stressors, further eroding resilience of the system.

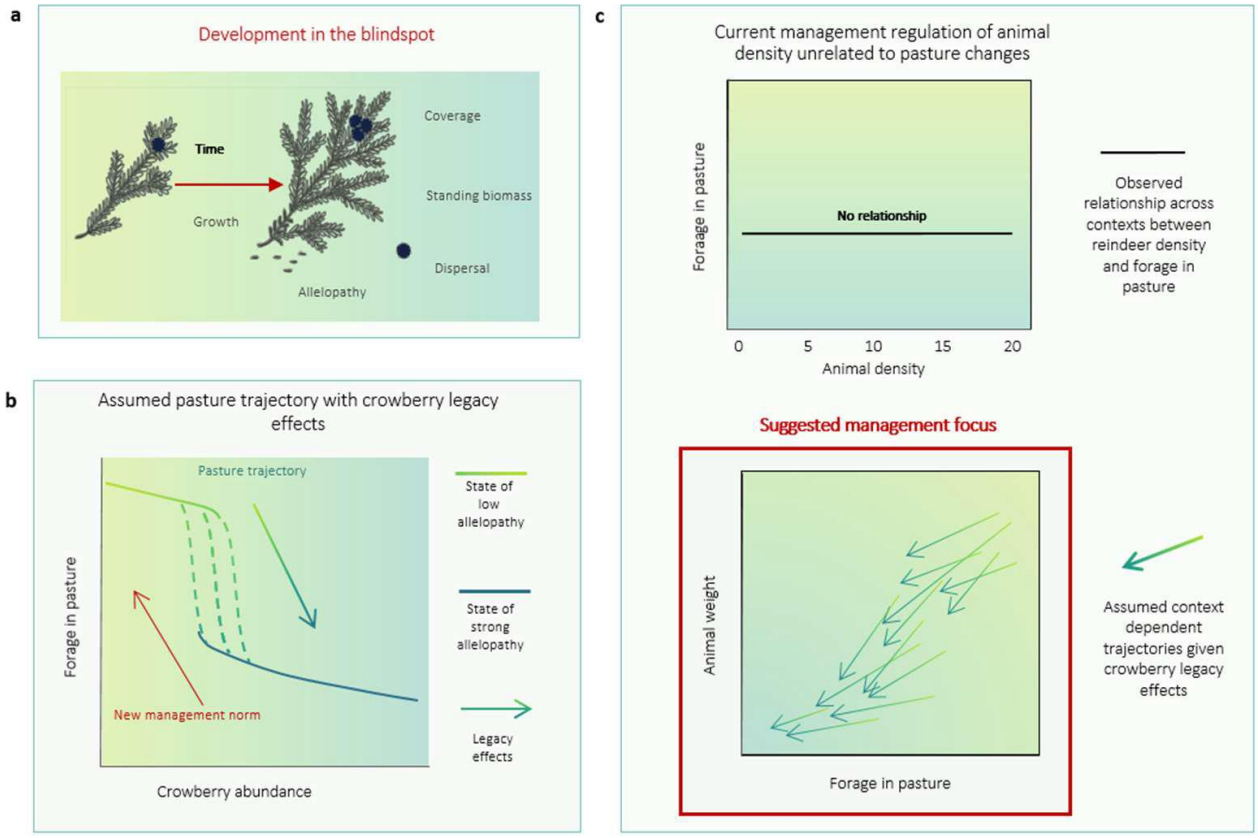

Figure 4. a) Mechanisms of crowberry encroachment and increased allelopathy over time. Growth of established plants results in infilling and increased biomass, leading to stronger allelopathic litter effects. Dispersal via seeds and clonal reproduction are means of lateral encroachment. Already an abundant 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.

193

194 *Evergreening: tundra pastures in transition*

195 As a strong niche-constructing species, crowberry can modify the environment once
196 established[14,33,38] and through legacy effects and reinforcing feed-backs, push the system
197 towards a state of strong allelopathy (Fig 4a-b, Table S1). Consequently, we suspect that the
198 legacy effects at the community- and ecosystem-level from crowberry allelopathy may
199 represent an ongoing shift with potential context-specific thresholds [55] (Fig 4b-c). Diminishing
200 diversity may happen gradually through reduced seedling recruitment [38,56], and over time
201 induce an extinction debt on the plant communities[57,58]. As a consequence of such reinforcing
202 feedbacks, along with the potential longevity, dense growth and poorly palatable leaves of

203 crowberry[35], crowberry-dominance of communities is likely to be a highly resilient
204 state[33,38,39,59], and once established, may require strong external disturbances to reverse (Fig
205 4a-b).

206 While we show that crowberry encroachment occurs in landscapes across northern
207 Fennoscandia, we also find large spatial variability in this encroachment, indicating there are
208 landscape areas and ecological contexts in which the shift seems weaker or absent (Fig 3b,
209 Table S3). Tundra vegetation changes are repeatedly found to be spatially heterogeneous
210 across scales[12,60,61] and can be linked to e.g., variation in microclimate or herbivory. For
211 instance, cyclic small rodent outbreaks across the resurveyed region can decimate dwarf-
212 shrubs and especially crowberry in patches across landscapes[31,62] (Fig S3) - a temporary
213 reduction even detectable from space[63]. However, strong localized rodent impact has not
214 limited the overall high-magnitude encroachment of crowberry documented here.

215 While neither small nor large herbivores may halt the trend of allelopathic
216 encroachment across tundra pastures, they are likely adversely affected by the observed,
217 extremely low abundance of forbs and diminishing prevalence of communities with little
218 crowberry[41,64]. Apart from reindeer, other endotherm herbivores, such as small rodents,
219 ptarmigans, domesticated sheep and musk-ox also rely on N-rich forage[65], and seek pastures
220 with high-quality food[41,53,66]. Furthermore, crowberry being a wind-pollinated plant[67], its
221 encroachment over forbs may over time also affect insect pollinators. In summary, crowberry
222 encroachment of the magnitude documented here raises significant concerns of cascading
223 effects onto the tundra ecosystem and human beneficiaries relying on them – including
224 pastoralists, sheep farmers and game hunters.

225

226 *Encroaching allelopathy in a management blind spot*

227 A trajectory towards stronger allelopathy (Fig 4b) – resulting in lowered pasture process rates,
228 forage availability and carrying capacity – induces a risk of mismanagement and loss of
229 resilience of the SES[68–70]. Therefore our results call for explicit inclusion of norms relating to
230 pasture plant diversity and productivity, especially that of forbs[71], in the management model
231 (Fig 4c), in line with intentions for sustainable reindeer husbandry (lovdata.no) and the
232 urgency of translating the IPBES Global Assessment to policy[72].

233 Presently, however, crowberry encroachment, and its ecological and socio-economic
234 impacts, remain largely unobserved and subject to high epistemic uncertainty[cf. 70,73] that can

impede development of management norms and objectives[54,74]. Validation and monitoring of Arctic vegetation change has relied heavily on remote sensing indices[9,11], which may not necessarily capture changes in functional composition[75], or indeed, distinguish greening and evergreening as functionally different processes[30]. Adaptive and long-term ecosystem and pasture monitoring programmes are key to mitigating uncertainty about climate-driven vegetation change[7,15,76]. Such programmes have recently been implemented, for example, in Iceland[77], and in the Varanger peninsula and Svalbard, in Norway[78].

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[79,80] and in European agri-environmental policy focused on preventing loss of open semi-natural grasslands[81]. Especially fire has the capacity to ameliorate soil conditions against crowberry's allelopathic effects[37,82], suggesting management through burning as a way to control ecosystem state shifts similar to that of coastal heathlands[80] or boreal *Pinus*-dominated forests[33,39]. Here, the challenge lies in the already scarce and diminishing herbaceous resource, the forbs[71], 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[83–85]. 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 (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 (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. [14,50]. 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

300 descriptions from 2003 (e.g., "transect was moved 10m backwards due to a lake") we accurately
301 relocated all resampled communities that were measured in 2003.
302 **Environmental data.** We estimated climatic trends between 1957 and 2019 in the studied summer
303 pastures for growing degree days (GDD), using data described in Pedersen [86]. We applied segmented
304 linear regression models using the R-package segmented [87] to explore trends and breakpoints in the
305 mean estimates for the regional climate.
306 We retrieved data on reindeer numbers from the onset of the reindeer herding year [cf. 45] for each
307 studied reindeer herding district (Ministry of Agriculture, accessed via reinbase.no), which we then
308 divided by summer pasture area (km^2) to obtain reindeer density for each district (individuals/km^2).
309 We used the average density from 1980 to 2003 as a predictor for the 2003 vegetation data, and
310 average density from 2003 to 2019 as a predictor for the 2020 vegetation data.
311 **Vegetation sampling.** We used the point-intercept method [88] with a triangular 3-pin frame to obtain
312 a measure of vascular plant abundance. We counted all hits of all vascular species in 11 $0.08m^2$ plots
313 spaced along each 50m transect. Prior to further analysis, we converted point-frequency hits per
314 species per plot to biomass estimates (g/m^2) using established calibration equations [31,89]. For analyzing
315 biomass data, we first pooled species-specific biomass estimates based on functional grouping to
316 forbs, graminoids, deciduous woody shrubs and dwarf-shrubs (deciduous woody), and crowberry.
317 Other groups not included in the analysis (Table S2) were other evergreen woody dwarf-shrubs, non-
318 woody evergreen plants and vascular cryptogams. We then averaged biomass of all 11 plots along
319 each transect to reach a community-averaged estimate of g/m^2 for forbs (non-zero sample size N_{year}:
320 N_{2003} = 136, N_{2020} = 136), graminoids (N_{2003} = 257, N_{2020} = 252), deciduous woody (N_{2003} = 282, N_{2020} =
321 279), and crowberry (N_{2003} = 261, N_{2020} = 269). We also calculated and analyzed the cover of crowberry
322 within each community, using plot-level presence-absence data and summarized numbers of plots
323 with crowberry present in each transect (results in Table S4).
324 **Statistical analyses.** To test our first two hypothesis, we used Bayesian linear multilevel models fitted
325 with the package *brms*[51] in the R statistical environment[90] (version 4.0.4/15.02.2021 and later). We
326 modeled biomass of each plant group and crowberry cover separately, with year (2003 vs. 2020) and
327 reindeer density and their interaction as population-level predictors. Landscape areas nested within
328 reindeer districts were set as the group-level predictors of the intercept. We fitted gamma-hurdle
329 models for biomass data and zero-inflated beta models for crowberry extent data. We used package
330 default weakly informative priors for population and group-level predictors and family parameters[51],
331 and evaluated convergence and independence of HMC chains based on the ^R statistics (< 1.1) and
332 effective sample size (> 1000)[91]. We confirmed model fit visually through posterior predictive checks

as well as comparing model-simulated data to observed data[91]. Data visualization was done with packages ggplot2[92] and ggdist[93].

Data availability

The datasets collected and analyzed in this study as well as reproducible R scripts for analysis are made publicly available (CC-BY license) via UiT repository (https://dataverse.no/) at DOI: ---.

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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.

Competing interests

The authors declare no competing interests.

Materials & Correspondence

Maria W. Tuomi (maria.w.tuomi@uit.no)

Kari Anne Bråthen (kari.brathen@uit.no)

Additional information

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.

Extended discussion.

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