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# The increase of an allelopathic and unpalatable plant undermines reindeer pasture quality and current management in the Norwegian tundra

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Ongoing Arctic greening can increase productivity and reindeer pasture quality in the tundra. However, greening may also entail proliferation of unpalatable species, with consequences for pastoral social-ecological systems. Here we show extensive greening across 20 reindeer districts in Norway between 2003 and 2020, which has reduced pasture diversity. The allelopathic, evergreen dwarf-shrub crowberry increased its biomass by 60%, with smaller increases of deciduous shrubs and no increase in forbs and graminoids, the most species rich growth forms. There was no evidence for higher reindeer densities promoting crowberry. The current management decision-making process aims at sustainable pasture management but does not explicitly account for pasture changes and reduced diversity. Large-scale shifts towards evergreening and increased allelopathy may thus undermine the resource base for this key Arctic herbivore and the pastoral social-ecological system. Management that is sensitive to changes in pasture diversity could avoid mismanagement of a social-ecological system in transition.

Rapid changes in the Arctic climate[1] are altering primary productivity, biodiversity, and ecosystem functions[2–5], with effects cascading to and interacting with herbivore populations and coupled social-ecological systems[6,7]. Prevalent warming-induced vegetation trends include increased productivity, biomass, and leaf area, identified as ecological greening of the Arctic[2], and shifts towards more resource-acquisitive plant species[8,9]. In practice, such changes are expected to manifest as an increased abundance of plants with taller stature and higher nitrogen (N) concentrations, especially willows and other deciduous shrubs, but also graminoids and forbs[8,10,11]. In areas where shrubs are already present or dominant, their growth can occur via increased cover, i.e., infilling of existing patches, or accumulation of biomass, i.e., vertical growth[12]. Recent observations, however, indicate that Arctic vegetation changes conceal functionally contrasting trends. Field observations show increases especially in evergreen dwarf shrubs across the circumpolar Arctic[13–19]. Evergreen plants often have high phenolic and low N content and can contribute to lowering ecosystem productivity[20,21]. An "evergreening" trend may therefore be functionally distinct from that of greening by deciduous plants, as it may suggest an ongoing decline in process rates, herbivore forage quality, and biodiversity[10], despite increasing biomass in vegetation.

The proliferation of poorly palatable vs. palatable plants will likely have distinct consequences for herbivore populations and associated social-ecological systems. In a rapidly changing Arctic, *Rangifer* (reindeer and caribou) herding systems are readily subject to multiple climate and anthropogenic stressors that affect food availability (e.g., rain-on-snow events that lead to impenetrable ice layers that prevent foraging) and access to pasture (e.g., tourism and infrastructure)[22,23]. Until now, however, changes in Arctic vegetation composition have been little considered among

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the novel threats to caribou and reindeer populations and indigenous pastoral systems[22,24,25].

*Rangifer* are the most numerous Arctic ungulates, with grazing systems that span the circumpolar area[25], and that are core to the indigenous Sámi livelihood and culture[26]. Akin to all extensive pastoral or grazing systems, *Rangifer* herding relies on high-quality plant resources[27,28]. Increasing plant productivity and abundance of N-rich and palatable herbaceous and deciduous species are expected to translate into higher survival and population growth rates of reindeer through positive bottom-up effects[28–30]. In contrast, poorly palatable species may reduce pasture productivity and quality to the extent that reindeer avoid areas where their dominance is high[31]. In a recent example, the satellite-derived greening signal in North America was negatively related to caribou population growth rates, which was attributed to the expansion of deciduous shrubs with high levels of anti-browsing defenses[32]. The balance between the proliferation of poorly palatable and palatable plant species in *Rangifer* pastures across space and time, however, is poorly known.

Arctic terrestrial ecosystems often host strong herbivore-plant interactions, with co-occurring bottom-up and top-down dynamics[33–35]. Arctic *Rangifer* has highly context-dependent impacts on vegetation[36], although they theoretically can strongly impact plant biomass along gradients of productivity through top-down effects[33]. In line with top-down effects, *Rangifer* has been found to modulate warming-induced vegetation changes. For instance, reindeer can counteract shrubification[37], e.g., keeping nutritious willows in a "browse-trap"[38], and thereby prevent the even more nutritious forbs and graminoids from being overgrown[39,40]. Suppression of palatable species may, however, not be representative of how herbivores affect less palatable plants. For instance, the ability of *Rangifer* to modulate warming-induced changes in dominant, nutrient-poor evergreen dwarf shrubs is less clear[15,16].

Central to many Arctic ecosystems and their change is the evergreen dwarf shrub crowberry (*Empetrum nigrum*), a niche-constructing, allelopathic species[10,41] (Supplementary Notes). In Fennoscandia, crowberry is already abundant and commonly dominant. As a boreal-Arctic species, it appears to thrive under a warming climate in the tundra and it tolerates various environmental stressors[42–45]. Owing to its low foliar nutrient concentrations, high levels of allelopathic polyphenolic compounds in its leaves, and a dense, clonal growth form, crowberry is highly unpalatable, and can substantially retard ecosystem processes such as litter decomposition, soil nutrient fluxes, and seedling establishment[41,42,46–48]. Its dominance is related to suppressed biodiversity and herbaceous plant growth in summer pastures[10] (Supplementary Notes), and reindeer have been found to avoid crowberry-dominated areas for most of the growing season[31].

In the present work, we analyze vegetation across 20 reindeer districts in Norway to assess both temporal changes and spatial variation in reindeer summer pastures, and to what extent the associated Norwegian reindeer management[49] is capturing these changes (Fig. 1). Summer pastures and their N-rich forage are critical for building up reindeer body mass to buffer against winter mass loss and starvation, especially for juveniles[50,51]. The current reindeer management decision-making process aims at sustainable management of pastures[49,52]. However, the indicators used in the decision-making process do not measure the summer pastures and their condition directly[53]. Instead, more feasibly measurable, indirect indicators that also link to the economic evaluation of the industry are assumed to reflect the state of the system[53]. Decision-making is thus based on an empirically supported negative density-dependent relationship between reindeer numbers and body mass as the primary indicator[54,55] (Fig. 1d, Supplementary Fig. 2), and this relationship is assumed to be unaffected by long-term changes[56]. The consequence is that long-term changes in productivity – a key determinant of the sustainability of pastures and the husbandry – are managed through mandatory reductions of reindeer densities, easing the assumed top-down regulation of the pastures (Fig. 1b, e) whenever animal slaughter weights (or other state variables indicative of reindeer body condition)[53] fall below a threshold. However, negative density-dependence in animal populations is not due only to changes in resources[56], and pasture

productivity and composition may develop independently of animal densities, leading to bottom-up effects (Fig. 1b, e).
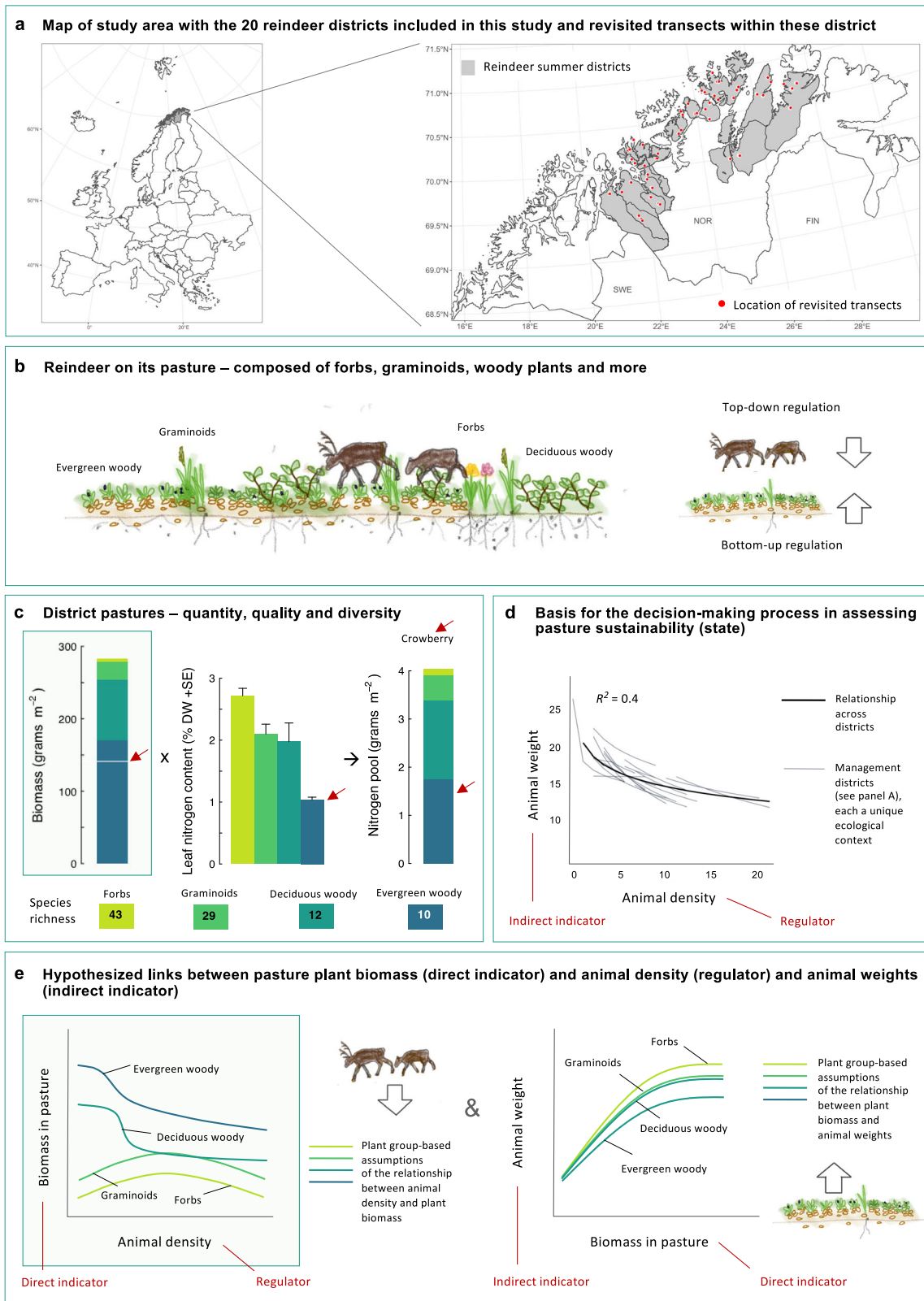
In contrast to the current management decision-making, which emphasizes short-term and homogeneous temporal and spatial effects of pastures on animal populations[53], a community ecological perspective sees the pastures themselves as neither stable nor uniform (Fig. 1b, c). There is a large variation in nutrient content between the plant functional groups in pastures (Fig. 1c), and the plant groups may respond differently to herbivory (Fig. 1e) and to other temporal and spatial factors, such as climate (temporal confounding) and bedrock nutrient content (spatial confounding). Therefore, plant responses to reindeer densities are likely to vary between plant functional groups in both time and/or space. Temporal and spatial patterns of plant groups and community compositions are thus important determinants of changes in summer pasture quality (Fig. 1c), and hence of reindeer nutrition and growth (Fig. 1e). For instance, pastures abundant with the most nutritious plant groups could support high calf weights, whereas weights may saturate at lower levels if pastures consist mainly of crowberry (Fig. 1c, e). In 2003, crowberry made up the majority of plant biomass across the northern Norwegian tundra, already resulting in pastures that were abundant in poor-quality forage of low nitrogen content (Fig. 1c).

We apply a unique, large-scale resurvey of 292 georeferenced plant communities within 56 landscape areas sampled in 2003 and 2020 across 20 reindeer summer districts in northern Norway (Supplementary Fig. 1), to assess variation in vegetation biomass and cover over time relative to reindeer densities. We used averaged reindeer densities from the previous 24 years for 2003 (1980–2003, same data as in ref. 57) and 18 years for 2020 to avoid temporal overlap in the data (2003–2020[58] accessed via reinbase.no), and decomposed these density values into temporal, spatial and residual components for analysis[50,59]. Here, the temporal component (one value for 2003 and 2020, respectively) captures the direction and extent of change. For instance, with an increase of over 100 growing degree days (GDD) in the studied summer pastures since the 1960s and 1970s[60] (met.no) (Supplementary Fig. 3a), the pastures have been subject to a prolonged growing season, which can be a key driver behind increased shrub growth[4,11,61]. In contrast, the average reindeer density across all districts barely changed from 1980–2003 to 2003-2019, increasing from 6.44 to 6.71 animals/km$^2$ (the numerical basis for the temporal component, Supplementary Fig. 3b). Reindeer density differed on the other hand strongly between districts (the spatial component in Supplementary Fig. 3b).

We ask (1) how preferred forage plants (forbs, graminoids, and deciduous dwarf shrubs) and less palatable evergreen dwarf shrubs – with a focus on crowberry – vary in time, and with reindeer density across space and in time among reindeer summer districts, and (2) what are the implications of these changes for reindeer management decision-making. Given the strong ongoing warming trend in the region, we hypothesize that all species and functional groups increase in abundance over time, including crowberry and other evergreen dwarf shrubs. However, if the existing decision-making process is adequate for achieving a sustainable management of pastures and husbandry, the variation in pasture plant composition and biomass should be linked to spatial variation in reindeer density, or to its district-level variation over time. We thus ask if palatable plant groups have a more positive abundance response in management districts with low-to-intermediate or decreased reindeer density (cf. Figure 1e) and if evergreen dwarf shrubs have a more positive abundance response in districts with high or increasing reindeer density.

## Results

Across the entire study area, crowberry standing biomass increased by 60% (Fig. 2a, Supplementary Table 1a), and crowberry cover by 14% (Supplementary Tables 1b and 2) from 2003 to 2020. The increase of deciduous dwarf-shrub biomass was nearly an order of magnitude smaller than that of crowberry's (Fig. 2a, Table 1), and we found no change in the cover of deciduous dwarf-shrubs (Supplementary Tables 1b and 2). The change in crowberry and deciduous shrubs was spatially consistent, as they increased

**a** Map of study area with the 20 reindeer districts included in this study and revisited transects within these district

**b** Reindeer on its pasture – composed of forbs, graminoids, woody plants and more

**c** District pastures – quantity, quality and diversity

**d** Basis for the decision-making process in assessing pasture sustainability (state)

**e** Hypothesized links between pasture plant biomass (direct indicator) and animal density (regulator) and animal weights (indirect indicator)

in biomass in 90% and 85% of the districts, respectively. The increase in the woody shrubs' biomass, crowberry in particular, was in sharp contrast with no change in the biomass and cover of forbs and graminoids (Fig. 2a, Table 1, Supplementary Table 2). The frequency of pasture communities in which more than 25% of total vascular biomass was crowberry, rose over this period from an already high 0.76 to 0.83.

We found that the spatial pattern in district-level reindeer densities had a negative relationship with forb biomass (Table 1, Fig. 2b). This effect was, however, relatively weak (Table 1). The shape of the relationship was also different from the expectation, with a non-significant quadratic term (Table 1). There was no evidence that the spatial differences in reindeer densities explained variation in any of the other plant groups.

**Fig. 1 | Role of summer pastures in the reindeer management system.** The current management decision-making process of reindeer in Norway applies reindeer density as the regulatory mechanism of sustainable pastures[49]. Autumn slaughter weight of animals, as a proxy for body condition, is used as the indicator for assessing the sustainability of the summer pastures (state of the system), and no measures pertaining to the pastures themselves. **a** The study area includes 20 management districts, spanning two latitudinal and six longitudinal degrees and representing different ecological contexts. Within each district, we analyzed transects for plant quantity, quality, and diversity in 2003 and in 2020. **b** Reindeer interact with the functional groups in their pasture through top-down and bottom-up effects. Approximate pasture functional group composition is visualized based on 2003 data[57]. **c** In 2003, across the studied summer pastures, the pasture consisted of plant functional groups of varying species richness[57], nitrogen content[120], and biomass[57]. Forbs, the most nutritious and species-rich group, made up the least biomass in the pastures. Conversely, the evergreen dwarf-shrubs, the least nutritious and species-poor group, made up the most biomass and with crowberry (red arrows) making up most of this biomass but not of the nitrogen pool. **d** The management decision-making applies animal weight as an indirect indicator of pasture condition, here expressed as density-dependence of calf body mass in 2000–2019 within and across the management districts of the current study[58]. **e** The role of plant biomass (direct indicator of pasture condition) in linking reindeer densities and weights[49,52]. The decision-making process implicitly assumes a negative top-down relationship between animal density and plant biomass and a positive bottom-up relationship between plant biomass and weights (see ref. [29]). Here, we inspect these assumptions further for plant functional groups. Forbs and grasses, as more grazing-tolerant groups, are expected to have an unimodal response to animal density[121]. Deciduous shrubs are expected to show patterns of a browsing-trap at densities above 5 animals/km2[38], whereas evergreen shrubs are expected to be little affected by browsing[31] but may decline under trampling effects[42]. Per biomass unit, we assume the most nutritious forbs to have the highest contribution to animal weights followed by graminoids, deciduous and evergreen shrubs in declining order of nutrient content respectively. Framed graphs in (**c**) and (**e**) are patterns and relationships that are empirically addressed here.

In the studied districts, average reindeer densities declined in 40%, increased in 55% and stayed stable in 5% of reindeer districts (calculated with a change threshold of 0.1 reindeer/km2, Supplementary Fig. 4). None of these district-specific deviations in density from the spatial and temporal means, i.e., the residual component, explained variation in any of the plant groups (Table 1, Supplementary Fig. 5). In our dataset, the spatial scale for important group-level effects differed between plant groups. Crowberry biomass varied substantially among landscape areas within reindeer districts, but little between districts (Fig. 2c, Supplementary Table 3). Deciduous shrubs and graminoids varied markedly between both districts and among landscape areas. In contrast, variation in forb biomass was largest between – and not within – districts (Fig. 2c, Supplementary Table 3).

## Discussion

In line with our first expectation and corroborating the hypothesized evergreening and greening trends, we found substantial increases in woody vegetation biomass in reindeer summer districts. The difference in magnitude between the evergreen and deciduous woody plant proliferation, however, was surprising, with pasture evergreening far outpacing greening by deciduous shrubs. We found no evidence that variation in woody species was linked with spatial density patterns nor with district-specific changes in reindeer densities. Therefore, it is plausible that the observed substantial changes are attributable to temporal effects such as the increase in growing degree days (Supplementary Fig. 3a)[62] or snow conditions[63]. Such causal links remain to be established. The proliferation of crowberry appears to mainly occur through accumulation of biomass (vertical growth), but also through infilling, whereby ever larger surface areas are potentially impacted by crowberry.

In contrast to the expectation of change over time, the least abundant, yet most species-rich and productive plant groups, the forbs and the graminoids, showed estimates of temporal change that were negative but not significant. This result was surprising, given the overall warming trend, which could be expected to favor herbaceous growth forms. Their increase was potentially inhibited by the more successful crowberry proliferation and increased allelopathy. Furthermore, there was no indication of a temporal change in forb and graminoid biomass related to reindeer density. The spatial negative relationship of forbs and reindeer density, also being present in 2003[57], may therefore not be informative to predict changes over time. Nevertheless, the continued low abundance of the most productive plant groups combined with the rapid proliferation of the least palatable evergreen dwarf-shrubs across landscapes is likely of high importance for pasture management and the pastoral social-ecological systems as well as for tundra ecosystem management in general.

Our results point at evergreening and crowberry proliferation as potential major bottom-up forcing on the pastures (Fig. 2a, c) (cf. ref. [64]), effectively decoupled from district-level variation in reindeer density. Sustainable management of tundra pastures and the pastoral social-ecological systems will be contingent on models that are representative of the managed system and its spatial and temporal uncertainties[65–67]. An insufficient decision-making process that misses influential variables or processes may severely undermine management objectives[68], and reduce the capacity of the system to adapt and maintain system resilience against undesirable states[69]. A pastoral management practice that does not monitor changes in the plant resource per se, such as the Norwegian reindeer management decision-making process, would likely remain functional or even thrive under increasing productivity and greening of palatable plants. However, managers would be ill-equipped to detect and manage bottom-up effects that slowly reduce pasture quality (Fig. 3). In the following, we argue that if left unchecked, allelopathic evergreening may have severe, adverse, long-term consequences for the diversity, productivity, and resilience of reindeer pastures and the pastoral social-ecological systems[70–72] (Fig. 3b, right panel).

Allelopathic evergreening involves a set of mechanisms, which potentially cause an ecosystem-state transition. As a niche-constructing species, crowberry can modify the environment once established[10,41,47], as allelochemicals in crowberry's leaves and accumulating litter can push the system towards a state of strong allelopathy (Fig. 3). The growth-inhibiting effects of crowberry litter can remain after the plant itself is gone[43,73,74], giving rise to legacy effects. Diminishing diversity due to allelopathy happens gradually through reduced seedling recruitment[47,75], and over longer time scales induce an extinction debt on the local plant communities[76,77], as local seed banks disappear (Fig. 3a). These legacy effects, along with the potential longevity, recovery potential, dense growth and poorly palatable leaves of crowberry[43], suggests crowberry dominance of communities is likely to be a highly resilient state[41,47,48,78]. Once established, the state may require strong external disturbances to reverse (Fig. 3b, left panel). Consequently, we hypothesize that the long-term effects from crowberry allelopathy at the community- and ecosystem-level may represent an ongoing shift with potential context-specific thresholds[79] (Fig. 3b, left panel) such as soil biological and chemical properties, disturbance regimes, or biotic interactions[80], affecting process rates in the tundra ecosystem.

While we show that crowberry proliferation occurs in landscapes across northern Fennoscandia, low variability at the district scale suggests spatial variation in large-scale factors is of less importance. However, we find spatial variability in crowberry proliferation especially at relatively local landscape scales, indicating there are ecological contexts in which the shift is stronger, weaker, or absent. Tundra vegetation changes are repeatedly found to be spatially heterogeneous across scales[8,81,82] 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[20,33] – a temporary reduction even detectable from space[83]. However, strong localized small rodent grazing before the summers of 2003 and 2020 (Supplementary Fig. 6) has not limited the overall high-magnitude, long-term encroachment of crowberry documented here.

**Fig. 2 | Modeled temporal and spatial variation in plant group biomass (forbs, graminoids, deciduous shrubs and dwarf shrubs, and crowberry).**
**a** Change in time. Estimates of posterior mean distributions of biomass of forbs, graminoids, deciduous shrubs, and crowberry, separately for each plant group in 2003 (gray) and in 2020 (green colors). Means and 95% confidence intervals from observed data for each year are provided as point intervals at the base of each biomass density plot (note a full overlap for forbs and graminoids).
**b** Association between plant group biomass and the spatial density component. Each point represents a reindeer district, showing the mean and model-derived 95% and 80% credible intervals of the estimated posterior mean distribution. The line represents the linear association across all districts.
**c** Model-derived estimates of the relationship of plant biomass and the (recomposed) reindeer density. Each short solid black line connects averaged model estimates in 2003 and 2020 in each district, and a regression line is fitted with log(density) across all districts. Data in all panels includes 100 draws from the posterior distribution, and the colored regression lines and adjusted $R^2$ across all districts are estimated with the package *ggpmisc* functions stat_poly_line and stat_poly_eq[119].
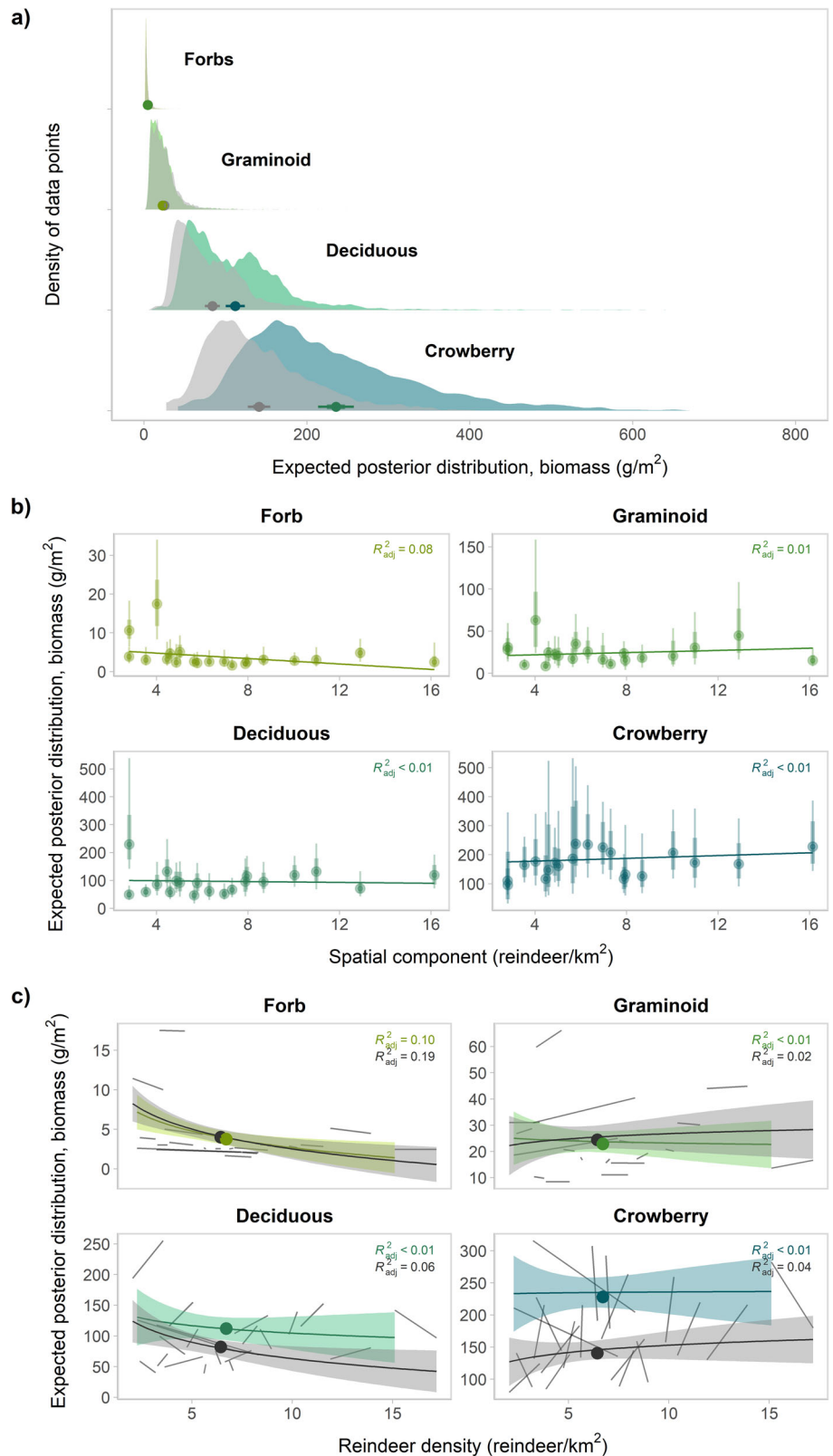


While neither small nor large herbivores may halt the overall trend of crowberry encroachment across tundra pastures, herbivores are also likely adversely affected by the observed low abundance of forbs and diminishing prevalence of communities with little crowberry[31,84]. Apart from reindeer, other endotherm herbivores, such as small rodents, ptarmigans, domesticated sheep, and musk-ox also rely on N-rich forage[85] and seek pastures with high-quality food[31,86,87]. Furthermore, crowberry being a wind-pollinated plant[88], its encroachment may over time also affect insect pollinators. In summary, crowberry encroachment of the magnitude documented here – and predicted e.g., for Arctic Greenland[19] – raises substantial concerns of cascading effects on the tundra biota, ecosystem, and human beneficiaries relying on them, including pastoralists, sheep farmers, and

**Table 1 | Model parameter estimates and credible intervals, with plant functional group biomass as response and decomposed reindeer density as predictors**

| Response | Parameter | Estimate | Q2.5 | Q97.5 |
|---|---|---|---|---|
| Biomass ~ spatial + spatial² + temporal + residual | | | | |
| Forbs | Intercept | 1.791 | 1.408 | 2.169 |
| | *Spatial* | *−0.403* | *−0.797* | *0.007* |
| | Spatial² | 0.205 | −0.086 | 0.480 |
| | Temporal | −0.044 | −0.181 | 0.095 |
| | Residual | −0.049 | −0.170 | 0.079 |
| Graminoids | Intercept | 3.103 | 2.776 | 3.439 |
| | Spatial | −0.047 | −0.419 | 0.310 |
| | Spatial² | 0.072 | −0.178 | 0.320 |
| | Temporal | −0.041 | −0.153 | 0.072 |
| | Residual | 0.042 | −0.052 | 0.137 |
| Biomass ~ spatial + temporal + residual | | | | |
| Deciduous woody | Intercept | 4.491 | 4.255 | 4.732 |
| | Spatial | 0.045 | −0.208 | 0.311 |
| | **Temporal** | **0.220** | **0.139** | **0.300** |
| | Residual | −0.041 | −0.111 | 0.028 |
| Crowberry | Intercept | 5.224 | 5.076 | 5.375 |
| | Spatial | 0.061 | −0.116 | 0.237 |
| | **Temporal** | **0.341** | **0.263** | **0.418** |
| | Residual | 0.014 | −0.050 | 0.077 |

Note that the temporal component is confounded with e.g., GDD (Supplementary Fig. 3a). For estimates of group-level standard deviation (random effects), see Supplementary Table 3. Error terms Q2.5 and Q97.5 represent the 95% credible interval. Bold font indicates strong support for the effect, and italic indicates relatively strong support for the effect, given the data.

game hunters. We therefore suggest that managing for resilience[7] of the tundra ecosystem, and the way forward for reindeer management, should include monitoring, and managing for, sustained pasture diversity.

Crowberry proliferation in summer pastures adds to a host of other stressors, including consequences of climate changes and anthropogenic land uses[22,23]. The changing climate is already undermining conditions for reindeer productivity in winter pastures. Rain-on-snow (ROS) events and freeze-thaw cycles prevent access to the winter pastures[89] and food such as ground lichens, edible meristems, and leaves. Deeper snow increases energy expenditure for mobility and reindeer vulnerability to predation[90], breaking into their energy reserves accumulated from summer pastures.

However, even in evergreening pastures, one would expect calf weights to increase when, in the management decision-making process, maximum allowed reindeer numbers are reduced, simply because there are fewer animals to share the limited resources – the system would appear to work as intended. Yet, this would not mean that the underlying sustainability of the pasture is safeguarded, given that summer pasture quality deteriorates independent of reindeer density. The result can be a loss of ecosystem function, where evergreening and crowberry proliferation forces slow but continuous reductions of reindeer numbers. The current decision-making process alone would not address the underlying cause for this trajectory, nor affect the loss of ecological, social, and economic resilience of the system. Similar dynamics can be expected for rain-on-snow events, where additionally adverse winter conditions increase the need for wintertime supplemental feeding with added direct economic and labor costs of husbandry[22] affecting economic sustainability.

Our results suggest that revision of the current reindeer management decision-making process[53] should add an adaptive component sensitive to long-term, decadal changes in pasture plant diversity and productivity. Along with local knowledge, this should be supplemented through adaptive monitoring[91] and assessment of pasture condition, plant diversity, and productivity, in line with intentions for sustainable reindeer husbandry[49] and adaptation of the IPBES Global Assessment in policy[92]. Development of pasture monitoring alongside demographic state variables is necessary to establish which aspects of summer pastures are most influential for reindeer productivity (e.g., calf weights) and susceptible to external forcing and should be targeted for management. A priori, in summer pastures, particular attention should be given to the most species-rich and nutritious, yet scarce growth form, the forbs[93], especially in regard to anthropogenic land-use stressors.

Presently, crowberry proliferation, and its ecological and socio-economic impacts, remain poorly understood. This can impede the development of novel management norms and objectives[94,95]. First, general acceptance and evidence-based baselines are often difficult to establish for slow and poorly detectable changes[96], such as the creeping infilling and biomass accumulation of a slow-growing dwarf shrub. The trajectory of evergreening is likely long, but large-scale empirical evidence goes back barely half a century[15,18]. Second, contemporary validation and monitoring of Arctic vegetation change has relied heavily on remote sensing indices[2]. Remote sensing may not necessarily capture changes in functional composition[97], distinguish greening and evergreening as functionally different processes[20], or document the species diversity of pastures. Long-term ecosystem and pasture monitoring programs are key to mitigating uncertainty about climate-driven vegetation change[12,24]. Such general programs have recently been implemented, for example, in Iceland[98], and in the Varanger peninsula, and Svalbard, in Norway[91]. Yet, targeted, policy-relevant, and goal-based monitoring protocols to also address important relationships between the resource base and reindeer productivity in summer pastures would support decision-making the most[99], recognizing where the reindeer husbandry context is distinct from ecosystem monitoring in general. Presently, only variation in lichen abundance on winter grazing grounds has been extensively monitored in Norway, as lichen is a critical indicator of the winter resource base, and susceptible to both reindeer activities and climate change[100,101].

Our results suggest that the current regulator of the management system (adjustment of maximum allowed reindeer numbers) may not function in an efficient manner to support resilient and sustainable pastures over the long term. Additional management strategies, interventions, and indicators that directly address spatial and temporal variation in diversity, productivity, and heterogeneity of pastoral landscapes, are needed. Such strategies have centennial or even millennial roots in extensive management practices of European coastal heathlands[102,103] and in European agri-environmental policy that has focused on preventing the loss of open semi-natural grasslands[104]. Fire has the capacity to ameliorate soil conditions against crowberry's allelopathic effects[46,105], suggesting management through burning as one potential way to locally control ecosystem-state shifts similar to those in boreal *Pinus*-dominated forests[41,48]. Regulating and optimizing fire intensity in summer pastures is likely important to ensure the recovery of herbaceous perennials over evergreen dwarf shrubs[106]. For any management action, the challenge lies in the already scarce and diminishing herbaceous resource, the forbs[93]. Scarcity begets scarcity through increasing seed limitation under encroaching crowberry dominance and allelopathic effects[47], and promotion of productive vegetation would likely require re-building seed banks alongside soil amelioration. Spatial rarity also poses challenges for monitoring efforts. Despite such challenges, we believe a resilient management approach to tundra reindeer pastures and pastoral social-ecological systems is both attainable and urgent.

## Conclusions

Evergreening puts increasing pressure on sustainable land-use planning and prioritization to preserve remaining forb and graminoid-rich pastures[107] and the biodiversity of tundra landscapes against rapid homogenization[18,19]. Evergreening through crowberry encroachment exemplifies the emergence of super-dominance among native species, a phenomenon linked with anthropogenic pressures or novel climates across biomes[108–110], with ecological consequences not unlike those of non-native invasive species.

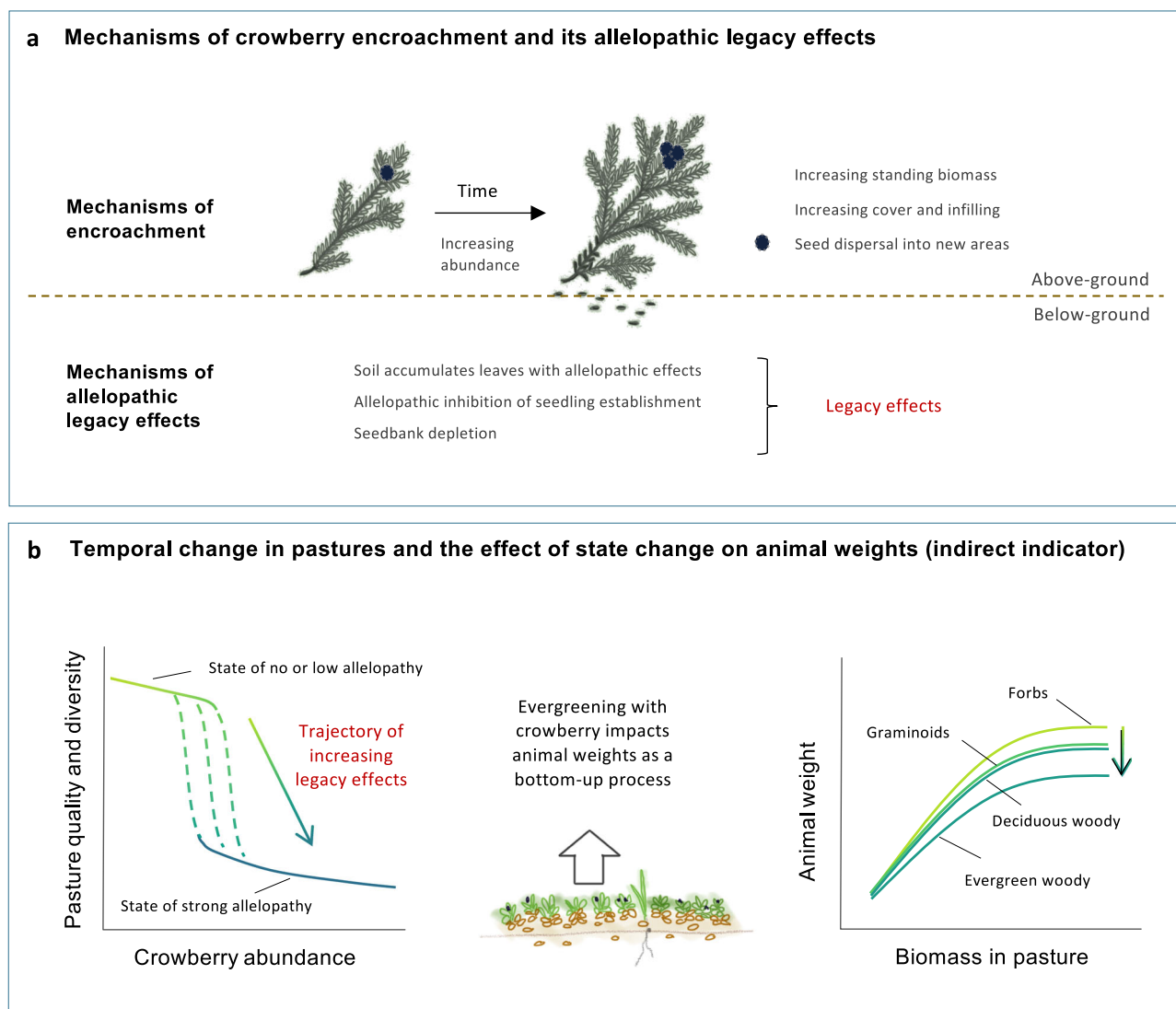**a    Mechanisms of crowberry encroachment and its allelopathic legacy effects**

**Fig. 3 | Mechanisms and consequences of crowberry proliferation. a** Mechanisms of crowberry proliferation and increased allelopathy over time. Already an abundant and long-lived species, slow growth may still cause substantial increments in abundance. The growth of established plants results in infilling and increased biomass, leading to increasing allelopathic litter effects in the soil. In addition, dispersal via seeds and clonal reproduction are means of lateral encroachment, increasing the areal extent of the plant. **b** Potential transition in pasture state and its implication for the state-indicator relationship. Increasing crowberry abundance may push the system towards a state of strong allelopathy. The state may be highly resilient, with litter and seed bank-mediated legacy effects that over time will reduce new plant establishment[47] at levels as low as 25% crowberry out of total community standing biomass[10]. Changing bottom-up effects and transition to increasing allelopathy in pastures may have adverse, yet slow impacts on reindeer conditions. The relationship between pasture biomass and animal weights is assumed dependent on plant composition, with effects of evergreening and crowberry proliferation on reindeer weights.

Overall, our results on crowberry encroachment suggest an ongoing decline in the quality of pasture land[31,87], adding to the ongoing loss of land with productive pastures due to human disturbance[23] and other stressors[22,94]. Loss of pasture quality may additionally amplify other stressors, further eroding the resilience of an increasingly vulnerable Arctic system.

Ignoring the capacity of native species to be drivers of change is a critical blind spot that threatens the biodiversity and sustainability of ecosystems. For the Arctic pastoral system studied here, the management of tundra ecosystems and pastoral social-ecological systems post-2020 should align targets for reindeer productivity and biodiverse pastures, and ensure resilience through targeted, policy-relevant monitoring and monitoring-informed adaptive management. This way, sustainable management of diversity in complex social-ecological systems will be possible in changing climates.

## Methods
### Study area and resurvey design
We conducted a vegetation survey of 292 remote, georeferenced vegetation communities in summer pastures of 20 reindeer herding districts across Northern Norway (Supplementary Fig. 1a) during peak growing seasons in 2003 and again in 2020. The study area (lat N69° 25.806′- N70° 58.471′, lon E20° 47.186′- E27° 31.099′) 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. We applied the original 2003 survey design[57], including the original a priori stratification, inclusion rules of transects, and sampling method. The sampling design (Supplementary Fig. 1b) was spatially nested within districts. Within each district, a 2 × 2 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 25 200 × 200 m squares (of the 100 possible squares constituting 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 50 m transect was placed from the midpoint towards an a priori randomly selected GPS position along a circle with a 50 m radius. The GPS positions of both the start and the endpoints were recorded in 2003 and used in 2020 to relocate the transects. We used the point-frequency method in 11 plots every 5 m along the transect to sample each community (Supplementary Fig. 1). Each plot was measured by placing a triangular frame with sides of 40 cm and one pin in each corner, counting all intercepts with the vegetation[111] (see "Vegetation sampling" section). Based on transect descriptions from 2003 (e.g., "transect was moved 10 m backward due to a lake") we deemed the relocation of communities accurate.

The resurvey design (Supplementary Fig. 1) followed the original design, with three exceptions. First, due to practical reasons, in 2020 we sampled a subset of 292 (of the original 1450) communities in 56 (of the original 151) landscape areas. Only plant communities resampled in 2020 were included in the analysis, making the dataset comparable between time periods. The re-sampling retained the geographic extent as well as most of the climatic and abiotic variability. Second, like the original design, the resurvey incorporated summer pasture areas of 20 reindeer districts, where adjacent districts of similar climatic conditions were organized into 10 district pairs. In the original design, these district pairs included a low and a high-density district based on the 1980 to 2003 average reindeer density. However, due to changes in district-specific densities from 2003 to 2020, this original density contrast did not apply to all district pairs in 2020, and the district pair level was not included in the analysis. Third, we were not able to retain the spatial extent of landscape areas within all districts, meaning that not all *siidas* (smaller reindeer herding units) within each district were represented in the resurvey dataset.

## Environmental data
We estimated climatic trends between 1957 and 2019 in the studied summer pastures for growing degree days (GDD)[60]. We applied segmented linear regression models using the R-package segmented[112] 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[55] for each studied reindeer herding district[58], which we then divided by summer pasture area (km²) to obtain reindeer density for each district (individuals/km²).

## Vegetation sampling
We used the point-intercept method[111] 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 m² plots spaced every 5 m along each 50 m transect. Prior to further analysis, we converted the point-frequency hits per species per plot to biomass estimates (g/m²) using established calibration equations[21,113]. For analyzing biomass data, we first pooled species-specific biomass estimates based on functional grouping to forbs, graminoids, deciduous dwarf-shrubs and shrubs (deciduous woody), and crowberry. Other groups not included in the analysis (Supplementary Table 1A) were other evergreen woody dwarf-shrubs, non-woody evergreen plants, and vascular cryptograms. Other evergreen woody dwarf-shrubs were not included in the statistical analyses as they responded very similarly to crowberry but with comparably low biomass. We then averaged biomass of all 11 plots along each transect to reach a community-averaged estimate of g/m² 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 the cover of the functional groups within each community, using plot-level presence-absence data and summarized numbers of plots with each functional group present in each transect.

## Statistical analyses
To test our hypothesis, we fitted Bayesian linear multilevel gamma-hurdle models with the package *brms*[114] in the R statistical environment[115] (version 4.0.4/15.02.2021 and later). We used the average reindeer densities from the previous 24 years for 2003 (1980–2003[57]), and the previous 18 years for 2020 to avoid overlap in the data (2003–2020[58], accessed via reinbase.no). We decomposed the reindeer density ($D_{s,t}$) to its spatial ($D_S$), temporal ($D_T$), and residual ($D_r$) components[50,59] to not convolute spatial and temporal effects (Eqs. 1–3), and standardized all three predictors to a mean of 0 and variance of 1 for better effect comparability and model convergence. For the spatial component, we averaged the density in each individual district (s) across the two years $t$ ($t = 1,2$). For calculating the temporal component, density was averaged across all districts s ($s = 1, …., B$), for each time period. The residual, a space-time anomaly, was then calculated as the difference between the original density and the spatial and temporal components.

$$D_{s.} = \frac{1}{2} \sum_{t=1}^{2} D_{s,t} \tag{1}$$

$$D_{.t} = \frac{1}{B} \sum_{s=1}^{B} D_{s,t} \tag{2}$$

$$D_r = D_{s,t} - D_{s.} - D_{.T} \tag{3}$$

While the temporal component is numerically derived from the reindeer density, it only tests whether there is a change in time over two time points. The spatial component tests for the effect associated with densities averaged over time in each district and the residuals of the district- and year-specific variation in reindeer densities from the spatial and temporal averages. To fully test the expectations in Fig. 1e, models for forbs and graminoids included a quadratic term for the spatial component, while models for deciduous woody and crowberry were included linear term only, and all models included block and district as group-level intercepts. We fitted the Bayesian generalized linear mixed models with weakly informative default priors[114] and checked model convergence and independence of HMC chains based on the $\hat{R}$ statistics (<1.002) and effective sample size (>2000)[116]. In addition, we fitted negative-binomial hurdle models for plant functional group cover in the same way as described above for biomass data. We used package default weakly informative priors for population and group-level predictors and family parameters[114]. We confirmed model fit visually through posterior predictive checks as well as comparing model-simulated data to observed data[116]. The lack of spatial autocorrelation in group-level effects and model residuals was assessed visually. Data visualization was done with packages ggplot2[117], ggdist[118], and ggpmisc[119].

## Reporting summary
Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability
The datasets collected for this study are publicly available (CC-BY license) via the UiT repository (https://dataverse.no/) at https://doi.org/10.18710/WZ5RSE.

## Code availability
Reproducible R scripts applied for the statistical analysis are publicly available (CC-BY license) via UiT repository (https://dataverse.no/) at https://doi.org/10.18710/WZ5RSE.

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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 with support from M.T., and based on discussions with C.W.A., V.G., S.B.H., I.S.J., F.I.P, K.S., T.Aa.U., D.A.W., N.Y., and S.Z. Data were collected by M.T., K.A.B., T.Aa.U., N.Y., and S.Z. The data analysis was planned by M.T., K.A.B., and N.Y. and M.T. analyzed the data and extracted the results. M.T. and K.A.B. led data interpretation, with C.W.A., V.G., S.B.H., I.S.J., F.I.P, K.S., T.Aa.U., D.A.W., N.Y. and S.Z. contributing to interpreting the results. M.T. wrote the manuscript with and support from K.A.B., and C.W.A., V.G., S.B.H., I.S.J., F.I.P, K.S., T.Aa.U., D.A.W., N.Y., and S.Z. contributed substantially to editing the manuscript.

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## Competing interests

We disclose a link of one co-author, an associate professor, to reindeer husbandry. The remaining authors declare no competing interests.

## Additional information