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Authors: Speed, James D. M., Austrheim, Gunnar, Hester, Alison J., and Mysterud, Atle

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The Response of Alpine *Salix* Shrubs to Long-Term Browsing Varies with Elevation and Herbivore Density

James D. M. Speed§*
*Gunnar Austrheim**
Alison J. Hester† and
Atle Mysterud‡

*Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway
†The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, U.K.
‡Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, NO-0316 Oslo, Norway
§Corresponding author: james.speed@vm.ntnu.no

Abstract

The widespread expansion of shrubs into arctic and alpine regions has frequently been linked to climatic warming, but herbivory can play a role in addition to, or in interaction with, climate. Willow (*Salix* spp.) shrubs are important constituents of alpine ecosystems, influencing community structure and providing habitat and forage for many species. We investigate the impact of browsing by domestic sheep (*Ovis aries*), the dominant herbivore in Norwegian mountains, on *Salix* stem density, height, and radial growth. We used a field experiment, replicated along an elevational gradient, with manipulated densities of sheep (no sheep, low density, and high density at 0, 25, and 80 sheep km^{-2}). We found that *Salix* shoot density and radial growth were greatest at high sheep density but only at low elevations, indicating that competition from field-layer vegetation at lower sheep densities reduced *Salix* performance. At higher elevations *Salix* shoot density and radial growth were lower at high sheep density than at low sheep density and in the absence of sheep. Thus at high elevations sheep browsing is likely to slow the expansion of *Salix* shrubs, whilst the removal of browsing is likely to constrain *Salix* expansion at lower elevations.

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Introduction

Shrubs are expanding in distribution and biomass in many parts of the world (e.g. Sturm et al., 2001; Naito and Cairns, 2011). Understanding the nature of expanding shrub distribution is vital due to close links between shrub expansion and ecosystem carbon balances and feedbacks to the global climate (e.g. Jackson et al., 2002; Bonfils et al., 2012). A range of potential drivers has been identified to explain this pattern of shrub expansion; however, climatic causes are most commonly investigated, particularly in Arctic and alpine regions (e.g. Sturm et al., 2001; Hallinger et al., 2010; Myers-Smith et al., 2011; Macias-Fauria et al., 2012). Concurrently, treelines are also advancing in elevation or latitude in many areas; a meta-analysis found that 52% of studied treelines had advanced, particularly in those areas where winter warming was strongest (Harsch et al., 2009). However, decreasing densities of herbivores can also cause rapid advances in treelines (Speed et al., 2010; Van Bogaert et al., 2011). Contrasting responses of shrub encroachment on the tundra have also been observed in the presence or absence of herbivores (Post and Pedersen, 2008; Olofsson et al., 2009). Thus shrub encroachment is unlikely to be solely influenced by climatic factors, and changes in herbivory may interact with climatic warming to determine shrub dynamics.

Willow species (*Salix* spp.) form an important constituent of Alpine and arctic vegetation, with large influences on ecosystem and community dynamics (Eldridge et al., 2011; Ims and Henden, 2012). *Salix* shrubs provide important forage and habitat for many taxa using alpine areas, including the characteristic and economically important reindeer (*Rangifer tarandus*) and grouse species (*Lagopus* spp.) (den Herder et al., 2008), as well as mountain hare (*Lepus timidus*) (Ehrich et al., 2012), moose (*Alces alces*), and other Cervidae and domestic sheep (Mobæk et al., 2009). Specific understory vegetation is also associated with canopy-forming willows (Pajunen et al., 2011). *Salix* shrubs are highly selected by browsing herbivores (Kitti et al., 2009; Tape et al., 2010) and therefore would be expected to be more strongly affected by herbivore densities than other less preferred species (Gill, 2006). Densities of vertebrate herbivores in the tundra are highly variable in time and space. Their effects on shrub species, such as *Salix*, are predicted to be highly spatially variable, yet this has been little studied (but see Ravolainen et al., 2013).

Populations of domestic and semi-domestic herbivores as well as wild herbivores are managed in alpine ecosystems (Apollonio et al., 2010; Austrheim et al., 2011). In mountainous areas of Norway, livestock (mostly sheep that are released into alpine areas for the summer season) are the dominant vertebrate herbivore, constituting over half of the total metabolic biomass of large herbivores in these regions (Austrheim et al., 2011). The European Alps also have a long history of grazing livestock, and the abandonment of this land use has been linked to afforestation and impacts on biodiversity (Dirnböck et al., 2003; Tasser et al., 2007). Thus there is considerable potential for livestock management in regions with histories of grazing to affect both wild cervids and other herbivore species through their effects on *Salix* shrubs as key browse and habitat provision species.

The response of *Salix* shrubs to browsing in addition to or in interaction with other pressures such as climate will likely determine long-term herbivore-vegetation dynamics in alpine ecosystems. For example, *Salix* patch structure, in terms of area and continuity, is associated with increased willow grouse (*Lagopus lagopus*) occupancy (Henden et al., 2011), and browsing by reindeer on upright *Salix* has been linked to decreases in ptarmigan (*L.* spp.) populations in subarctic tundra (Ims et al., 2007). A recently recorded collapse in the avian community of the subarctic tundra with a halving of species richness could also be linked to browsing-induced decline in *Salix* shrubs (Ims and Henden, 2012). Expansion

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and increases in biomass of erect *Salix* shrub canopies have been observed in the absence of herbivory (Myers-Smith et al., 2010; Ravolainen et al., 2011), and whilst the radial growth of *Salix lanata* has been shown to respond to climatic conditions, it has been suggested that browsing by ungulate herbivores may also play a role in regulating such growth (Forbes et al., 2010). Analyses of annual radial growth have been used to separate the effects of browsing and climate on the growth of mountain birch (Speed et al., 2011a). However, attempts to study the interactions between herbivory and climate on the widespread *Salix* shrubs, which are key species in Arctic and alpine ecosystems, are lacking.

In this study the density and growth response of upright *Salix* stems to browsing were investigated along an elevational gradient, and growth ring analyses used to investigate the different influences of temperature and browsing on radial growth. By using experimentally controlled and replicated densities of enclosed herbivores, we have been able to directly link the response of shrubs to actual densities of herbivores, something that previous studies have not attempted. We tested the hypotheses that *Salix* stem density and height decrease with elevation, and this interacts with browsing such that the elevational decreases in density and height are less where unbrowsed. We also predict that temperature and browsing interact to determine radial growth, with growth increasing at higher temperatures, but with a lower increase when browsed.

Methods

STUDY SITE

A replicated landscape-scale enclosure experiment in the mountains of southern Norway was used to investigate the influence of browsing on *Salix* stems. Nine sub-enclosures with a mean area of 0.3 km^2 were constructed in 2001 located at 7°55′ to 8°00′E, and 60°40′ to 60°45′N. The sub-enclosures were positioned on a south-facing elevational gradient from the forest line (closed birch forest canopy) and into the alpine zone (approximately 1050 to 1320 m a.s.l.). Using a randomized-block design, the nine sub-enclosures were stratified between three herbivory treatments, each with three replicates (Fig. 1). The herbivory treatment involved three densities of the domestic sheep of the Norwegian-white breed, with 0, 25, and 80 sheep km^{-2}, representing no sheep, and low and high densities. Permanent vegetation plots (50 × 50 cm) were established in 2001; these were located by stratification according to vegetation type and elevation, with 20 per enclosure and 180 in total (see Austrheim et al., 2008, for further information). The sheep were grazed within the experiment every summer from 2002 to 2011, from late June to early September in accordance with standard livestock management practice in the region. Wire mesh fencing was used to construct the enclosures. Fences did not prevent access of hare (which could pass through the mesh), and moose or reindeer (which could jump over the fences); however, these herbivores were rarely observed in the enclosures and their impacts were likely negligible.

SAMPLING

In 2010, after 9 years of experimental manipulation of herbivore density, the stem diameter and height distribution within *Salix* shrub patches were sampled. These were selected using all the permanent vegetation plots where at least one stem of any upright species of *Salix* had been recorded at least once in the period 2001 to 2009. The locations of these plots are shown in Figure 1. At each plot, two 5-m transects were positioned at 90° (orientated North–South and East–West) and centered on the northwest corner

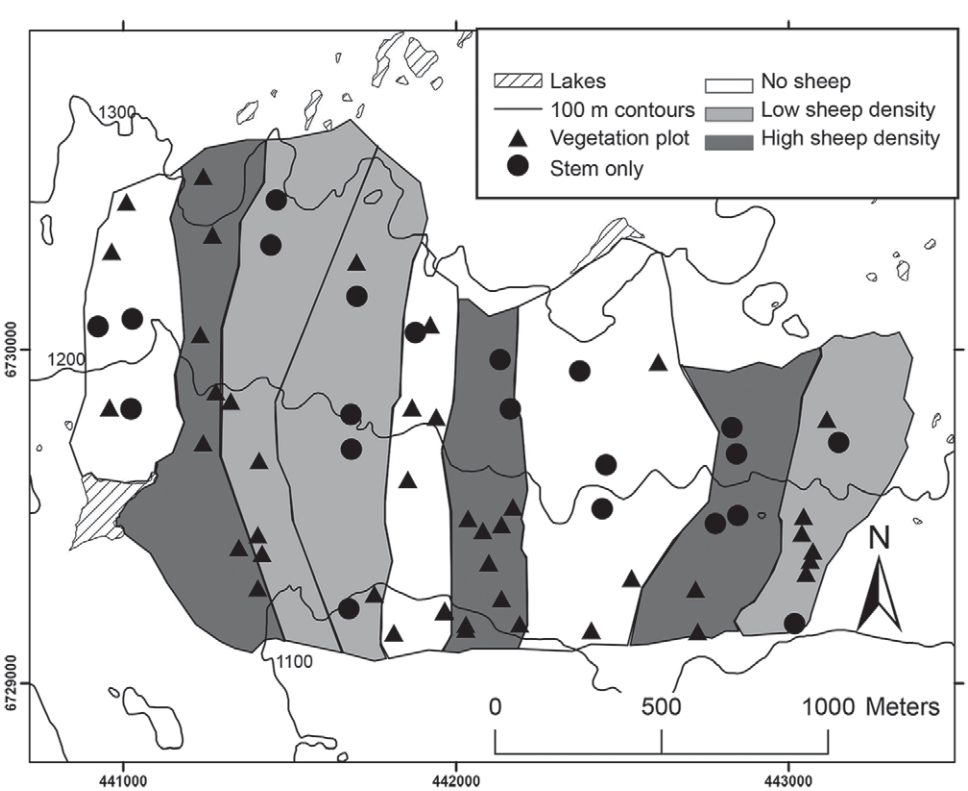

FIGURE 1. Map of experimental site showing sheep density treatments and *Salix* sampling points. UTM coordinates are in zone 32V.

marker of the permanent plot. All upright *Salix* stems intersecting with transect lines were sampled, including *S. lanata*, S. *lapponum*, *S. hastata*, and *S. glauca*. Prostrate species such as *S. arctica* were not recorded since we focus on canopy forming species. The distance of the intersection along each transect was recorded along with the species, vertical height (not stretched, to the nearest 1 cm), and basal stem diameter (measured as close to ground level as possible using a set of calipers to the nearest 0.5 mm) of each *Salix* stem.

RADIAL GROWTH

In 2011 stem basal sections were sampled from the same transects (but outside of the permanent vegetation plots). Additional samples were taken from further localities to increase the range of sampled elevations. These localities were selected randomly within elevational bands to achieve a better balance of elevations (Fig. 1). For each locality, the three closest *Salix* stems were destructively sampled after recording the species, height, and stem basal diameter. Stem basal discs were cut and air dried (for at least two months) prior to preparation for dendrochronological analyses. The upper surface of each disc was cut smooth with a scalpel, and zinc cream was applied to increase the contrast between early and late wood (Hofgaard et al., 2009). Ring widths were measured to the nearest 0.001 mm using a Leica MZ16-A microscope and Leica DFC420 digital camera with Leica Application Suite 3.2 imaging and analysis software (Leica Microsystems, Wetzlar, Germany). Up to four radii separated by 90° were sampled, or the maximum number for which a full chronology could be measured (i.e. where not prevented by e.g. damage). A total of 9 stems were discarded due to poor visibility of rings within the discs. Rings widths from each radius were cross checked for the presence of partial (incomplete) rings. Radial sequences that did not include partial rings were dropped. Next, mean chronologies for each stem base were calculated by averaging across the remaining radii for each stem; this accounts for asymmetrical growth around the stem. The stem-average series were aligned across all stems, imputing missing values (''NAs'') in the case of simple missing rings.

Radial ring widths were converted to annual basal area increment (assuming a circular cross section), as an area-based measure was considered a more reasonable approximation for stem growth than a linear measure, because a 1-mm annual increase in radius represents a larger increase in area for a stem of larger diameter than a stem of smaller diameter (Phipps, 2005; Biondi and Qeadan, 2008). We employed regional curve standardization to account for differential growth across different ages of stem. Basal area increment was plotted against the age of the ring and a site level model fitted to estimate predicted basal area increment for a given *Salix* stem age. Linear and exponential models were tested, and the exponential model was found to give the best fit. The residuals from this model (i.e. the deviation from the expected site-level radial increment for a ring of given age) were used for statistical analyses. We also estimated the intra-annual asynchrony of growth between individual stems within each enclosure. This was expressed as the coefficient of variation (standard deviation divided by the mean) of radial growth between shrubs within each sub-enclosure for each year, averaged across the period of experimental browsing.

Plot-level measures (shoot density and variance in shoot size) were analyzed using generalized linear models with the plot as the unit, whilst stem-level measures (diameter, height, and height-to-diameter ratio) used generalized linear mixed models with the stem as the unit of observation and the plot as the random factor because many stems were measured per plot (Bolker et al., 2009). Basal increment analysis also used generalized mixed models with the ring as the observation unit, and stem nested within plot as the random factors. Temperature data for the site was provided by the Norwegian Meteorological Office as an interpolation from nearby weather stations to the mid-point and elevation of the experimental site. Mean summer temperature (June to August 1957 to 2010) was used as a hypothesized explanatory variable since this period coincides with sheep presence within the experiment as well as the growing season. Statistical processing and analyses were performed in R version 2.15 (R Development Core Team, 2012), using the package dplR for dendrochronological analysis (Bunn, 2008, 2010). To determine whether the response of *Salix* shrubs to sheep density treatment varied among species, we investigated whether *Salix* radial growth during the years of experimental browsing was predicted by an interaction term between sheep density treatment and species. This measure was used, as radial growth was expected to be the most susceptible to browsing.

Results

A total of 1533 stems were sampled. *Salix glauca* was the most commonly sampled species with 833 stems, with *S. lapponum* and *S. lanata* also abundant in the sample (453 and 239 stems, respectively). One stem of *S. hastata* was sampled, along with 7 stems of hybrid individuals (*S. glauca* × *myrsinifolia*). There was a significant trend for increasing mean summer temperature at the study site (linear regression, $F_{1,52} = 9.6$, $P = 0.003$, $R^2 = 0.14$), and the mean summer temperature during the period of herbivore density manipulation (8.9 °C, 2002 to 2010) was greater than the long-term mean (7.9 °C, 1957 to 2010; Fig. 2). However, there was a high level of inter-annual variability in temperature.

PLOT-LEVEL

The density of *Salix* shoots increased with elevation in the absence of sheep, but decreased with elevation at low and high densities of sheep (Fig. 3, Table 1). At low elevations there was a lower density of *Salix* shoots in the unbrowsed treatment (with around 2 stems of *Salix* intersected per meter of transect line) than at high sheep density (5 m^{-1}), but at high elevations the density of *Salix* shoots was higher where unbrowsed (with around 6 shoots per meter) than at either browsed treatment (where there were less than 3 shoots per meter). The variation in *Salix* shoot stem diameter (expressed as the coefficient of variation to allow for differences in mean stem diameter) did not differ between treatments or along the elevational gradient (Analysis of Variance, Treatment: $F_{2,40} = 0.55$, $P = 0.58$; Elevation: $F_{1,41} = 0.0003$, $P = 0.99$).

STEM-LEVEL

There were no significant differences in stem diameter (One-Way ANOVA: $F_{2,23} = 1.96$, $P = 0.16$) and height (One-Way ANOVA: $F_{2,23} = 1.23$, $P = 0.13$) among the three most abundant species of *Salix*, with the mean stem diameter being between 9 and

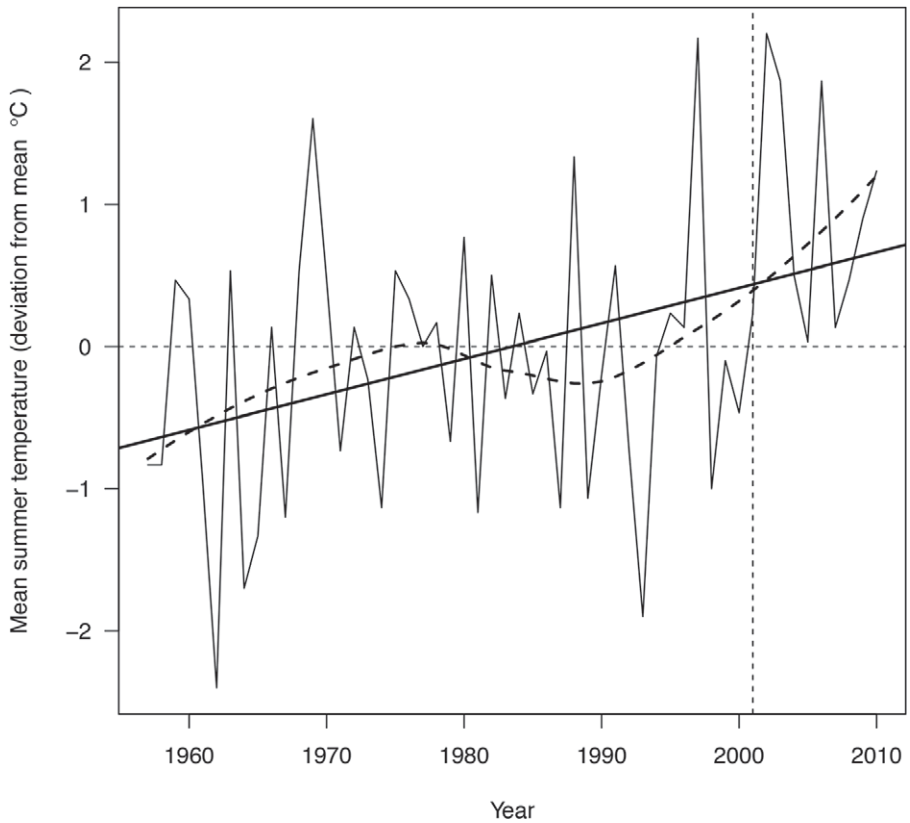

FIGURE 2. The deviation of summer temperature (mean June, July, and August) from the long-term mean (1957–2010). The solid line is the linear regression of deviation against year ($F_{1,52} = 9.6, P = 0.003, R^2 = 0.14$), and the dashed is a second-degree polynomial loess line. The broken vertical line shows when the experimental manipulation began, and the broken horizontal line shows the 1957–2010 mean.

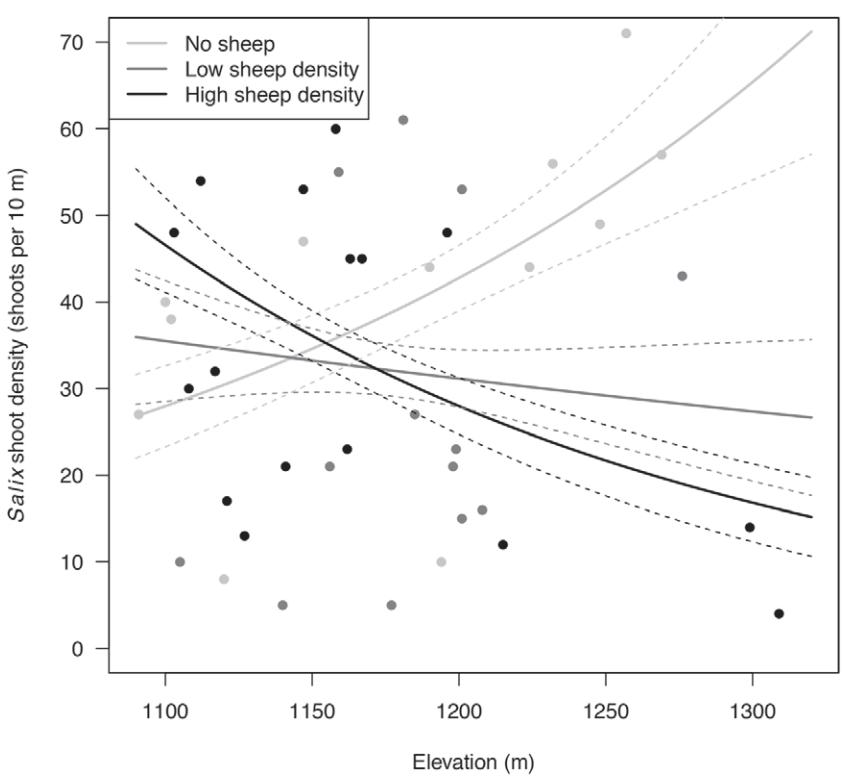

FIGURE 3. Density of *Salix* shoots intersecting with a transect plotted against elevation and sheep density treatment. Lines show predictions from a Poisson generalized linear model (see Table 1) and dotted lines the 95% confidence intervals.

TABLE 1

ANOVA output for Poisson-family model of *Salix* shoot density. Estimates from this model shown in Figure 3.

	d.f.	Deviance	Residual d.f.	Residual deviance	*P*
	42	579.04			
Elevation	1	0.22	41	578.83	0.64
Sheep density treatment	2	14.56	39	564.26	<0.001
Elevation × Sheep density treatment	2	75.005	37	489.26	<0.001

12 mm and the mean height being between 40 and 50 cm. Stems of the different species did not show contrasting responses to browsing (Gaussian linear mixed model, Likelihood Ratio: $F = 2.23$, $P = 0.69$) and were thus analyzed together (see Table 2).

Salix stems were significantly larger (in terms of stem diameter) and taller at high sheep density than where ungrazed (Fig. 4, parts a and b). The mean stem diameter and height across the elevational gradient was 13.1 mm and 52.5 cm, respectively, at high sheep density and 7.4 mm and 32.5 cm in the absence of sheep. The height to stem diameter ratio was significantly higher in the absence of sheep than at high sheep density (Fig. 4, part c). Stem diameter, height, and height to stem diameter ratio all decreased with elevation (Fig. 4, parts a–c). There was no significant interaction (at $P < 0.05$) between elevation and sheep density for stem diameter, height, or height to stem diameter ratio (Table 3). However, at low elevations, stem height tended to be highest at high sheep density, whilst at higher elevations stem height tended to be lowest at high sheep density, although this was only marginal ($F = 2.76$, $P = 0.077$; Table 3).

RADIAL GROWTH

There was a mean correlation between all 174 *Salix* stem chronologies of $r = 0.47$ (Pearson product-moment correlation coefficient). For the period of the grazing experiment (2002 to 2010) the mean correlation between all chronologies was $r = 0.76$. Following regional age standardization, annual ring growth (expressed as basal area increment) was related to mean summer temperature, elevation, and sheep density treatment for two separate periods: prior to the start of experimental manipulation of sheep density and during the experimental manipulation period. In the period prior to the experimental manipulation of sheep density (2001 and before), treatment was not a predictor of basal area increment of *Salix* stems (Gaussian linear mixed model, $F_{1,56} = 55.4$, $P = 0.057$). However, during the experimental period, the sheep density treatment was a significant predictor of *Salix* stem basal area increment, and also in interaction with elevation, but in addition to summer temperature (Table 4). Predicted radial growth is shown in Figure 5, plotting predicted age-standardized basal area increment against elevation and summer temperature. At low elevations, *Salix* radial growth was higher at high sheep density than in the absence of sheep and at low sheep density, but at higher elevations radial growth was lower at high sheep density than in the other treatments. Radial growth did not differ between low sheep density and in the absence of sheep. The variation in radial growth across the elevational gradient and over the range of summer temperatures was thus highest at high sheep density and lowest in the absence of sheep (Fig. 5). However, growth asynchrony, when expressed as the coefficient of variation (the deviance in annual growth standardized by the mean calculated across each enclosure), was significantly higher in both the low sheep density ($t = 2.8$, $P = 0.031$) and high sheep density treatments ($t = 2.7$, $P = 0.034$) than where sheep were removed (Fig. 6).

Discussion

Shrub encroachment in tundra ecosystems is generally linked to a warming climate (Sturm et al., 2001; Hallinger et al., 2010). However, our study supports the hypothesis that shrub encroachment in alpine lands with a history of grazing occurs under decreased herbivory in addition to climatic warming. The density of *Salix* shoots at high elevations was found to increase in the absence of sheep grazing, with a higher number of recruiting *Salix* shrub stems of low height and small stem diameter. Tall *Salix* shrubs have also been observed to show positive responses in terms of biomass to exclusion of both large and small herbivores in arctic vegetation (Ravolainen et al., 2011). In our study, we were also able to show how browsing (sheep density) interacts with climate (summer temperature) to determine stem radial growth. We also found that the synchrony of radial growth between stems was reduced in the absence of sheep, showing that browsing, which by nature differs in occurrence and intensity over time and space (Mobæk et al., 2009) leads to variation in individuals' performance. Growth and recruitment limitations caused by herbivory, and interactions between herbivory and climate to determine radial growth, have also been observed within the same experiment for mountain

TABLE 2

ANOVA likelihood ratio table testing the significance of a browsing *Salix* species interaction in determining radial growth of *Salix* stems.

Predictors	d.f.	ΔAIC	Log likelihood	*F* Likelihood ratio	*P*
Sheep density treatment × species	11	5.77	−2875.9		
Sheep density treatment + species	7	0	−2877	2.32	0.6931

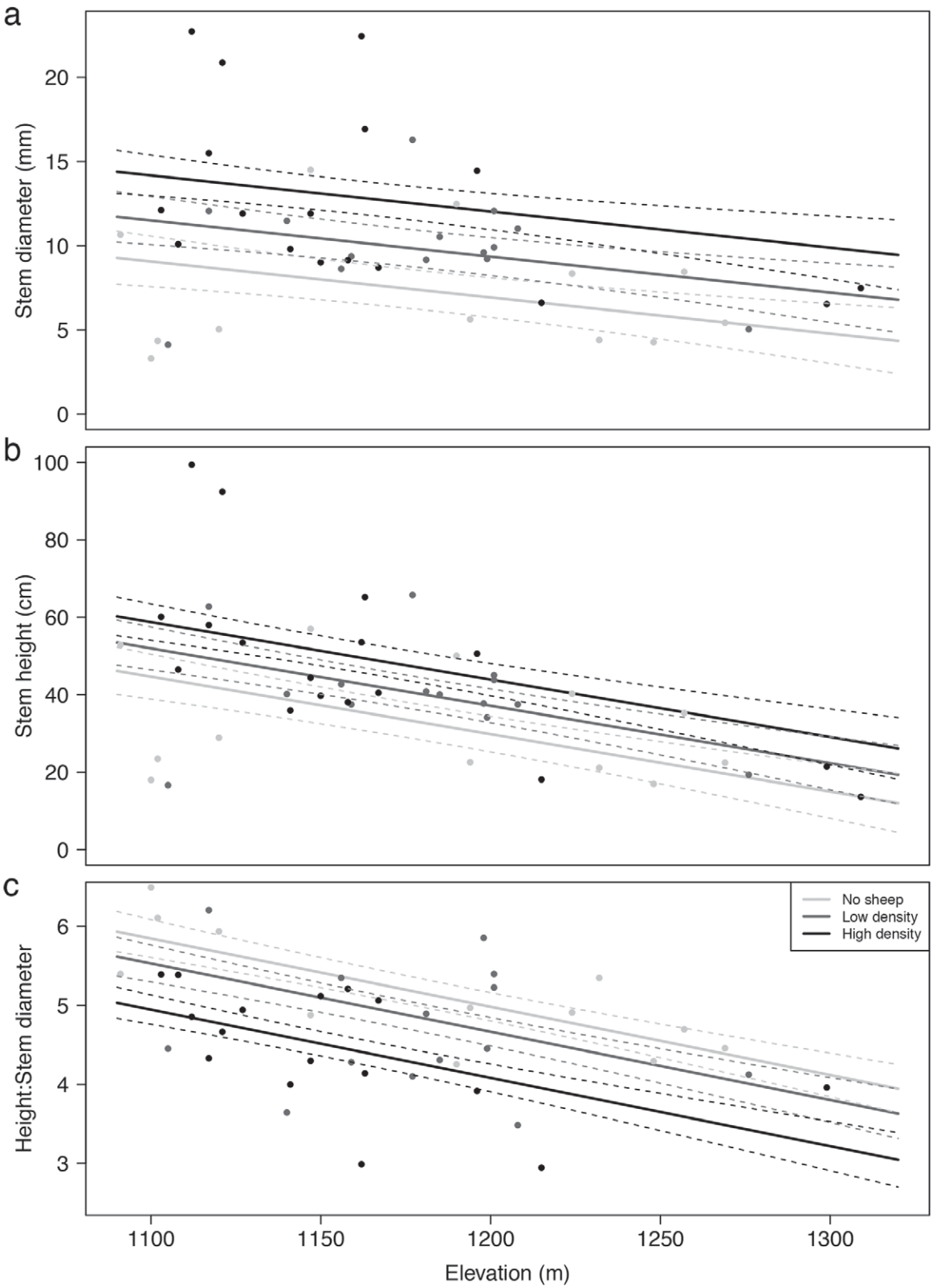

FIGURE 4. (a) Stem diameter, (b) height, and (c) height:stem diameter for three sheep density treatments along elevational gradient. Regression lines are predictions from mixed-effect models for each treatment (see Table 3) with standard errors shown by dotted lines.

TABLE 3

ANOVA output table for model of *Salix* diameter, height, and height to stem diameter ratio. Estimates from these models are shown in Figure 4, parts a–c. The elevation grazing treatment interaction was not retained in any of the three models.

	Numerator	Denominator	Stem diameter		Stem height		Height:Stem diameter	
	d.f	d.f	*F*	*P*	*F*	*P*	*F*	*P*
Intercept	1	1490	276.36	<0.001	299.1	<0.001	2394.66	<0.001
Sheep density treatment	2	39	6.87	0.0028	4.21	0.0221	3.62	0.0361
Elevation	1	39	3.49	0.0692	11.21	0.0018	21.31	<0.001

birch (Speed et al., 2011a, 2011b), further supporting a role of herbivory in regulating shrub encroachment. The contrasting effects of sheep grazing at lower elevations, with greater shoot density and stem radial growth of *Salix* (as well as a marginally greater stem height) at high sheep density than in absence of sheep, suggest that the influence of increased competition from the rest of the plant community in the absence of grazing sheep outweighed the negative influence of sheep browsing on *Salix* shrubs at lower elevations.

In support of our proposal for plant competition increasing at low elevations in the absence of sheep, vegetation height was found to both decrease with elevation and be lower at high sheep densities than where ungrazed (Austrheim et al., 2008). Furthermore, the height to stem diameter ratio was greater in the absence of sheep, and lowest at high sheep density, which implies that height growth may be more limited than radial growth by browsing. This supports the premise that interspecific competition, most likely from fast growing herb species that are highly selected by sheep in low alpine habitats (Evju et al., 2009), limits *Salix* growth in the absence of sheep: Indeed, cover of understory herbs has been linked to *Salix* shrub volume (Pajunen et al., 2011). Other recent work has also highlighted that herbivore density can affect the elevational distribution of plant communities (Speed et al., 2012). Thus in the absence of sheep, lowland communities may be expected to move upslope, potentially reducing *Salix* performance at higher elevations as well.

Other studies have reported similar patterns of woody plant growth in relation to browsing. *Salix myrsinites* has been found to have lower growth at lower elevations, which was also attributed to competition with the field layer (Gilbert, 2011). Greater height growth has also been observed for ash (*Fraxinus excelsior*) growing in higher sheep densities; again, this was attributed to competition suppressing ash seedling growth in the absence of herbivores (Hester et al., 1996). A study of the effects of herbivore exclusion on regeneration of montane *Salix* species concluded that the dense vegetation that develops in the absence of herbivores precludes survival of *Salix* seedlings that tend to germinate in bare ground patches (Shaw et al., 2010).

Salix species' responses to sheep density varied with elevation, which we attribute to competition from surrounding vegetation. In contrast, mountain birch (*Betula pubescens* ssp. *czerepanovii*), which is also selected for by foraging sheep, showed a clear negative response in recruitment, height growth, and radial growth to increasing sheep density within the same experiment (Speed et al., 2010, 2011a, 2011b). This genera-specific difference highlights that woody plant encroachment is driven by a complex suite of interacting factors leading to differential responses for different species and under different conditions. *Salix* shrubs exhibit clonal growth, and as such, the response of individual stems to browsing, as well as other drivers including climate, will depend on the clonal network of which they are part. For example, through translocation of resources within clonal individuals, we may expect that stems that form parts of larger clones are less negatively impacted by browsing. It is not clear how clonality varies with elevation in this study or in these species, but there was lower synchrony in growth between trees in both of the low and high sheep treatments than in the absence of sheep. Long-term browsing itself can impact the spatial structure of *Salix* patches (Ravolainen et al., 2013), thus the response of *Salix* shrubs to browsing is complex and includes feedbacks between the vegetation and herbivore populations.

While temperature and herbivory are regularly linked with encroaching shrubs, it is becoming clear that a range of other factors

TABLE 4

ANOVA output for model of *Salix* radial growth. Estimates from this model are shown in Figure 5. Summer temperature refers to mean temperature June to August; linear and quadratic terms were included in the model.

	Numerator d.f.	Denominator d.f.	*F*-value	*P*
(Intercept)	1	1294	21.80	<0.001
Sheep density treatment	2	168	3.86	0.023
Summer temperature^2	1	1294	27.75	<0.001
Summer temperature	1	1294	44.21	<0.001
Elevation	1	168	14.35	<0.001
Sheep density treatment × Elevation	2	168	5.01	0.007

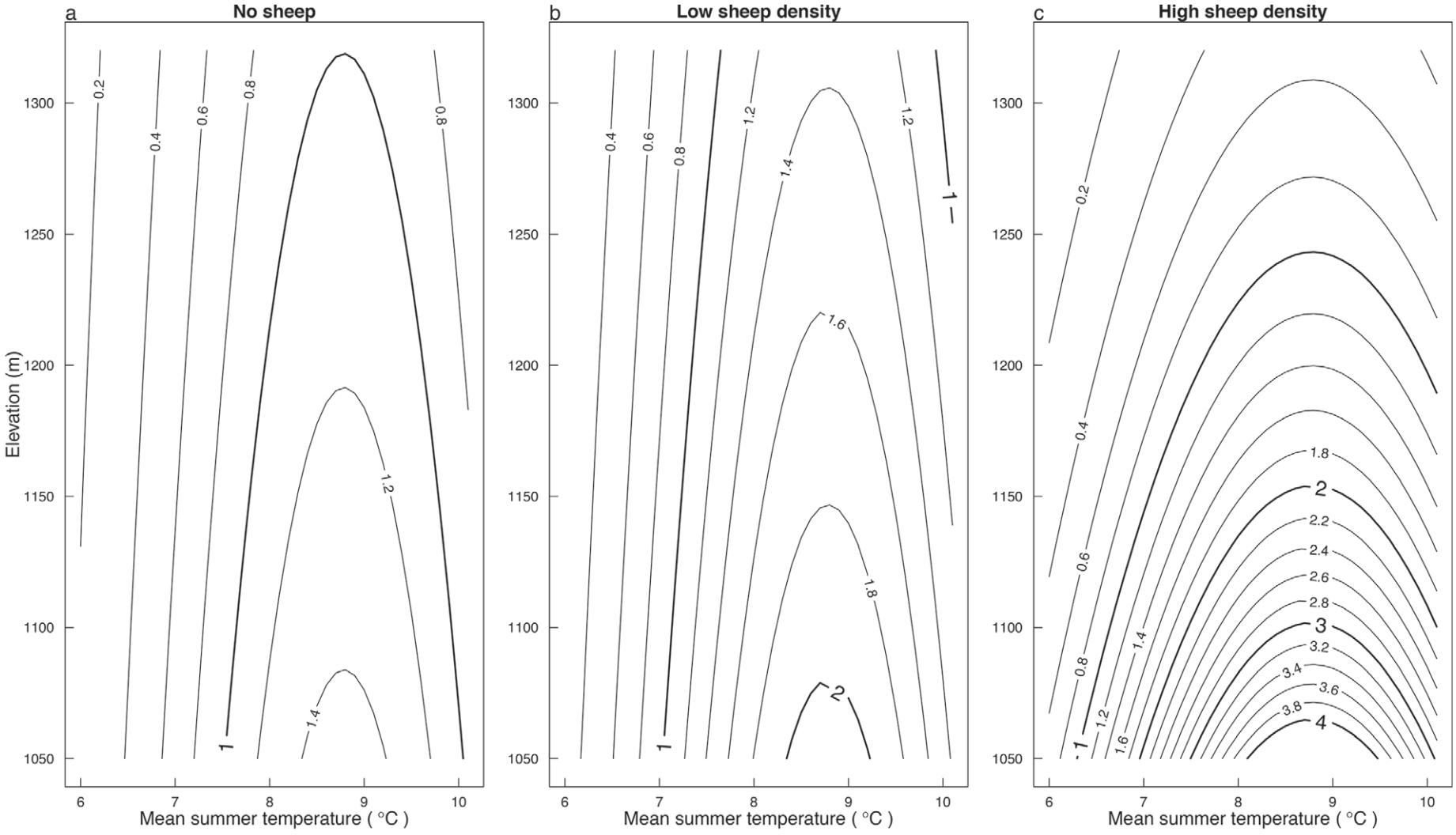

FIGURE 5. Radial growth (standardized basal area increment) of *Salix* stems estimated across mean summer temperatures (x) and elevation (y) in three sheep density treatments during the period of experimental manipulation of sheep density (2002–2010). Contour values show predicted radial growth for a given mean summer temperature, elevation, and sheep density.

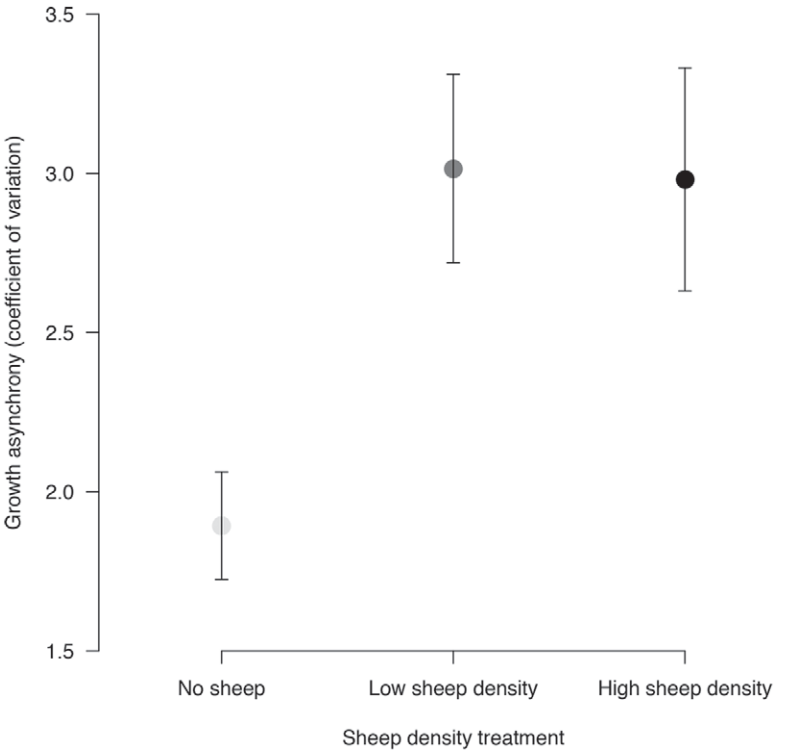

FIGURE 6. Intra-annual growth asynchrony (expressed as coefficient of variation) of radial growth of *Salix* shrubs within each sheep density treatment, averaged across the period of sheep density manipulation. Mean and standard errors at the enclosure level ($n = 3$) are shown.

may modulate these impacts including competition from field layer vegetation (this study), substrate composition (Macias-Fauria et al., 2012), snow cover/depth (Hallinger et al., 2010), and disturbance (Lantz et al., 2009; Myers-Smith et al., 2010). Since vegetation develops in interaction with the herbivore communities, decreases in herbivory can cause changes within ecosystems that have developed in the presence of herbivores (Milchunas et al., 1988). Thus shrub expansion is expected to be driven by decreasing densities of herbivores in regions that have previously been used by high densities of herbivores, and particularly livestock.

Conclusions

Salix shrubs are a key component of alpine and arctic ecosystems (den Herder et al., 2008). Thus the impacts of sheep browsing on *Salix* shrubs are likely to impact other aspects of alpine communities. Here we have shown that the impact of domestic herbivores on *Salix* shrubs at high elevations is the opposite of predicted climatic changes and thus there is the potential for management of alpine ecosystems through livestock grazing to buffer against the predicted climate-driven shrub encroachment. However, it should be noted that this study shows how this buffering using high densities of domestic sheep can also alter the structure and dynamics of *Salix* canopies, which serve as an important resource in terms of both forage and shelter provision for many alpine species.

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