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PRACTICE AND TECHNICAL ARTICLE

# Impacts of Highland cattle browsing on encroaching *Alnus viridis* shrubs

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## Abstract

**Introduction:** In several European mountain chains, the expansion of the tall shrub *Alnus viridis* into mountain pastures has altered vegetation structure and composition, reduced plant species diversity, and diminished forage quality. Recent woody encroachment research has explored the use of robust livestock breeds, such as Highland cattle (*Bos taurus taurus*), as a potential agroecological restoration tool to reduce *A. viridis* encroachment. However, empirical evidence on their medium-term (5 years) impact on shrub cover remains limited.

**Objectives:** To address this gap, we evaluated over 5 years how different grazing pressures of Highland cattle impacted *A. viridis* shrubland structure.

**Methods:** A field experiment was conducted in *A. viridis*-encroached pastures, where three paddocks were grazed over five consecutive summer seasons. For 344 *A. viridis* shrubs, we classified shrub position (border vs. interior of the shrubland), measured their basal diameter and proportion of dead trunks, the understory light availability, and the proportion of trunks with resprouts. Each year, 8–10 cows (approximately 400 kg on average) were equipped with Global Positioning System collars, and cattle stocking density was calculated within a 10 m buffer around each shrub.

**Results:** The increase in livestock density led to a significant increase in trunk mortality and understory light availability, particularly at the shrubland edges. The number of resprouts also increased with higher stocking densities.

**Conclusions:** Our findings show that Highland cattle browsing reduces *A. viridis* cover and increases understory light availability, promoting favorable conditions for grassland restoration. Nevertheless, the resprouting response of *A. viridis* indicates that a 5-year grazing period is insufficient to control *A. viridis* encroachment at the plot scale.

**Implications for Practice:** By reducing *Alnus viridis* cover and improving light penetration, the integration of Highland cattle into mountain pasture restoration programs can favor the reestablishment of grassland species and the enhancement of biodiversity and ecosystem functioning in formerly encroached areas. However, to strengthen *A. viridis* control, prevent regrowth and re-encroachment, grazing should be implemented over longer periods and using targeted techniques that increase livestock stocking densities, such as the strategic use of attractive points.


**Key words:** Alps, grassland restoration, green alder, mountain pastures, woody encroachment

## Introduction

*Alnus viridis* (Chaix) DC—commonly known as green alder—has been widely documented as a woody encroaching species in large areas of European mountain pastures, primarily because of reduced pastoral management and land abandonment (Caviezel et al. 2017). It is a pioneer species capable of fixing atmospheric nitrogen through symbiosis with the actinomycete *Frankia alni* (Huss-Danell 1997). It forms dense canopies reaching 2–5 m in height and, under them, soil becomes nitrogen saturated, while light and temperature decrease, and humidity increases (Bühlmann et al. 2016). As a result, only a few shade-tolerant and nitrophilous species can persist and dominate the understory vegetation within encroached areas (Svensk et al. 2021), with a consequent decline in plant and animal diversity and forage quality (Zehnder et al. 2020).

Restoring encroached ecosystems is a global concern, and the use of robust livestock breeds offers a promising strategy for the agroecological restoration of grasslands invaded by woody species (Yantes et al. 2025). In general, robust breeds, such as Highland cattle, can better forage on shrub leaves and low-quality herbage that are typically avoided by production-oriented breeds, show lower selectivity, have lower maintenance energy requirements, and can utilize steep, marginal, and less productive areas (Pauler et al. 2020). For instance, the proportion of woody species in the diet of Highland cattle can range from 15 to 46%, depending on the vegetation composition of

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the pasture and the abundance of woody plants (Nota et al. 2024), whereas cattle diets typically include no more than 5–10% of woody forage in most breeds (Oikonomou et al. 2025). More specifically, *A. viridis* leaves can constitute a significant forage resource for Highland cattle in early summer (Svensk et al. 2024). However, although Highland cattle have been proposed as a tool to control shrub encroachment in various ecosystems and regions, studies evaluating the potential of this breed to control woody encroachment have assessed only short-term impacts on vegetation (e.g. 1-to-3-year of Highland cattle grazing, Cromsigt et al. 2018; Svensk et al. 2021, 2022).

Cattle may impact woody vegetation not only through browsing, but also by trampling, scratching, bark rubbing, and breaking trunks and branches as they pass through shrublands (Huntly 1991). Previous studies have shown that the defoliation intensity was approximately 2.5 higher around attractive points (i.e. molasse-based blocks) with high densities of Highland cattle than in control areas. Moreover, woody species cover in these same areas after grazing was approximately four times lower than in control areas (Svensk et al. 2022). In this way, these animals have the potential to increase light availability at ground level in the medium term (i.e. when grazing is repeated for at least 4–5 years). Greater light penetration through a reduced canopy cover, combined with seed and nutrient dispersal through livestock zoochory, can thus promote favorable ecological conditions for the establishment of light-demanding grassland species, which could then enhance both understory biodiversity and forage quality (Kohler et al. 2006).

Plant compensatory responses to browsing can modulate the impact of cattle on vegetation. Indeed, morphological and physiological adaptations allow plants to sustain growth and reproduction despite tissue removal from herbivory (Tiffin 2000; Díaz et al. 2007). Compensatory growth responses of woody plants to browsing may include alterations in leaf size, shoot growth, branching patterns, and resprouting capacity (Bellingham & Sparrow 2000; Michielsen et al. 2017). As such, browsing can promote shrub resprouting and increase branching (Archibald & Bond 2003; Mochi et al. 2023), creating positive feedback on shrub growth that can potentially limit the medium-term effectiveness of cattle browsing for woody encroachment control.

Various subspecies of *A. viridis* have been documented to exhibit strong resprouting capacity and rapid recolonization following disturbances, a trait that underlies their recurrent success in post-harvest and post-fire environments (Mallik et al. 1997; Lantz et al. 2010). This response may be driven by root and collar sprouting, underground bud banks, carbohydrate reserves (Bond & Midgley 2001), and symbiotic associations with *Frankia alni* and mycorrhizal fungi (Chen et al. 2020). These plant functional traits must be carefully evaluated when aiming to restore *A. viridis*-encroached pastures using livestock, as resprouting capacity may influence long-term shrub suppression. Even though multiple field studies report high post-disturbance abundance and frequent recovery of *A. viridis* following harvesting and fire, knowledge on its regrowth capacity after browsing is lacking.

We evaluated over 5 years how different livestock pressures of Highland cattle impacted *A. viridis* shrubland structure. We hypothesized that, through browsing, trampling, scratching, bark rubbing, and trunk breakage, Highland cattle would significantly impact *A. viridis* shrubs. Since cattle tend to spend more time in open areas (Allred et al. 2013; Raynor et al. 2021), and grazing activity is likely to be higher along the borders between open pastures and shrubland than in the inner parts of *A. viridis* stands (Svensk et al. 2021), we hypothesized that the strongest effects would occur on shrubs located at the edges of the shrubland. We predicted that the proportion of dead trunks and understorey light availability would increase with increasing livestock stocking density around the shrubs.

## Methods

### Study Site and Grazing Management

This study was conducted in the Swiss Alps, in the summer pasture of Bovonne (N46°16′20.109″, E7°6′47.327″, Vaud, Switzerland, Fig. S1), where in the last decades *Alnus viridis* largely encroached previously open mountain pastures, because of extensive undergrazing. Three paddocks were established, and targeted grazing by Highland cattle was carried out during the summers from 2019–2020 to 2023. These paddocks were placed on the upper and steeper area of the summer pasture, that in the last 40 years was undergrazed by a dairy cow herd before the experiment started in 2019. The paddocks had a similar surface (mean: 7.66 ha, Table S1), and they were comparable in elevation (mean: 1811 m) and slope (mean: 23°), comprising a mosaic of small open pastures and large and ungrazed areas dominated by *A. viridis*. Planet Labs basemap mosaic images with a 5 m resolution (Planet Team 2026) were used to manually classify the vegetation cover of the three paddocks at the beginning of the experiment (2019). In each paddock, vegetation cover was classified as forest, open pasture, or *A. viridis* shrubland. *A. viridis* cover averaged 74.3% (70% in paddock 1, 75.8% in paddock 2, and 77% in paddock 3; Fig. S1). The rest of the vegetation cover consisted of open pastures (mean 18.6%) and forest (mean 7.1%). The Highland cattle herd included cow/calf pairs and heifers, varying in age from 1 month to 13 years; they grazed each year from the middle of June to the beginning of September, rotating among the paddocks with a mean annual stocking rate of 0.22 livestock units (LU) $ha^{-1}$ $yr^{-1}$ (see Table S1 for grazing period details). Eight to 10 cows were equipped with Global Positioning System (GPS) collars each year (Followit AB, Tellus GPS System collars, Sweden), which recorded their position every 10 minutes over the whole grazing period, with an accuracy of 2–5 m.

### Data Collection and Analysis

At the beginning of the experiment in 2019, shrubs were of similar age and showed no signs of previous browsing (i.e. shrubs were intact and had no broken branches). In 2024, after 5 years of Highland cattle grazing, *A. viridis* shrubs were randomly selected both at the shrubland borders and in the adjacent inner zone (hereafter referred to as "border" and "interior," respectively). Border shrubs were defined as those located in the first row adjacent to the open pasture or as isolated shrubs near the edge, whereas interior shrubs were those with the main trunk located in the second row or further inside the shrubland. A total of 344 shrubs (180 classified as on the border and 164 on the interior) were georeferenced and surveyed (Fig. S1). For each shrub, we recorded basal diameter, trunk condition, understory light availability, and the proportion of trunks with basal resprouts. Trunk condition was assessed on 20 trunks per shrub and classified as undamaged (no visible signs of damage), damaged (partially broken or browsed), or dead (dried-out and without vitality). The proportion of available light in the understory was quantified as the ratio between photosynthetically active radiation (PAR; 400–700 nm) at the ground level beneath the canopy and that in adjacent open areas. Measurements were done under clear-sky conditions with a LI-191R line quantum sensor connected to a LI-250A light meter. Four PAR readings were taken in the four cardinal directions beneath each shrub and then averaged. In addition, the presence or absence of basal resprouts was recorded for each trunk. The survey was conducted in early July 2024, after the *A. viridis* canopy had fully developed following spring season and before grazing started in these paddocks.

A 10-m radius buffer was created around each selected *A. viridis* shrub, and livestock stocking densities were calculated by counting the number of GPS fixes using QGIS software (version 3.36.1-Maidenhead, QGIS.org 2024). The average annual stocking density (LU $ha^{-1}$ $yr^{-1}$) around each shrub was calculated by computing the 5-year mean of yearly GPS fixes, which were weighted according to the number of LU, GPS collars, and grazing days in each paddock each year.

Statistical analyses were performed using R (version 4.3.3; R Core Team 2024). We fitted three models to evaluate the effects of livestock stocking density on the proportion of dead trunks, the proportion of available light in the *A. viridis* understory and the proportion of trunks with resprouts. The proportion of dead trunks and the proportion of trunks with resprouts were analyzed using generalized linear mixed models (GLMMs, glmmTMB package, Brooks et al. 2017), with trunk-level measurements as response variables. Light availability in the *A. viridis* understory was analyzed using a generalized additive model (GAM, *mgcv* package, Wood 2017). Fixed effects in all models included livestock stocking density (ranging from 0 to 2.2 LU $ha^{-1}$ $year^{-1}$), shrub position (border vs. interior), and their interaction. The GLMMs for the proportion of dead trunks and for the proportion of resprouts were fitted assuming a binomial error distribution and the GAM for light availability was fitted assuming a beta error distribution. In all the models, livestock stocking density was log-transformed and spatial autocorrelation was accounted for using the $X$ and $Y$ coordinates of each shrub. Shrub diameter was included as a covariate in the GLMMs and as a smooth term in the GAM for light availability. For the GLMMs, a random intercept for shrub ID was included to account for repeated measurements within the same shrubs. Model assumptions were evaluated using the DHARMa package (Hartig 2024) for the GLMMs and the *gam.check* function from the *mgcv* package for the GAM. Statistical significance of fixed effects was assessed using Wald $z$-tests based on the model summaries for GLMMs and approximate significance tests for smooth and parametric terms in the GAM.

## Results

While increasing livestock density significantly increased the proportion of dead trunks at the border and in the inner parts of shrublands, its impact was significantly stronger at the border ($p < 0.05$). Indeed, increasing livestock density was associated with a steeper increase in the probability of dead trunks at the border than in the interior (Table S2; Fig. 1).

The proportion of available light in the understory varied markedly depending on shrub position and livestock stocking density. At the border with open pastures, increasing stocking densities were associated with higher light availability ($p < 0.\ 05$), whereas no significant effect was detected in the shrubland interior ($p = 0.24$; Fig. 2). Shrub diameter had a significant non-linear effect on light availability in the GAM (smooth term: $p < 0.05$), with a sharp decline up to approximately 11 cm followed by a plateau (Table S3; Fig. S2).

Finally, the proportion of trunks with resprouts was affected by the interaction between livestock stocking density and shrub position ($p < 0.05$). In both environments, the probability of resprouting increased with livestock density, but the slope was steeper at the border than in the interior (Fig. 3). The proportion of trunks with resprouts increased with shrub diameter, indicating that larger shrubs resprouted more ($p < 0.05$, Table S2).

## Discussion

Our study provided evidence on how targeted grazing by Highland cattle impacted *Alnus viridis* shrubs within encroached mountain pastures, over a 5-year period. As hypothesized, livestock density significantly increased trunk mortality. These results highlighted the medium-term cumulative livestock impacts that had already been reported by a previous short-term study, which documented trunk breakage and *A. viridis* defoliation during the first year of grazing (Svensk et al. 2022). After 5 years, we also found that *A. viridis* trunk mortality was highest at the borders of encroached stands, but it also increased in their inner parts with increasing stocking density. These findings are consistent with a recent study showing that Highland cattle tend to spend more time along the edges of *A. viridis* shrublands, gradually moving into the interior over time (Mochi et al. 2026). Consequently, cattle impacts are initially concentrated at shrubland edges and progressively extend into stand interiors, consistent with patterns reported for African savannas (Porensky et al. 2013).

Consistent with previous studies and in agreement with our hypothesis, the proportion of light reaching the soil in the shrubland understory increased with increasing livestock stocking density (Kohler et al. 2006), especially along the borders (up to approximately 5 m) with open pastures. Together with earlier findings showing that Highland cattle can reduce the cover of tall herbs and ferns through grazing

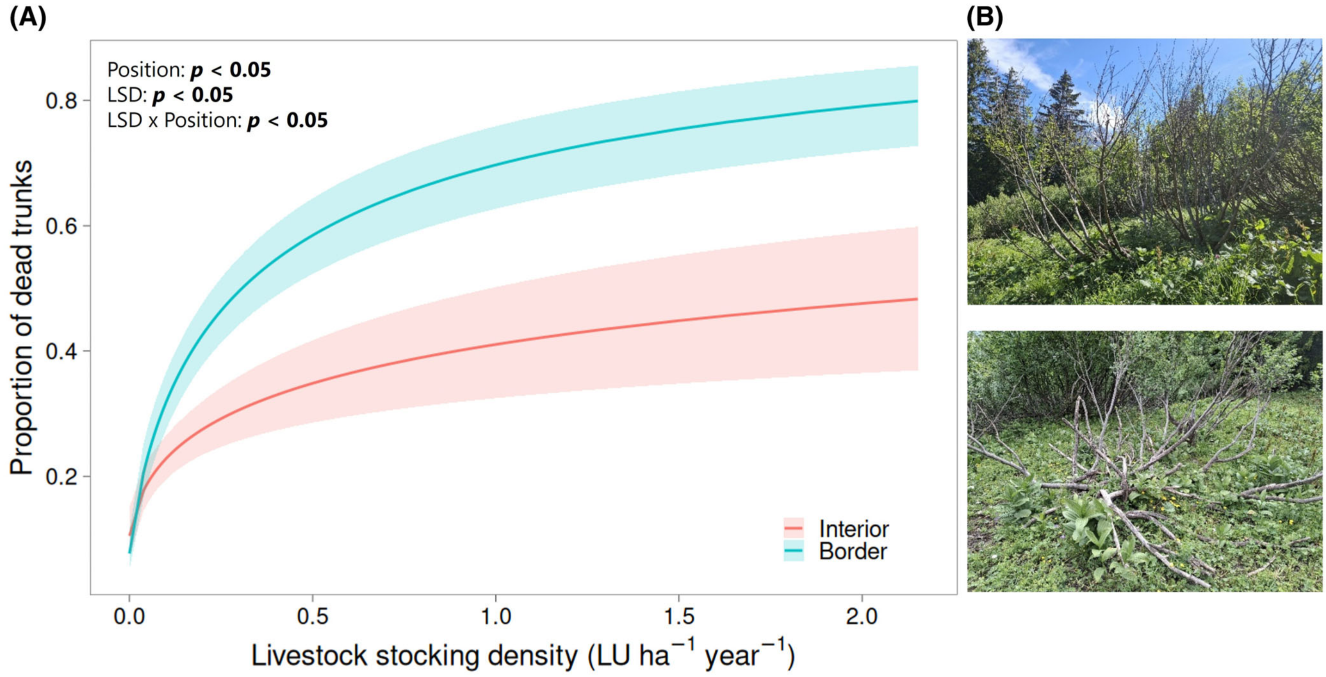


Figure 1. (A) Proportion of dead trunks as a function of average annual LSD (livestock stocking density expressed in Livestock Units ha$^{-1}$ yr$^{-1}$) from 5 years of Highland cattle grazing at the borders of *Alnus viridis* stands (blue line) and in the adjacent interior zone (red line). The shaded areas represent 95% confidence intervals. (B) Example of two *A. viridis* shrubs located at the borders of a *A. viridis* stand, measured during the survey, showing damaged and dead trunks.

and trampling (Svensk et al. 2022), these findings highlight their potential role in restoring the forage provisioning function of mountain pastures. By opening the canopy and increasing light penetration, together with a reduction in the cover of shade-tolerant species, cattle browsing may promote a shift from shade-tolerant to light-demanding species,

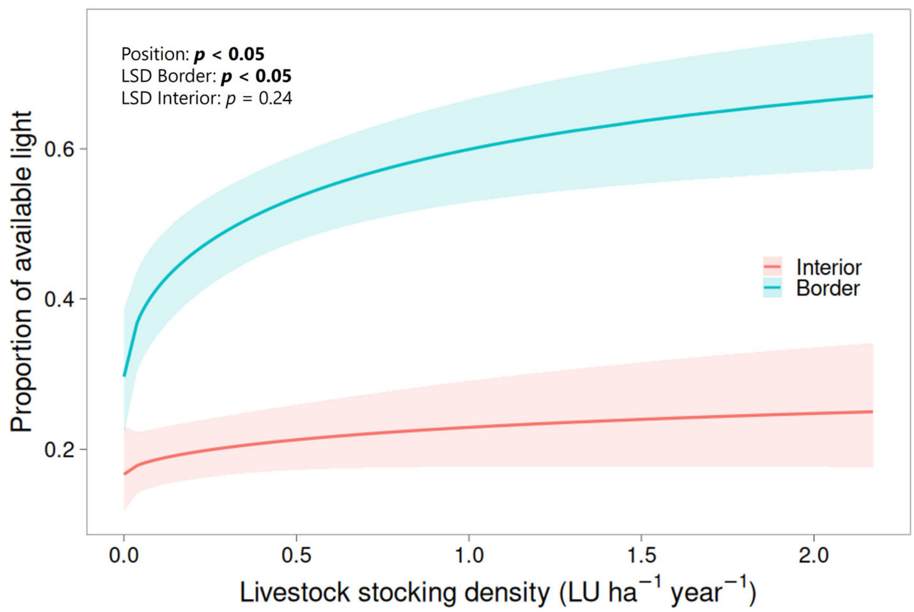


Figure 2. Proportion of available light, as a function of average annual LSD (livestock stocking density, expressed in Livestock Units ha$^{-1}$ yr$^{-1}$) from 5 years of Highland cattle grazing on the *Alnus viridis* understory, at the borders of *A. viridis* stands (blue line) and in the adjacent interior zone (red line). The shaded areas represent 95% CIs.

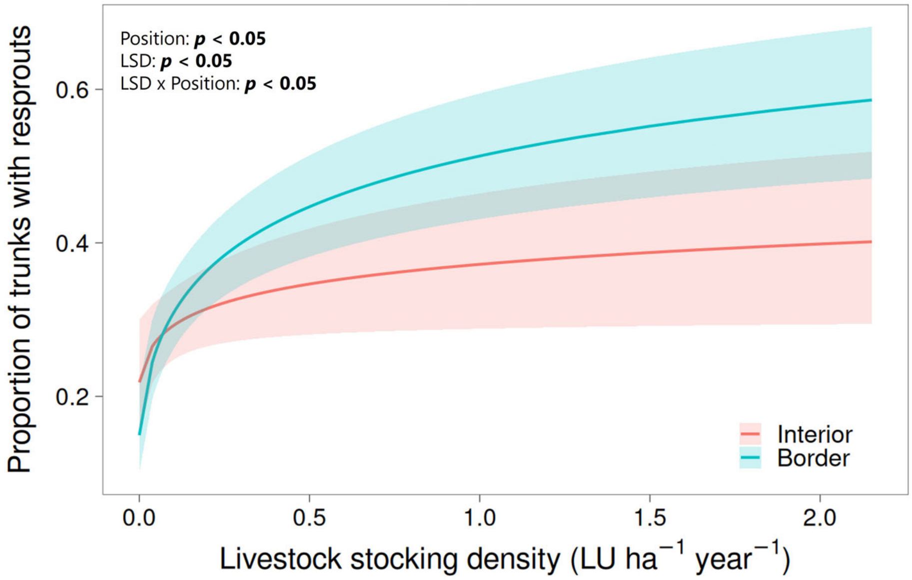


Figure 3. Proportion of trunks with resprouts, as a function of average annual LSD (livestock stocking density, expressed in Livestock Units ha$^{-1}$ yr$^{-1}$) from 5 years of Highland cattle grazing on the *Alnus viridis* understory, at the borders of *A. viridis* stands (blue line) and in the adjacent interior zone (red line). The shaded areas represent 95% CIs.

favoring the recolonization of typical grassland plants and thus enhancing both biodiversity and pastoral value (Probo et al. 2016). Furthermore, maintaining a mosaic of open and encroached patches within cattle paddocks can increase seed dispersal by livestock, thereby contributing to the recolonization of typical grassland species on encroached areas (Traba et al. 2003). Indeed, Mochi et al. (2026) demonstrated that the use of Highland cattle has increased plant diversity and pastoral value in these environments over a 5-year timespan. Our results presented here help to explain the mechanisms behind this pattern—notably the enhanced light penetration in shrublands driven by browsing pressure—as a key process underlying grassland recovery.

However, livestock density also affected the probability of *A. viridis* resprouting. Indeed, even after 5 years of browsing, shrubs exposed to the highest Highland cattle densities showed an increased presence of resprouts, highlighting the strong tolerance of *A. viridis* to browsing. Destruction of the apical meristem frequently stimulates new trunk development through lateral or subterranean buds, resulting in changes in plant architecture that improve light interception and subsequent resource capture following damage (Stowe et al. 2000). This compensatory resprouting could lead to a shorter and denser architecture through over-compensatory branching (Archibald & Bond 2003; Mochi et al. 2023), which protects inner tissues and thereby reduces accessibility of the canopy to large herbivores, such as cattle. This response suggests that, to limit *A. viridis* encroachment, livestock grazing pressure should be managed with a long-term perspective, as effective control necessarily requires sustained pressure to restrict plant regrowth and weaken *A. viridis* shrubs in the long term. Indeed, a recent work (Mochi et al. 2026) showed that vegetation diversity continued to increase and shrubland cover continued to decrease even 15 years after the introduction of Highland cattle, supporting the idea that long-term grazing could further enhance mountain grassland restoration.

Overall, our study underscores that sustained Highland cattle grazing pressure can be considered a valuable agroecological restoration tool in encroached agroecosystems. Indeed, targeted Highland cattle grazing effectively reduces *A. viridis* cover and enhances understory light availability, thus promoting ecological conditions that support pasture restoration in the medium term. However, the strong resprouting capacity of *A. viridis* indicates that long-term grazing management of woody encroachers is needed. Therefore, effective restoration programs that prevent re-encroachment require careful and sustainable planning of grazing intensity and duration, as well as the implementation of rotational grazing systems and the strategic use of attractive points to target grazing pressure for the management of woody encroaching vegetation and the restoration of mountain grassland biodiversity.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Location of the study site and surveyed shurbs across the three study paddocks.
**Figure S2.** GAM-predicted relationship between shrub diameter and light availability.
**Table S1.** Grazing periods of the three green alder-encroached paddocks during the 5 years
**Table S2.** Summary of statistical models assessing the effects of livestock stocking density, shrub position, and shrub diameter on trunk mortality and resprouts.
**Table S3.** Summary of the Generalized Additive Model (GAM) analyzing the proportion of available light in the *A. viridis* understory.

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