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RESEARCH ARTICLE

Thinning the thickets: Foraging of hardy cattle, sheep and goats in green alder shrubs

Caren M. Pauler[1] | Tobias Zehnder[1,2] | Markus Staudinger[1,2] | Andreas Lüscher[1] | Michael Kreuzer[2] | Joël Berard[2,3] | Manuel K. Schneider[1]

[1]Agroscope, Forage Production and Grassland Systems, Zurich, Switzerland

[2]ETH Zurich, Institute of Agricultural Sciences, Zurich, Switzerland

[3]Agroscope, Animal Production Systems and Animal Health, Posieux, Switzerland

Correspondence
Manuel K. Schneider
Email: manuel.schneider@agroscope.admin.ch

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Abstract

1. Green alder shrubs *Alnus viridis* increasingly overgrow European mountain pastures but hinder natural forest succession. This nitrogen-fixing, autochthonous invasive species has numerous negative effects including the loss of biodiversity and landscape aesthetic, eutrophication of soils and downstream waters, and greenhouse gas emission. Over centuries, *A. viridis* encroachment was impeded by grazing livestock, particularly goats. However, in modern agriculture, livestock numbers decreased on remote mountain pastures and goat farming became unprofitable.
2. A grazing experiment tested if hardy breeds of the more economically attractive livestock species, cattle and sheep can replace goats as *A. viridis* antagonists. On a subalpine pasture heavily encroached by *A. viridis*, space use and debarking (bark foraging) by Dexter cattle, Engadine sheep and Pfauen goats were analysed using GPS tracking and vegetation mapping.
3. Dexter cattle used space least evenly (Camargo evenness: cattle = 0.39; sheep = 0.52; and goats = 0.47) and preferred flat slopes and open pastures. They spent least time foraging in *A. viridis* stands (relative presence while foraging: cattle = 0.55; sheep = 0.76; and goats = 0.80). Dexter cattle did not debark any *A. viridis*, but damaged shrubs by trampling.
4. Engadine sheep visited *A. viridis* stands nearly as often as goats, but preferred flat slopes, short vegetation and shrub edges more clearly than goats. This sheep breed debarked significantly more *A. viridis* branches (average 244 branches per paddock; 7.4% of all *A. viridis* branches) than goats (45; 0.8%). Goats preferred mountain-ash shrubs *Sorbus aucuparia* covering only 2% of the shrub layer.
5. *Synthesis and applications*. Green alder shrubs, controlled by goats traditionally, overgrow valuable mountain pasture ecosystems today. Cattle, kept instead of goats, may slow down but not hinder shrub encroachment, because they avoid shrub stands and do not debark green alder. However, this study is the first to show that Engadine sheep are even better suited for green alder clearance than goats. Moreover, if management goals include forest re-establishment, Engadine sheep outperform goats, because they debark green alder (which hinders forest

regeneration), but do not destroy elderberry—a valuable forest pioneer. Hardy breeds are an important tool to maintain biodiverse, open pastures, restore natural mountain forests and mitigate the negative environmental effects of shrub encroachment.

KEYWORDS
Alnus viridis, browsing, cattle, debarking, goat, hardy breed, sheep, shrub control

1 | INTRODUCTION

Shrub encroachment is a global phenomenon affecting the structure and function of grasslands (Eldridge et al., 2011). In the European Alps, mainly green alder shrubs *Alnus viridis* [Chaix] DC. expand into formerly open habitats of the subalpine zone (Brändli et al., 2020; Tasser & Tappeiner, 2002). This shrub is not native to most habitats where it occurs today, but only emerged due to human impact. In the post-glacial era, large areas of the European Alps were covered by dense forests in which *A. viridis* cannot prevail. Thus, it was restricted to naturally non-forested habitats, namely wet sites and avalanche aisles. In the Bronze Age, early farmers settled the Alps (Gilck & Poschlod, 2019). Woodcutting and livestock grazing thinned the post-glacial forests and finally created open grasslands below the natural tree line. Palaeobotanical pollen records in alpine lake sediments demonstrate that *A. viridis* appeared during this period, remarkably, simultaneously with typical grassland species (Schwörer et al., 2014). This indicates that *A. viridis* rapidly populated the newly deforested, open areas by spreading beyond its initial habitats. Livestock grazing thus enabled establishment of *A. viridis* shrubland, but simultaneously limited its expansion into subalpine pastures because high grazing pressure prevented the growth of *A. viridis*.

In the last century, social and agricultural transformations favoured the expansion of *A. viridis*. Depopulation of mountainous areas and non-agricultural employment have decreased the labour availability in the agricultural sector (Muñoz-Ulecia et al., 2021). Today, livestock is concentrated in favourable, intensively managed locations, whereas less productive grasslands are underused (Tasser & Tappeiner, 2002). Consequently, shrubs like *A. viridis* overgrow these extensively managed grasslands (Anthelme et al., 2003; Zehnder et al., 2020), which are among the most biodiverse habitats on earth (Wilson et al., 2012).

This process has been enforced by a shift in livestock species. Ruminants differ in their preferred type of forage. Goats, as opportunistic mixed feeders, eat woody plants, whereas grazers like sheep, and even more notably cattle, are supposed to avoid them (Lu, 1988; Wood, 1987). During the last century, European agricultural systems changed and smallholder goat farming became unprofitable (Boyazoglu et al., 2005). Accordingly, the number of goats in Switzerland has decreased by 80% since 1876 (Figure 1). They were widely replaced by cattle and, to some extent, sheep. Consequently, there are not only fewer animals on marginal pastures, but the remaining animals are less inclined to eat shrubs like *A. viridis*.

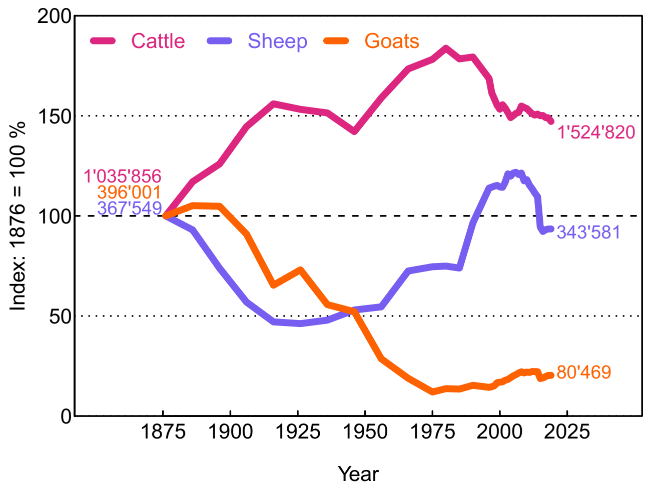

FIGURE 1 Development of ruminant livestock population numbers in Switzerland from 1876 to 2019. Data extracted from Swiss statistical yearbooks (Swiss Federal Statistical Office, 1891–2019)

In contrast to other shrub species, *A. viridis* fixes atmospheric nitrogen (N) by a mutualistic relationship with actinomycete *Frankia alni*. Thus, its expansion into subalpine grasslands has far-reaching consequences for these initially nitrogen-poor ecosystems and the wider environment:

1. Due to the high N supply, *A. viridis* and a few fast-growing understorey species, such as *Adenostyles alliariae* or *Peucedanum ostruthium*, out-compete most other plant species and thus, biodiversity declines tremendously (Anthelme et al., 2003) and clearly more than with other shrub species (Zehnder et al., 2020).
2. While N leaching in open pastures is close to zero, surplus N continuously leaches from *A. viridis* stands (Bühlmann et al., 2016). It eutrophicates soils and efflux waters (Bühlmann et al., 2016) or is emitted as greenhouse gases (N_2O, NO) due to incomplete denitrification (Hiltbrunner et al., 2014). Thereby, *A. viridis* affects both the immediate and the broader environment.
3. *A. viridis* stands seem to be a dead end of forest succession because *A. viridis* grows faster than most trees and out-competes them in the eutrophicated environment. On many sites in the Alps, *A. viridis* encroachment prevents the development of mountain forests that could serve as avalanche protection (Huber & Frehner, 2013).

4. Finally, most people perceive shrublands as unappealing, which is unfavourable in mountain regions that rely on tourism (Soliva et al., 2010).

Grazing by goats is assumed to effectively mitigate shrub encroachment (Wehn et al., 2011; Wood, 1987), but is rarely practiced due to its unprofitability. Clearing scrubs mechanically is laborious, expensive and often infeasible in the rough mountain terrain. Therefore, we tested whether there are effective livestock alternatives to goats and mechanical clearance.

Animals potentially impair shrubs in two ways: (a) By visiting the stands, animals damage branches and seedlings and thereby thin the thickets via *trampling*. This is a function of body weight, which is largest for cattle. However, cattle may be too large in size to enter the densest parts of the *A. viridis* stands and to visit the steepest slopes. Sheep and goats are therefore better able to penetrate the thicket. Especially goats, whose wild ancestors prefer steep slopes and areas providing hiding places (Zobel et al., 2018), are expected to visit shrubland often and thereby trample the shrubs. (b) More efficiently, woody plant species are damaged by *debarking*. If the bark of a branch is stripped all around, it dies off due to the irreversible interruption of water and nutrient transport. Sheep and goats bite off fodder using lips and teeth, whereas cattle rip off the grass mainly using the tongue. Therefore, cattle are not expected to debark and sheep prefer woody plants less than goats (Wood, 1987). However, farmer's observations and unpublished, preliminary studies have suggested a different pattern in certain hardy sheep breeds, which may be uniquely suited for shrub control.

Although several studies have analysed how ruminant livestock deal with some shrubs (e.g. Iussig et al., 2015; Rogosic et al., 2006; Wehn et al., 2011; Wood, 1987), there is a lack of scientific knowledge on the specific response to *A. viridis*.

We hypothesized that due to the outlined differences between livestock species:

1. cattle, sheep and goats visit *A. viridis* stands, but the depth of shrubland penetration, time spent in the shrubs and evenness of space-use decrease in the order goats >> sheep > cattle (*Space-use hypothesis*);
2. cattle, sheep and goats debark different amounts of *A. viridis*, with decreasing intensity in the order goats >> sheep > cattle (*Debarking hypothesis*);
3. at high stocking rate, animals visit *A. viridis* stands more often and debark more intensively (*Grazing pressure hypothesis*).

2 | MATERIALS AND METHODS

2.1 | Animals

We compared the foraging and movement behaviour of hardy goats as a positive control with the behaviour of low-productive, hardy cattle and sheep breeds expected to tolerate the harsh environmental and poor nutritive conditions of subalpine pastures. To represent hardy cattle, we used Dexter cattle (Figure 2a), a particularly small (withers height of cows: <110 cm), light (<350 kg body weight) and agile dual-purpose breed, supposed to cope well with rough terrain (The Dexter Cattle Society, 2021). Hardy sheep were represented by the autochthonous dual-purpose breed Engadine sheep (Figure 2b), originating from the Engadine Valley, where the experiment was conducted (Engadine sheep association, 2021). This breed was selected due to postulations of Bühlmann et al. (2014) indicating a preference for *A. viridis*. Goats (Figure 2c) were of the local, hardy Pfauen breed (purebreds and some crosses with chamois-coloured mountain goat).

2.2 | Study location

A. viridis occurs all over the alpine arch (Figure 3a). The experiment was conducted on subalpine pastures in the middle of this area, that is in the Eastern Swiss Alps (46.5812°N, 9.9029°E; 13.4 ha; elevation: 1,925–2,200 m a.s.l.; average slope: 55.5%; annual precipitation: 713 mm; and average temperature: 1.9°C), from June to August, which represent the entire grazing period at this elevation. The study area (Figure 3b) was partially covered by dense *A. viridis* stands including single *Sorbus aucuparia* L. shrubs (Raspé et al., 2000). The shrubland was surrounded by heterogeneous, mostly nutrient-poor

FIGURE 2 Three hardy livestock breeds, used for assessing movement and foraging behaviour: (a) Dexter cattle equipped with GPS logger (arrow), (b) Engadine sheep and (c) Pfauen goats; photo: ProSpeciesRara

grassland, dwarf-shrub heathland and sparse forest, dominated by *Larix decidua* Mill. and *Pinus cembra* L. We classified the vegetation types (Figure 3c; for details see Appendis S1) according to Dietl et al. (2002) and mapped them by combining field observation and high-resolution orthophotos.

2.3 | Grazing experiment

Animals were grouped into five herds: one goat herd of seven adult she-goats and seven yearlings; two sheep herds consisting of seven ewes and three lambs each; and two cattle herds with eight heifers each. We defined 15 paddocks according to estimated forage availability and topographic structures that allowed fence installation. Three paddocks were consecutively grazed by the goat herd in two rotations. The two cattle herds consecutively grazed six paddocks rotationally, and the two sheep herds grazed the other six paddocks. Half of these cattle and sheep paddocks were small (mean size cattle paddocks: 0.90, sheep: 0.52 ha) and thus, the grazing pressure was high (cattle: 0.63, sheep 0.42 LU ha^{-1} $year^{-1}$; 1 livestock unit LU = 500 kg). The other half of the paddocks were larger (cattle: 1.45, sheep: 0.86 ha) and thus, were grazed with low pressure (0.40 and 0.25 LU ha^{-1} $year^{-1}$ respectively). The single goat herd grazed its three paddocks under low grazing pressure (0.75 ha; 0.21 LU ha^{-1} $year^{-1}$). We maintained cattle under higher grazing pressure than sheep and goats, because we expected them to visit or consume *A. viridis* only under high stocking rates. The stocking rate was calculated based on metabolic live weight (i.e. body $weight^{0.75}$) accounting for the higher turnover rate of smaller animals. Because all paddocks were stocked for the same duration, stocking rate directly corresponds to stocking density.

Each herd grazed one paddock for, on average, 12 days and was then moved to another paddock. Thereby, the herds alternatingly grazed small and large paddocks. This procedure was repeated until

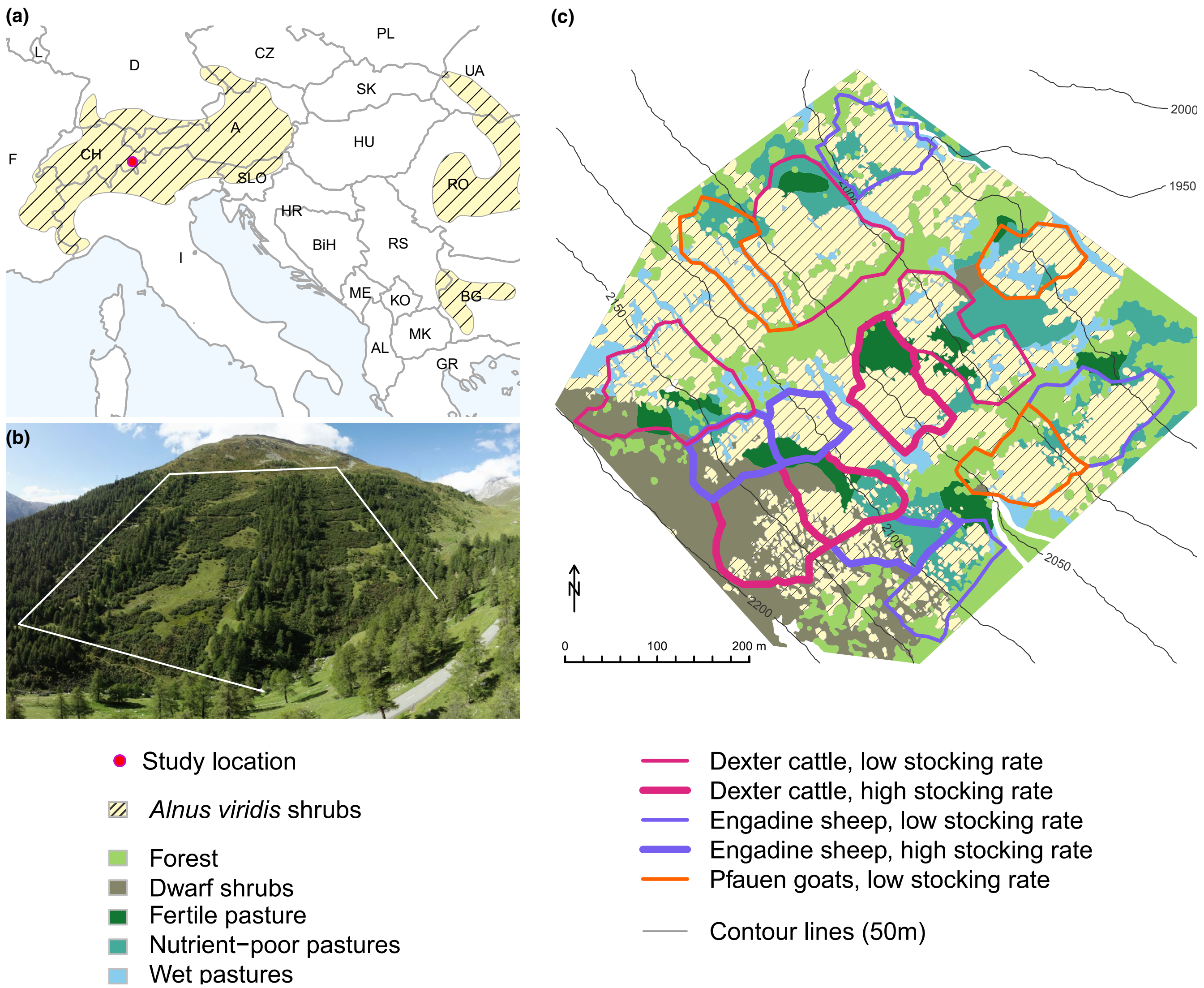

FIGURE 3 (a) European distribution area of *Alnus viridis*, based on data of Caudullo et al. (2017); (b) study area; and (c) vegetation types of the study area and paddocks of the experiment grazed by cattle, sheep and goats with either low or high stocking rate all cattle and sheep herds had visited each of their six paddocks once. The single goat herd visited each of their three paddocks twice. More details of paddock occupation are given in Appendix S2.

Shrub-encroached subalpine pastures pose a challenge for conducting controlled experiments because they are heterogeneous, steep and rocky. Since defining and fencing out identical paddocks is impossible in this environment, we spaced out the inherent heterogeneity evenly across the livestock species. For instance, each paddock contained zones of high and of low forage quality, slope, percentage cover of *A. viridis* and vegetation height (for further details, see Appendix S3).

To track movement behaviour, animals were equipped with GPS loggers recording a position every 10 s. After a paddock had been grazed (i.e. twice per paddock), we quantified debarking by recording the location of debarked branches (debarking occurrence) in the entire stand and the total number of debarked branches at each location. Debarking intensity was calculated as the counted number of debarked branches relative to the estimated number of non-debarked branches per shrub species. Technical details on GPS logging and debarking assessment are given in Appendices S4 and S5. The animal experiment was approved by the veterinary office of Grison (licence GR_2016_18). No permission was needed for other fieldwork.

2.4 | Data analysis

In all analyses, the paddock was used as the unit of observation. The five treatments (a) cattle at low and (b) high stocking rate, (c) sheep at low and (d) high stocking rate and (e) goats at low stocking rate were each repeated in three paddocks ($n = 15$). All calculations were completed using R 4.0.4 (R Core Team, 2021).

The recorded GPS positions were classified as resting or foraging using a simple algorithm based on speed (see Appendix S6 for details). Only foraging data were used for the subsequent analysis since shrub damage is normally caused by foraging (i.e. feeding and searching for forage) and not resting. We assigned the vegetation type to each GPS position recorded. Subsequently, we calculated the relative presence while foraging in *A. viridis* stands (RPA) as the proportion of GPS positions within *A. viridis* stands normalized by the relative area of *A. viridis* in the paddock. Values <1 indicate avoidance, 1 indifference and >1 preference for *A. viridis*. Moreover, we totalled the number of GPS positions classified as foraging within 5 × 5 m grid cells and computed Camargo's index (CI) of space-use evenness (Pauler, Isselstein, Suter, et al., 2020). Because not all tracked animals per herd had the same number of GPS positions, RPA and CI were calculated per animal and averaged per paddock, weighted by the number of recorded positions. Means were compared by post hoc Tukey tests at 5% significance level using the package MULTCOMP (Bretz et al., 2016).

To explain the spatial distribution of space use and debarking, we calculated three variables at 5 × 5 m grid resolution: (a) distance to open pasture, that is the Euclidean distance to the boundary between open pasture and *A. viridis* stands, set to zero in all open pasture cells; (b) the percentage slope based on the swissALTI3D elevation model (swisstopo, Wabern, Switzerland; resolution: 2 m); and (c) height of vegetation as the difference between the swissALTI3D and a digital surface model obtained using a fixed-wing drone (for details, see Appendix S7). Space use was aggregated at the paddock level by averaging the relative number of GPS positions in each grid cell for all monitored individuals in each paddock. Since the relative numbers ranged from zero to one, we used a multiple linear regression model with a beta likelihood and a spatially structured error term (Homburger et al., 2015). The model was fitted by integrated nested Laplace approximation using the package R-INLA (Rue et al., 2009). Model code and output is given in Appendix S8.

The debarking data also contained a high number of zeros and was bounded below one, so a zero-inflated beta model was fitted using the package GLMMTMB (Brooks et al., 2017). Logit links were used for the zero-inflated component (debarking occurrence) and for the conditional component (debarking intensity) of the model (for details, see Appendix S9).

3 | RESULTS

3.1 | Differences in space use

3.1.1 | Space-use differences among livestock species

All three animal species used the space unevenly (Figure 4), and resting was more clustered than foraging, as indicated by CI ($CI_{foraging} = 0.45$ and $CI_{resting} = 0.11$, $p < 0.001$). Moreover, cattle spent more time foraging (41.2%) than sheep (34.5%) and goats (38.9%; data not shown).

All livestock species visited the *A. viridis* stands, but they differed in space-use evenness and relative presence in *A. viridis* stands, although the differences were rarely significant due to large variability. Dexter cattle used space least evenly (mean $CI_{cattle} = 0.39$; Figure 5a) and avoided *A. viridis* stands more clearly than the other livestock species (mean $RPA_{cattle} = 0.55$; Figure 5b). High stocking rate increased the space-use evenness of cattle ($CI_{cattle\_low} = 0.33$; $CI_{cattle\_high} = 0.44$) but did not significantly affect their preference of vegetation types ($RPA_{cattle\_low} = 0.49$; $RPA_{cattle\_high} = 0.60$). Engadine sheep avoided shrubs slightly, but less clearly than the cattle. Consequently, sheep used the space more evenly (mean $CI_{sheep} = 0.52$). At a high stocking rate, sheep visited *A. viridis* stands more frequently than under low grazing pressure ($RPA_{sheep\_low} = 0.67$; $RPA_{sheep\_high} = 0.86$) and highly stocked sheep avoided *A. viridis* stands least compared to all other treatments. Consequently, the space-use evenness of sheep increased with stocking rate ($CI_{sheep\_low} = 0.45$; $CI_{sheep\_high} = 0.59$). However, sheep used the space less evenly than goats when kept under comparably low stocking rate ($CI_{goats} = 0.47$). While foraging, the relative presence in *A. viridis* stands was similar in sheep and goats (mean $RPA_{sheep} = 0.76$; $RPA_{goats} = 0.80$).

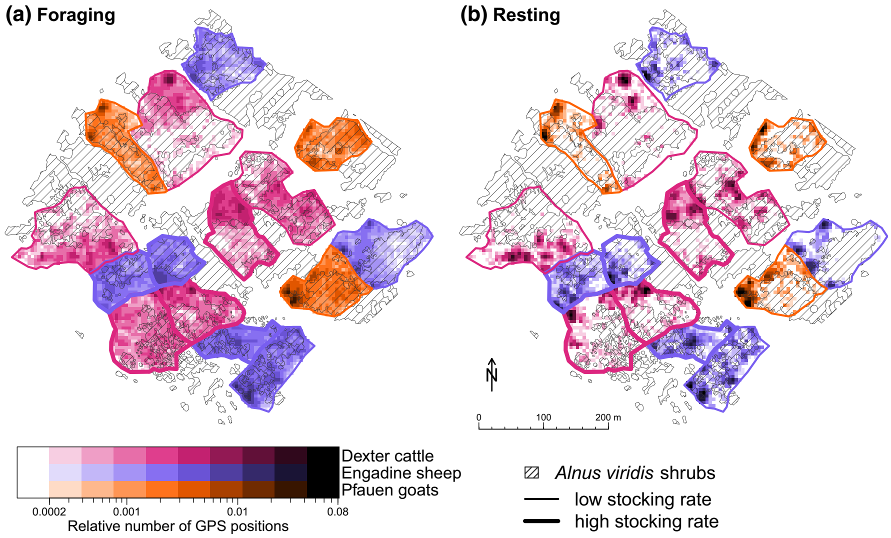

FIGURE 4 Space-use patterns of cattle, sheep and goats under low or high stocking rate on pastures partially covered by *Alnus viridis* stands. Colour intensity of grid cells indicates the number of GPS positions relative to the total number per paddock, classified as (a) foraging and (b) resting, averaged over the entire grazing period

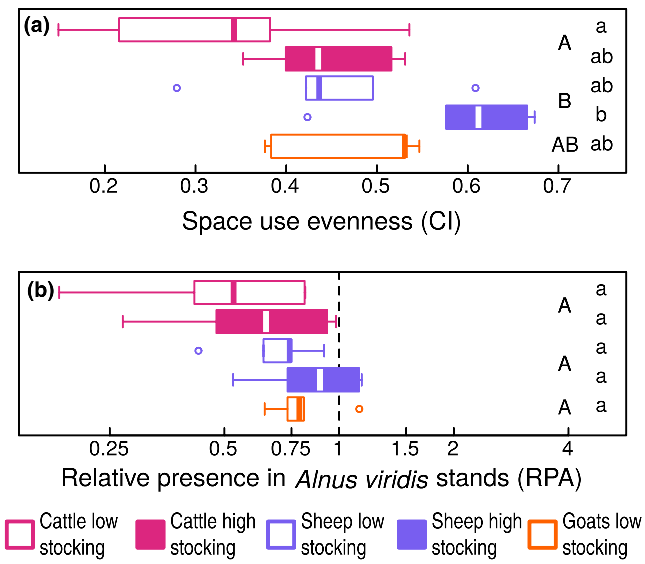

FIGURE 5 Space use of cattle, sheep and goats while foraging as measured by GPS: (a) evenness of space-use measured as Camargo index (CI) and (b) the relative time spent in *A. viridis* stands normalized by the area covered by shrubs. After selecting GPS positions classified as foraging, data of all animals grazing a paddock simultaneously were averaged. Thus, each boxplot is based on six data points. Values annotated without common letters are significantly different at $p < 0.1$. For effects on space use while resting, see Appendix S10

3.1.2 | Parameters explaining space use

The regression analysis highlighted several parameters explaining space use, especially of cattle. The steeper the slope (Figure 6a), the larger the distance to open pasture within *A. viridis* stands (Figure 6b) and the higher the shrubs (Figure 6c), the less frequently cattle visited an area. Consequently, cattle preferred flat areas with short vegetation and mainly explored the edge of *A. viridis* stands. Under low stocking rate, cattle avoided steep areas and places deep inside the *A. viridis* stands more strictly than under high grazing pressure.

Engadine sheep also were indifferent to slopes and tended to avoid the depth of the *A. viridis* stands. The impact of slope and of distance to open pastures on sheep's space use was only slightly affected by stocking rate. However, under high grazing pressure, they preferred tall vegetation, which contrasts observed cattle behaviour.

In contrast to cattle and sheep, goats were not deterred by, but were rather attracted to steep slopes. The impact of distance to open pasture was slightly negative, as it was for sheep. As with the sheep, goats slightly preferred the edges over the depth of *A. viridis* stands, however not as clearly as was observed for cattle. Goats significantly preferred tall vegetation.

3.2 | Differences in debarking

3.2.1 | Debarking occurrence and intensity of different livestock breeds

The three livestock breeds differed significantly in their debarking activity. For cattle, no debarking was registered (Figure 7a), but they were often observed foraging the understorey vegetation and leaves of *A. viridis* (not quantified). Engadine sheep debarked 7% of all *A. viridis* branches (Figure 7b), that is, on average 244 branches per paddock (Figure 7c). However, there were large differences in debarking intensity among paddocks as indicated by a large standard deviation (*SD* = 7.4%). The debarking behaviour of goats was most surprising: they debarked fewer branches (185 per paddock) than sheep and most were not branches of *A. viridis* shrubs, but of *S. aucuparia*. (*S. aucuparia*: 140 debarked branches per paddock = 82.3%; *SD* = 7.9%; *A. viridis*: 45 branches = 0.8%; *SD* = 0.7%). *Sorbus aucuparia* shrubs were equally distributed over the stands and covered about 2% of the shrub layer. Sheep did not debark any *S. aucuparia*.

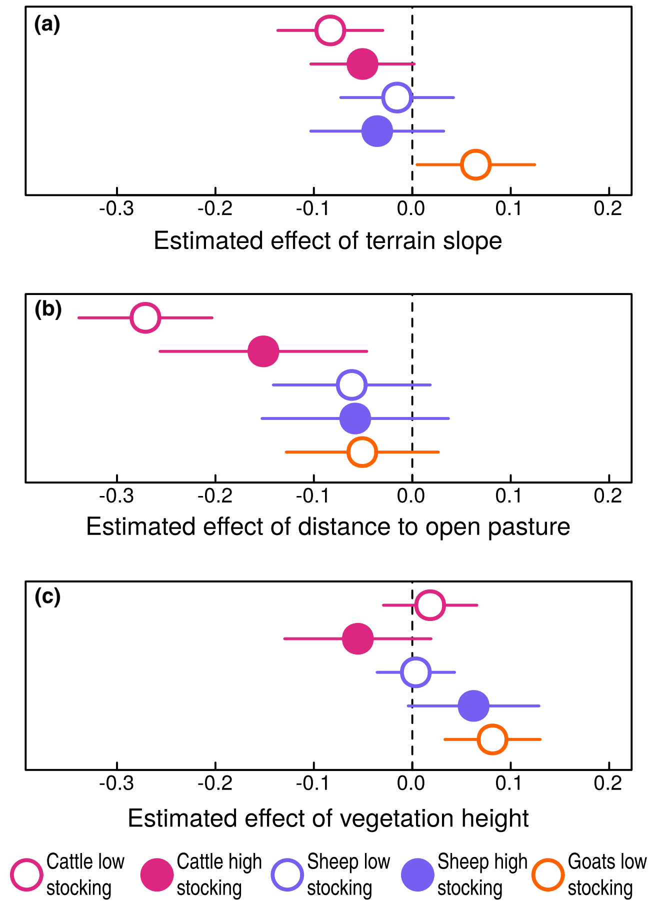

FIGURE 6 Estimated effects (regression coefficients) on space use of cattle, sheep and goats while foraging at low or high stocking rate on heterogeneous pastures partially covered by *Alnus viridis* stands. The dependent variable of the regression model is the average relative density of GPS positions classified as foraging. Explanatory variables are (a) terrain slope, (b) distance to open pasture and (c) vegetation height standardized to mean 0 and 1 standard deviation. The model accounts for spatial autocorrelation. Positive values indicate preference, zero indifference, negative values indicate avoidance [circle: median; whisker: 95% credibility interval]

3.2.2 | Parameters explaining debarking

Upon closer examination, several parameters explained the occurrence of *A. viridis* debarking (i.e. presence or absence of debarking; Table 1a) and the intensity of *A. viridis* damage (i.e. the relative number of debarked branches where debarking was found; Table 1b). Cattle did not strip any *A. viridis* bark (i.e. all values were zero), so it was not possible to include them in the model.

Remarkably, the occurrence of *A. viridis* debarking (Table 1a) was lower in paddocks of goats, than in those of sheep ($p_{goats} < 0.001$). Taller vegetation and greater distance to open pasture reduced the probability that sheep would debark *A. viridis* ($p_{veg.heigth} < 0.001$; $p_{distance} < 0.001$); in other words, they preferred debarking at the edges of the stands and at locations with short vegetation. In contrast, tall vegetation clearly increased debarking occurrence in goat paddocks ($p_{goats*veg.height} < 0.001$). Goats were also less deterred by large distances to open pastures than sheep ($p_{goats*distance} = 0.045$). The effect of slope on debarking by sheep and goats was small but significantly negative for sheep ($p_{slope} = 0.02$).

Debarking intensity (Table 1b) was less affected by the tested parameters than debarking occurrence (Table 1a). Hence, parameters more strongly impacted the animals' decisions of where to debark rather than how intensively to debark once they had chosen a certain location. Of all parameters evaluated for both goats and sheep, only distance to open pasture significantly reduced the intensity of debarking by sheep ($p_{distance} = 0.0098$); in other words, they debarked more branches at the edges of *A. viridis* stands.

4 | DISCUSSION

4.1 | Goats – The benchmark to beat

Over centuries, goats have been one of the most important livestock species in Europe (Boyazoglu et al., 2005) and have efficiently controlled shrub expansion. Therefore, we used goats as the benchmark for shrub consumption in our study. Goats differ from most other ruminant livestock in terms of their feeding strategy. As opportunistic mixed feeders they readily switch between grass and browse fodder (Lu, 1988). Their tolerance of a broad spectrum of feed resources was clearly observed in our study: goats used the available space most evenly (*Space-use hypothesis*) and debarked both available shrub species (*Debarking hypothesis*). They exploited nutrients from herbaceous and woody sources found in open pastures or shrub stands respectively. The feeding behaviour observed in our study corroborates farmers' experiences and former studies conducted in other shrub encroached ecosystems (e.g. Wehn et al., 2011 in birch and heathlands; Rogosic et al., 2006 in Mediterranean maquis). We complemented these observations, by demonstrating that hardy goats penetrate high shrub stands more than hardy breeds of other ruminant species, likely because they originate from wild *Capra* species, which prefer habitats providing shelter (Zobel et al., 2018). Accordingly, we found that goats prefer tall vegetation, which mainly grow deep within shrub stands. This suggests that hardy goats may not only supplement their diet when occasionally visiting the shrub edges, but may largely subsist on shrub fodder and thus explore the depths of a shrub stand where taller vegetation occurs.

4.2 | Goats prefer *Sorbus* over *Alnus*

Goats have the potential to (re-)transform shrubland into open pasture as previously shown for other shrub species (Wehn et al., 2011; Wood, 1987). However, our study showed that goats are not the ideal *A. viridis* antagonists, because they preferred *S. aucuparia*, which was much less abundant in the study area. The *Debarking hypothesis* must, therefore, be rejected. Generally, mixed feeders are expected to select single plant individuals in shrub stands (Iussig et al., 2015), whereas grazers forage less

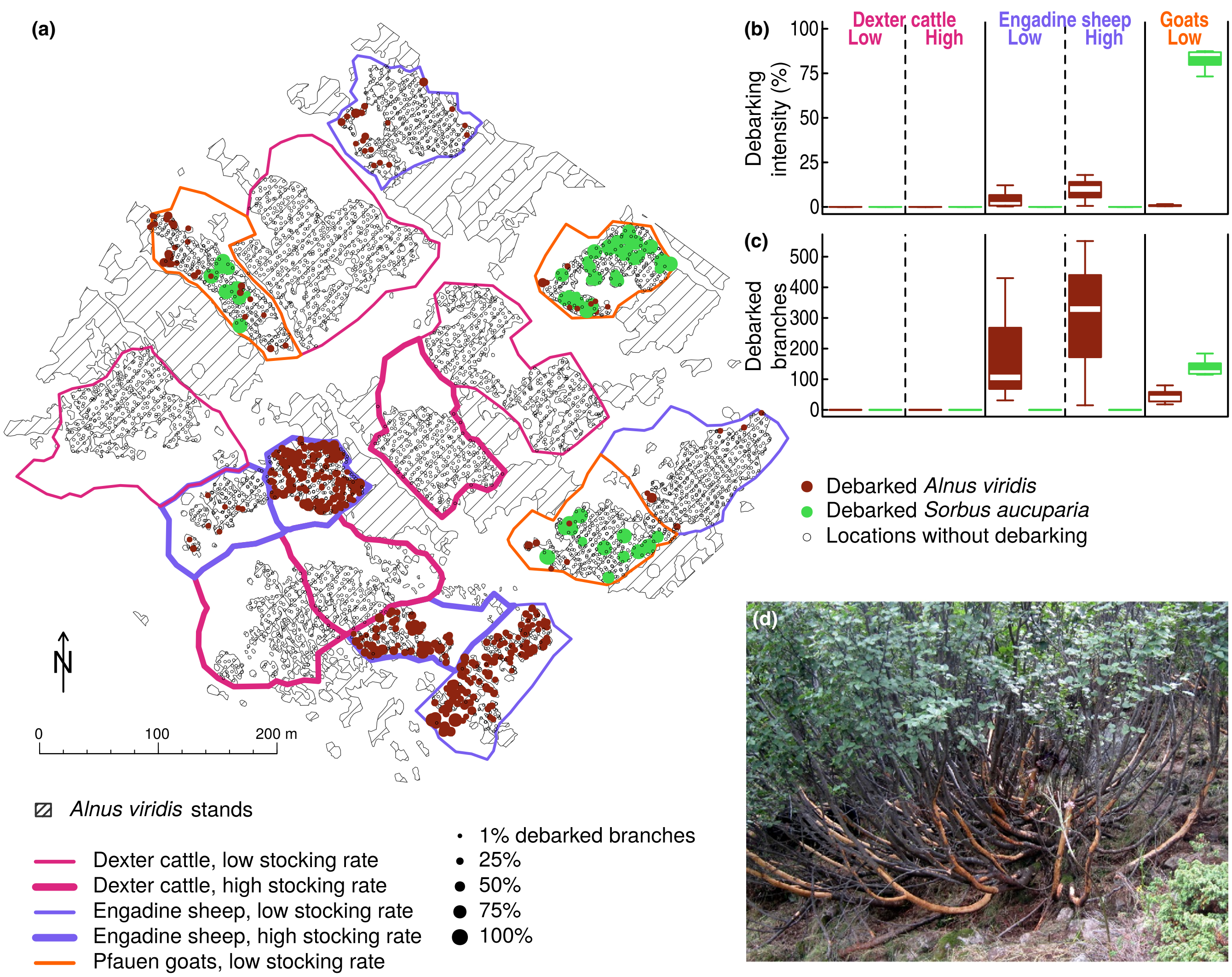

FIGURE 7 (a) Debarking occurrence (circles) and intensity (circle size) of cattle, sheep and goat grazing pastures partially covered by shrublands. Circles represent shrub locations with (coloured) or without debarking (grey). Debarking intensity: (b) proportion of *Alnus viridis* and *Sorbus aucuparia* branches debarked by the livestock breeds and (c) absolute numbers of debarked branches per paddock at the end of the experiment. The shrub layer was composed by about 98% *A. viridis* and 2% *S. aucuparia*. (d) Debarked *A. viridis* branches, which likely die off within a year

selectively on open pastures. In that respect, goats in our study behaved as hypothesized by primarily selecting *S. aucuparia*. Nevertheless, goats are appropriate for re-establishing open pastures because they also debark *A. viridis*, though clearly less than Engadine sheep.

However, goats are inappropriate if the management aim is to re-establish high forest on abandoned pastures, as in the case of protection against avalanches or other natural hazards. *A. viridis* prevents reforestation, because it out-competes tree saplings with fast growth, effective shading and late leaf shedding, which cause high humidity inside the stands, long snow cover and fungal infestation (Huber & Frehner, 2013). Few tree species are able to compete under these conditions: the most valuable pioneer of forest succession is *S. aucuparia* (Emmer et al., 1998), which goats preferably debarked in our study.

4.3 | Cattle slightly affect *A. viridis* by trampling

Cattle as grass and roughage feeders were not expected to debark shrub branches, because their forage technique—ripping off forage by tongue—does not facilitate stripping off bark. And indeed, cattle were never observed debarking in this study. Thus, cattle seem to constrain shrubs less effectively than goats and sheep. Although cattle spent less time in the shrubs—likely due to their larger body size and lower adaptation to rough terrain—than sheep and goats, the differences were not statistically significant. Cattle did not avoid the stands completely, but visited the shrubland and especially its edges frequently (*Space-use hypothesis*). Hence, cattle do not destroy *A. viridis* quickly by debarking. However, they were observed foraging seedlings, leaves and understorey, breaking off branches and trampling down young shrubs when moving inside the stands (not

TABLE 1 Effects of livestock species (sheep and goat) and terrain parameters (vegetation height, distance to open pasture and slope) on (a) occurrence and (b) intensity of *Alnus viridis* debarking. Sheep were defined as baseline (grey cells); cattle could not be modelled due to zero debarking. Estimates are obtained using a zero-inflated generalized mixed-effects model in which inverted coefficients of the zero-inflated component indicate the occurrence of debarking (a) and the conditional component indicates the intensity of debarking (b). Note: both components are proportions (a: of zeros, b: of branches) and estimates are on the logit scale

	(a) Debarking occurrence			(b) Debarking intensity		
	Estimate	*SE*	*p*-value	Estimate	*SE*	*p*-value
(Intercept)	−0.08	0.33	0.80	−1.42	0.30	<0.001
Goats	−3.43	0.91	<0.001	−0.27	0.71	0.71
Veg. height	−0.37	0.08	<0.001	+0.002	0.06	0.97
Goat × Veg. height	+0.84	0.21	<0.001	+0.03	0.19	0.89
Distance	−0.09	0.02	<0.001	−0.06	0.02	0.0098
Goat × distance	−0.16	0.08	0.045	−0.02	0.09	0.82
Slope	+0.001	0.004	0.02	0	0.004	0.98
Goat × slope	−0.005	0.01	0.68	−0.003	0.008	0.76

quantified). Thereby they probably thin the thickets slowly. Since beef is easier to place on the market than goat meat, hardy cattle could be a more profitable alternative for shrub control in the long term.

4.4 | Engadine sheep damage *A. viridis* more severely than hypothesized

As hypothesized, Engadine sheep used the space more evenly, visited *A. viridis* stands more often and penetrated them deeper than cattle (*Space-use hypothesis*). Similar to goats, they were rather indifferent in their relative presence in *A. viridis* stands, at least under high stocking rate. Thus, the trampling impact of sheep is comparable with goats, whereas cattle are a less suitable alternative to goats.

While the *movement* behaviour of sheep confirmed the *Space-use hypothesis* under comparable stocking rate, their *debarking* behaviour *Debarking hypothesis* was counter-intuitive. We presumed they would forage leaves of the shrubs at best and would have a smaller destructive impact on *A. viridis* than goats. However, we demonstrated for the first time that Engadine sheep debarked more shrubs of the species *A. viridis* than goats. Therefore, Engadine sheep are ideal animals to control the spread of *A. viridis*. Furthermore, because they did not debark the forest pioneer *S. aucuparia*, they could also be useful in the resettlement of forest by weakening the competitive *A. viridis* shrubs and increasing the survival of light-demanding tree saplings.

However, the large variability of debarking observed among paddocks in this study suggests the presence of additional, yet unidentified, parameters that influence the debarking behaviour of sheep. The differences in debarking cannot be explained by differences in slope; soil humidity; proximity to forest or water; per cent cover of shrubs; or by an effect of herd or stocking rate, because sheep paddocks with lower debarking damage were equally distributed with respect to these parameters. Large variation in shrub consumption by sheep was also reported by Celaya et al. (2007). Further investigations are necessary to identify additional drivers of sheep's debarking behaviour.

4.5 | Grazing pressure influences foraging behaviour

A higher stocking rate is generally assumed to lower forage selectivity, equalize space use and increase shrub consumption of ruminants (e.g. Pauler, Isselstein, Berard, et al., 2020; Pittarello et al., 2017; Utsumi et al., 2010). Indeed, cattle and sheep used space more evenly under high grazing pressure (*Grazing pressure hypothesis*). However, the difference was much clearer for sheep than for cattle. This indicates that cattle have a more clearly defined and stable feeding niche of herbaceous fodder, whereas the foraging behaviour of sheep is more opportunistic. This concurs with Sanon et al. (2007) who found that if less herbaceous fodder was available, sheep and goats increased browsing time, whereas cattle replaced grazing time by resting and ruminating. Although cattle were kept under higher stocking rate than sheep and goats, they visited *A. viridis* least and did not debark a single branch. This underlines their preference of herbaceous roughage. This has important management implications: an even higher grazing pressure would likely not substantially increase *A. viridis* debarking by cattle, but could raise animal welfare issues, because they could be underfed. Contrastingly, goats and sheep (at least of the Engadine breed) have a broader spectrum of potential forage and will more frequently debark *A. viridis* under higher grazing pressure.

4.6 | Breed matters in *A. viridis* control

In our study, we only observed hardy breeds, because they are expected to be better adapted to the rough, subalpine conditions and to control shrub expansion.

Hardy Dexter cattle can slowly thin the thickets as has been suggested of other hardy cattle before (Meisser et al., 2014; Pauler, Isselstein, Suter, et al., 2020; Svensk et al., 2021). Since their main impact is trampling, heavier hardy cattle breeds like Highland cattle may be more destructive. Heavy, production-oriented cattle, however, were recently shown to use the space less evenly (Pauler, Isselstein, Berard, et al., 2020) and thus, may avoid shrub stands altogether. Consequently, we assume that production-oriented, conventional cattle breeds are less appropriate for *A. viridis* clearance.

Hardy breeds of sheep and goats have been reported to forage less selectively and to consume more shrubs than production-oriented breeds (Brand, 2000; Glasser et al., 2012). However, it remains to be clarified whether the newly detected debarking preference for *A. viridis* is a general pattern in hardy sheep or a unique behaviour of the Engadine breed. The unexpected, beneficial behaviour of these local sheep underlines the general importance of preserving rare hardy livestock breeds.

5 | CONCLUSIONS

We assessed the movement and foraging behaviour of ruminant livestock in *A. viridis* stands to estimate if hardy breeds of cattle and sheep can replace goats as *A. viridis* antagonists. We conclude that the adequate livestock choice depends on the management objective: (a) If a pasture covered by *A. viridis* stands is just to be used for grazing, all hardy livestock breeds included here are appropriate: all visited the shrubland and consumed at least the leaves and understorey. Even hardy cattle, which are economically more attractive than goats (and sheep), can use such pastures. (b) Alternatively, if management aims at reducing shrub cover to restore biodiverse open grasslands, this study suggests that Engadine sheep would outperform the other species. For the first time, we demonstrated that this local breed of sheep debarked *A. viridis* more effectively than expected for sheep in general and even better than goats. Engadine sheep may not only slow down *A. viridis* expansion but effectively thin the thickets. Therefore, they seem to be especially suited for *A. viridis* clearance. Cattle, however, are inappropriate for this management goal because not even the undemanding, hardy Dexter cattle debarked *A. viridis*. (c) Finally, if management aims at the succession towards a subalpine forest, this study suggests that only Engadine sheep are appropriate because only they debarked *A. viridis* without affecting pioneer trees of forest succession, as the goats did. It seems worth investigating the long-term impact of grazing on *A. viridis* stands and if other local sheep breeds offer comparable benefits. Our findings underline that hardy breeds are a powerful option to control the negative environmental impacts of shrub encroachment and to sustain the structure, function and outstanding biodiversity of mountain grasslands.

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CONFLICT OF INTEREST

No conflict to declare.

AUTHORS' CONTRIBUTIONS

J.B., M.K., A.L. and M.K.S. conceived the ideas and designed the methodology; T.Z., M.S. and M.K.S. collected the data; C.M.P. and M.K.S. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Zenodo repository https://doi.org/10.5281/zenodo.4751171 (Pauler et al., 2022).

ORCID

Caren M. Pauler https://orcid.org/0000-0002-7872-2711
Andreas Lüscher https://orcid.org/0000-0001-8158-1721
Michael Kreuzer https://orcid.org/0000-0002-9978-1171
Joël Berard https://orcid.org/0000-0002-7222-632X
Manuel K. Schneider https://orcid.org/0000-0002-3842-2618

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