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Highland cattle grazing reduces shrubland cover and increases plant diversity in green alder-encroached pastures

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ABSTRACT

Alnus viridis is a shrub species encroaching mountain pastures in Central Europe, with negative economic and ecological consequences. Targeted grazing with robust livestock breeds may limit its spread and help to restore pastures, but its effectiveness on recovering plant diversity and forage quality remains unclear. This study was conducted on two summer pastures in the Alps encroached by *A. viridis*: Val Vogna in Italy, where Highland cattle were introduced in 2009, and Bovonne in Switzerland, where they were introduced in 2019. We characterised vegetation cover changes over the past decades using images analyses, evaluated animal movement patterns using GPS tracking, and conducted vegetation surveys to assess Highland cattle impact on plant diversity and pastoral value between 2019 and 2024. Shrubland cover decreased by 8 % at Val Vogna and 4 % at Bovonne after cattle introduction. Species richness increased from 25.5 to 32.2 at Bovonne and from 30.6 to 32.9 at Val Vogna, alongside an increase in the effective number of species. Pastoral value of open pastures at Bovonne improved from 12.9 to 17.7. Patterns of animal movement indicated a preference for pastures rather than shrublands; though at Bovonne they increasingly grazed within *A. viridis* stands over time. Differences between sites may partly reflect the longer grazing history and habits of Highland cattle at Val Vogna, where they were introduced a decade earlier. Overall, our study highlights the potential of Highland cattle as an effective tool to counteract *A. viridis* encroachment and restore the plant diversity of encroached pastures.

1. Introduction

Woody encroachment threatens grassland ecosystem functions worldwide (Eldridge et al., 2011; Archer et al., 2017; Stevens et al., 2017). Green alder (*Alnus viridis* (Chaix) DC) is one of the most widespread shrub species in central Europe and plays a dominant role in woody encroachment processes in former open mountain pastures, primarily due to the abandonment or reduction of agricultural activities (MacDonald et al., 2000; Anthelme et al., 2007). Indeed, 70 % of the shrublands in Switzerland are dominated by this species (Brändli, 2010). Although *A. viridis* is typically found on moist, north-facing, steep slopes, recent studies have shown that its ecological niche is much broader than previously assumed, and that climate change is accelerating its encroachment by expanding its upper distribution limit to higher elevations (Körner, 2012; Caviezel et al., 2017; Skoczowski, 2021). Consequently, *A. viridis* has the potential to spread over larger areas of abandoned pastures.

As a pioneer species, *A. viridis* forms dense canopies reaching 2–5 m in height and it presents a symbiotic relationship with the nitrogen-fixing actinomycete *Frankia alni* (Huss-Danell, 1997). Consequently, its expansion leads to nitrogen enrichment, resulting in nitrogen-saturated soils (Bühlmann et al., 2016). Combined with reduced light and temperature, as well as increased soil moisture under its canopy, these conditions contribute to a decline in plant and animal species diversity, along with a reduction in forage quality (Anthelme et al., 2001; Koch et al., 2015; Zehnder et al., 2020). Indeed, only a few shade-tolerant and nitrophilous species, such as *Adenostyles alliariae* (Gouan) A. Kern, *Cicerbita alpina* L. (Wallr.) and ferns such as *Athyrium filix-femina* (L.) and

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Dryopteris dilatata (Hoffm.), among others, can grow and they largely dominate the understory vegetation community (Svensk et al., 2021). Additionally, *A. viridis* encroachment prevents forest succession and, in contrast to coniferous forests, *A. viridis* stands do not provide protection against erosion and avalanches on steep slopes, mainly due to the elasticity of their branches (Caviezel et al., 2014).

Robust livestock has the potential to be managed as a tool for the agroecological restoration of woody-species encroached grasslands. Previous short-term studies have shown that Highland cattle can strongly impact *A. viridis*-encroached pastures through grazing and trampling (Svensk et al., 2022). Specifically, cattle were observed to consume green alder leaves, break its branches, and significantly reduce the cover of typical species of the *A. viridis* understory—such as ferns and tall forbs—while increasing bare soil cover. It has also recently been demonstrated that *A. viridis* leaves can constitute a valuable forage resource for robust livestock, especially at the beginning of summer (Svensk et al., 2024). Moreover, Highland cattle have an effective role in the translocation of the ingested nitrogen from *A. viridis*-encroached areas to adjacent pastures (Svensk et al., 2023). This evidence, combined with this breed's low maintenance energy requirements and low grazing selectivity (Berry et al., 2002; Pauler et al., 2020a), highlights the potential of Highland cattle to open encroached vegetation patches and trigger vegetation composition changes that can contribute to the restoration of mountain pastures. However, it remains unclear whether these short-term impacts persist and effectively help to reduce shrubland cover and enhance plant diversity and forage quality over time.

Animal tracking can be used to better understand the factors that influence livestock behaviour and movement, and to determine how grazing pressure and livestock management could be beneficial as a restoration tool in degraded ecosystems. Global Positioning System (GPS) technology provides an accurate and consistent measure of livestock distribution across the landscape. Together with remote sensing data, it enables to assess how landscape characteristics influence livestock distribution (Turner et al., 2000; Ungar et al., 2005; Forin-Wiart et al., 2015). Several studies have shown that the most important factors influencing livestock grazing location are forage quality and availability, topography, and distance to water (Homburger et al., 2015; Pauler et al., 2020a; Rivero et al., 2021). However, as most of these studies have been carried out over short time periods (1–2 years), little is known about the stability of movement patterns over a longer period and across multiple years. Indeed, a recent review paper summarizing information from articles using GPS-tracking has shown that in the period 2000–2020, among 87 articles, the average duration of tracking was 1.4 years, and only 3.4 % of the articles had a duration of 5 years or more (Rivero et al., 2021). Moreover, 96 % of the studies were conducted with beef cows, heifers or steers, and 4 % on dairy cows and no specific information on robust breeds was provided. Therefore, there is a lack of medium-term studies that determine robust cattle movement patterns to evaluate the effectiveness of their grazing management as an agro-ecological restoration tool.

In this study, we evaluated the effect of targeted grazing by Highland cattle on two summer pastures encroached by *A. viridis* in the Swiss and Italian Alps, combining a long-term, landscape-scale approach based on aerial and satellite data analysis with local-scale, a medium-term five-year livestock GPS tracking and vegetation surveys. The two summer pastures had a different grazing history, with the Italian site, located at Val Vogna that had already been grazed by a Highland cattle herd for 10 years before this study started in 2019, while Highland cattle grazing started in 2019 in the Swiss site, located at Bovonne. Here, we specifically aimed to investigate the changes in shrubland and pasture cover over the past decades at both sites, with a particular focus on the period since 2019. We also evaluated the patterns of cattle movement and the botanical changes in the last five years at both sites. We hypothesized that:

(i) Highland cattle grazing would reduce woody encroachment and promote vegetation cover and composition changes in shrublands through trampling, grazing, and seed and nutrient redistribution. These processes were expected to lead to shrub canopy opening and increased light availability at the soil level, which could enhance herbaceous plant colonization in previously encroached areas. Consequently, we predicted a reduction in shrubland cover after cattle introduction, along with shifts in the understory plant community, including increases in plant species diversity and forage quality over time.

(ii) Highland cattle would initially prefer open pastures but gradually increase their use of edges and inner areas of *A. viridis* stands. This spatial use shift was expected to limit *A. viridis* cover from the shrubland edges inward. In this regard, the progressive livestock penetration into *A. viridis* stands could exert pressure on shrubs and understory vegetation, further reinforcing canopy opening and promoting vegetation changes. These may include increased plant diversity, shifts in community composition, and the recovery of grassland species in formerly encroached areas.

(iii) Grazing patterns would evolve following Highland cattle introduction, becoming more consistent over time. Accordingly, we expected cattle movement patterns to be more stable at Val Vogna, where grazing was established 10 years earlier. In contrast, we predicted that cattle spatial patterns—along with vegetation cover, plant diversity and forage quality—would show more pronounced changes at Bovonne, where Highland cattle had been introduced more recently.

2. Methods

2.1. Study sites and grazing management

This research was carried out between 2019 and 2024 in two study sites in the Alps, where *A. viridis* encroached formerly open pastures (Fig. S1). The first site was located in Bovonne (N46°16'20.109'' E7°6'47.327'', Vaud, Switzerland), and had three paddocks grazed in rotation during the summer period, covering a total grazable area of about 23 ha. The second site was in Val Vogna (N45°46'18.815'' E7°54'9.198'', Vercelli, Italy), and consisted of four paddocks grazed during the summer. For the purpose of this study, a single large and heavily encroached paddock with 18 ha of grazable surface in Val Vogna was selected and included in the experiment. Both sites had similar topographical conditions with a mean elevation of 1820 m a.s.l. and 102.15 °N aspect in Bovonne, and 1897 m and 105.38 °N in Val Vogna. In both sites, areas highly encroached by *A. viridis* were located at comparable elevations, from 1660 to 1960 m.

The site at Bovonne was a summer pasture historically grazed by 70–80 dairy cows during the summer. Before 1985, 80–100 goats were also herded together with dairy cows during the summer grazing season, but goat farming was abandoned in that year. In 2019 Highland cattle were introduced in the area and grazed the three paddocks for five consecutive summers. Val Vogna was historically grazed by a Swiss brown breed herd (~ 80 cows), and since 2009 it has been grazed exclusively by Highland cattle, with a similar stocking rate. Highland cattle herds included cow/calf pairs and heifers, varying in age from 1 month to 13 years in Bovonne, and from 3 months to 18 years in Val Vogna. They grazed each year from the middle of June to the beginning of September (see Table S1 for details on grazed areas, stoking rates and grazing periods). Six to ten cows from each herd were equipped with GPS collars each year (Followit AB, Tellus GPS System collars, Sweden). The collars recorded their position every 10 min over the whole grazing period, with an accuracy of 2–5 m.

2.2. Vegetation analyses

2.2.1. Long term changes in vegetation cover

To describe long-term changes in vegetation cover at both sites and to test hypotheses (i) and (iii), we manually classified vegetation cover from orthophotos and satellite images from multiple years. For Bovonne, historical orthophotos dating back to 1946 were provided by the Federal Office of Topography Swisstopo (https://www.swisstopo.admin.ch/en/orthoimages) with a spatial resolution of 0.5 m from 1946 to 2016, and 0.25 m from 2016 onward. Images from 1946 to 1988 are black and white, while those from 1989 onward are in RGB. According to the availability and quality of the orthophotos, we analyzed images from 1946, 1957, 1960, 1980, 1992, 1998, 2004, 2007, 2010, 2013, 2016, 2020 and 2023. For Val Vogna, historical orthophotos were provided by the GeoPortal of the Piedmont Region (https://geoportale.igr.piemonte.it/cms/), and those from 1978, 1986, 1991, 2000, 2010, 2015, 2018, and 2021 were retained for the analysis. The spatial resolution was 1.3 m for orthophotos from 1978 and 2000, 1.6 m for those from 1986, 1991, and 2010, and 0.5 m for orthophotos from 2015, 2018, and 2021. In order to include an annual analysis of vegetation cover from the period since this research started (2019), we used PlanetLab basemap mosaic images at a 5-m resolution (Planet Labs, 2024; https://www.planet.com/) for the years in which high-resolution orthophotos were not available (2019, 2021, 2022 and 2024 for Bovonne and 2019, 2020, 2022, 2023 and 2024 for Val Vogna). Mosaic images from the month of July were selected, as they best correspond to the period of the year when vegetation is most developed and easily distinguishable due to its phenological state. The images were filtered for clouds, shadows, and snow-cover. The area of each vegetation cover type was calculated for each year using QGIS software (version 3.36.1-Maidenhead, QGIS.org, 2024). Finally, we used a random sampling approach to calculate the accuracy of land cover classifications between both image sources by site—orthophotos and PlanetLabs basemap images. This was done for three specific years at the Bovonne (2016, 2020 and 2023) and Val Vogna (2015, 2018 and 2021) based on orthophotos availability. The results showed a high level of agreement between the two sources, with an overall accuracy that averaged 0.90 (Table S2). Based on the analysis of aerial and satellite imagery for both sites, three vegetation classes were identified according to the specific characteristics of each area: shrubland, pasture, and forest in Bovonne; and shrubland, pasture, and unvegetated areas in Val Vogna—the latter corresponding to rock-dominated zones.

To better interpret the vegetation cover changes over time in relation to livestock management, we gathered historical information on grazing management from archives in the municipality of Bex, Switzerland, and from interviews with farmers at both study sites. Furthermore, to develop a better understanding of the impact of Highland cattle on vegetation cover compared to dairy cow grazed areas, we carried out the same manual classification on two other control paddocks (42.6 ha in total) at the Bovonne site. These paddocks were not grazed by Highland cattle but by dairy cows over the same period. In this case, the same imagery sources as the ones used for the study plots were analysed. At Val Vogna, there were no available control areas, as the entire site was exclusively grazed by Highland cattle.

2.2.2. Medium-term changes in plant diversity and forage quality

2.2.2.1. Field surveys. To complement the long-term vegetation cover analysis, vegetation surveys were also carried out to assess the medium-term effects of Highland cattle on plant diversity and composition. A total of 60 vegetation surveys were carried out in 2019 and resurveyed in 2024 along permanent transects (*i.e.*, 36 transects in Bovonne and 24 in Val Vogna). Transects were placed in patches with homogeneous botanical composition and vegetation structure, representative of the plant communities of each study site. Vegetation surveys were performed using a vertical-point method (Daget and Poissonet, 1971) along 12.5-m linear transects, in which all the plant species touching a steel needle at 50 cm intervals (*i.e.*, 25 measurements per transect) were identified and recorded. To complete the list of all the species per transect, including occasional or rare species, other plant species which did not touch the needle but were present within a 1-m buffer around the line were also recorded (Kohler et al., 2004). Taxonomic nomenclature followed Aeschimann et al. (2004). Transects were classified as “open pastures” or “encroached areas” according to their main environment.

2.2.2.2. Data analyses. Plant diversity was assessed for each transect by computing species richness and the Effective Number of Species (ENS), which was calculated as the exponential of the Shannon index (Jost, 2006) by using species relative abundance (SRA). We also calculated the Pastoral Value (PV) for each transect, an index summarizing forage yield, quality, and palatability, which has been widely used and validated in the Alps (Daget and Poissonet, 1969, Pittarello et al., 2018). For this purpose, an index of specific quality (ISQ), which depends on plant preference, morphology, structure, and productivity and ranges from 0 (low) to 5 (high) was attributed to each species (Cavallero et al., 2007; Pittarello et al., 2024). Then, the PV was calculated as follows (Daget and Poissonet, 1971):

$$PV = \sum_{i=1}^{n} (SRAi \times ISQi) \times 0.2$$

where SRAi is the species relative abundance, and ISQi is the index of specific quality value of the species i. The PV ranges from 0 to 100.

The frequency of occurrence of each species touching the needle along the transect was converted to 100 measurements (*i.e.*, multiplying by 4 the measured frequency values) to calculate the percentage cover for each plant species (%SC) (Pittarello et al., 2016). A value of 0.3 was attributed to all the occasional plant species recorded in the 1-m buffer area but not along the transect line (Tasser and Tappeiner, 2005). Plant species were pooled into Social Behaviour Types (SBT, *sensu* Troiani et al., 2016, and Tardella et al., 2018), which represent groups of species with a similar ecological behaviour. To accomplish this, firstly the phytosociological optimum at the class level was attributed to each plant species according to Aeschimann et al. (2004). Secondly, species belonging to different phytosociological classes with floristic, ecological and physiognomic similarities were pooled in SBT according to Theurillat et al. (1995). Four out of 12 SBTs were included in our further analyses: nutrient-rich grassland species, nutrient-poor grassland species, woodland and scrub species, and fringe-tall herbs (Table S3). The other SBTs were not considered, given that they represented a very low and negligible vegetation cover. For each transect, the sum of the %SC values for each SBT was calculated.

To evaluate changes on plant species richness, ENS, PV, and %SC according to SBTs over the years, linear mixed-effect models (LMMs) were performed at each site (*lme* function in *nlme* package; Pinheiro et al., 2022). The year and the environment in which each transect was located (open pasture vs encroached area) were set as fixed factors, while the transect ID was considered as a random factor to take into consideration the paired data structure at each transect. For the Bovonne models, the paddock was also considered as a random factor. Since the residuals were not normally distributed, a square root transformation was applied to the PV as well as to the variables assessing changes on the species cover according to SBTs. Model assumptions were checked using *check_model* function, *performance* package (Lüdecke et al., 2021).

Additionally, we evaluated the relationship between changes in the vegetation and livestock grazing intensity. For this purpose, a 10-m buffer was created around each transect and the stocking density was computed by counting the number of GPS fixes with QGIS software (version 3.36.1-Maidenhead, QGIS.org, 2024). The total livestock stocking density (LU ha^{-1}) for each transect was estimated by adding up yearly GPS fixes, weighted according to number of animals (converted in

Livestock Units) present in each paddock in each year. We performed Generalized Additive Models (GAMs) to evaluate whether changes between 2019 and 2024 (calculated as $\Delta_{2024\text{–}2019}$) of species richness, ENS, PV and %SC of SBTs were related to stocking densities for transects in open and encroached areas separately, at both sites. The GAMs were fitted using the *mgcv* package, with smooth terms fitted using thin-plate regression splines (tp) as implemented by default in *mgcv*, and assuming a Gaussian distribution with identity link function (Wood, 2017).

Finally, species turnover, as well as the proportion of species gained and lost in the period from 2019 to 2024, were calculated for each type of environment and study site separately (*codyn* package, *turnover* function, Hallett et al., 2020). We determined the significance of the environment using a likelihood ratio test (Bolker et al., 2009; Bar-Massada and Hadar, 2017). In this way, we evaluated whether the likelihood of a model containing the effect of the environment was significantly larger than the likelihood of a reduced model without it.

2.3. Cattle movement pattern analyses

To test hypotheses (ii) and (iii), we used GPS tracking data and modelled livestock spatial use in relation to environmental characteristics. All statistical analyses were performed using R (version 4.3.3, R Core Team, 2024).

First, each paddock was divided into 10 × 10 m cells. Slope, vegetation cover type, distance to attractive points (such as streams, water troughs and salt blocks), and distance to the edge inside *A. viridis* stands were calculated for the centroid of each cell. For the distance to the edge of *A. viridis* stands, larger distances indicate a greater depth within the shrublands. Terrain slope for the Swiss site was extracted from an elevation model with a resolution of 2 m (https://www.swisstopo.admin.ch/en/height-model-swissalti3d, swissALTI^{3D}, Swisstopo, 2023) and scaled up to 10 × 10 m. For the Italian site, the slope was extracted from a digital elevation model with a 10 m resolution provided by the Istituto Nazionale di Geofisica e Vulcanologia (TINITALY, Version 1.1; Tarquini et al., 2007, 2023). The vegetation cover type of each cell was described by identifying the dominant vegetation present in each cell. For these analyses, a vegetation cover classification has been validated through field observations in 2019, allowing for the most detailed categorization in our long-term analysis based on satellite imagery. In this context, in Val Vogna, we could distinguish between two types of shrublands: those dominated by dwarf shrubs and those dominated by *A. viridis*. Therefore, our classification included three vegetation cover types in Bovonne—open pasture, *A. viridis* shrubland, and forest areas—and four in Val Vogna: open pasture, *A. viridis* shrubland, dwarf shrubland, and unvegetated areas.

Second, to study patterns of Highland cattle movement, we fitted a generalized mixed-effect model with a negative binomial error distribution to the number of GPS fixes per grid cell. The negative binomial distribution was chosen over a Poisson distribution because the GPS count data per cell were overdispersed (overdispersion was tested with the *qcc* package, Scrucca, 2004). Vegetation cover type, slope, distances to attractive points and to the edge inside *A. viridis* were included as fixed effects, together with year and the interaction terms between each variable and year. To account for spatial and temporal autocorrelation in the GPS data, the models included both structured and unstructured spatial random effects. Specifically, we implemented a spatially structured error term using a two-dimensional second-order random walk (RW2), which allows neighbouring grid cells to share similar values and thus captures spatial autocorrelation. Additionally, we included an unstructured spatial random effect to capture location-specific variation not explained by the structured component. Temporal variation was addressed by including a random intercept for year. For Bovonne, we additionally included a random intercept to account for variation among paddocks. Prior to analysis, we evaluated correlations among quantitative variables (*i.e.*, slope, distance to attractive points, and distance to the edge inside *A. viridis* stands) using the *cor* function to identify highly correlated variables. Since for Val Vogna the slope and the distance to attractive points were highly correlated ($r > 0.67$), we retained only the distance to attractive points in our model. Model fitting was performed using Integrated Nested Laplace Approximation (INLA; Rue et al., 2009; Illian et al., 2013). Distance variables were log-transformed. To evaluate the relative density of GPS fixes in relation to each year of the studied period, a linear regression model for each cell was also performed. The resulting coefficient of each cell indicates the temporal trend in use: positive slopes reflect increased use over time, while negative slopes indicate decreased use.

3. Results

3.1. Vegetation changes

3.1.1. Long term changes in vegetation cover

Long-term image analyses showed that before the introduction of Highland cattle, shrubland cover increased at Bovonne (from 9.7 ha in 1946 to 17 ha in 2019), while it remained stable at Val Vogna (from 34.9 ha in 1974–34.6 ha in 2010; Fig. 1). At Bovonne, shrubland expansion accelerated during the 1990s, about five years after goat grazing ceased, and pasture cover decreased from 8.6 ha in 1992 to 4.2 in 2019. According to farmers, in 2013 a 0.32 ha area (1.39 % of the total surface) was clear-cut in one of the study paddocks (Fig. 1A). At Val Vogna, on the other hand, continuous grazing by Swiss Brown cattle before Highland cattle introduction contributed to a more stable pattern of vegetation cover over time. However, after Highland cattle were introduced, image classification revealed that shrubland cover declined at both sites: from 17 to 16.3 ha over five years at Bovonne, and from 34.6 to 31.8 ha over 14 years at Val Vogna (Figs. 1A and 1C). In contrast, control paddocks grazed by dairy cows showed an increase in shrubland cover—from 11.6 ha in 1957 to 17.5 ha in 2019, and then up to 18.3 ha in 2024 (Fig. 1B).

3.1.2. Medium term changes on plant diversity and forage quality

Across the vegetation surveys conducted in 2019 and 2024, a total of 255 species were identified (Table S3), with 83 species exclusive to Bovonne, 97 to Val Vogna, and 75 species shared between the two sites. Over the studied period, the species richness and the ENS increased at both sites, with generally higher values recorded in transects within open pastures rather than in encroached areas (Fig. 2A and Fig. 2B). At Bovonne, the PV increased over time in open pastures, whereas at Val Vogna it was consistently higher in these areas compared to encroached ones, but it did not change over the years (Fig. 2C).

At both sites, the %SC of nutrient-rich pasture species increased over time (Fig. 3A). While at Bovonne the %SC of nutrient-poor pasture species showed no significant change, it increased at Val Vogna (Fig. 3B). In particular, this trend was driven by the increase of the cover of *Festuca nigrescens* Lam. and *Ranunculus montanus* Willd (Table S4). At Bovonne, the %SC of species typical of woodland and scrub habitats did not change, while it increased at Val Vogna (Fig. 3C). This result is explained by the increase in the %SC of herbaceous and woody plants typical of dwarf-shrublands, such as *Viola biflora* L., *Vaccinium myrtillus* L., and *Rhododendron ferrugineum* L (Table S4). Finally, while the %SC of fringe and tall herbs decreased at Bovonne, it increased at Val Vogna (Fig. 3D). These results are explained by a reduction in the %SC of herbaceous species typically associated with green alder understory at Bovonne, such as *A. alliariae*, *Chaerophyllum hirsutum* L., *Geranium sylvaticum* L., *C. alpina*, and *Peucedanum ostruthium* (L.) W. D. J. Koch, along with the %SC of ferns, such as *Athyrium distentifolium* Opiz. At Val Vogna, on the other hand, the %SC of *C. hirsutum*, *P. ostruthium*, *Rumex alpestris* Jacq., and *Poa chaixii* Vill. increased (Table S4).

Of all the GAMs assessing changes in species richness, ENS, and PV as a function of livestock stocking density on the transects where vegetation surveys were performed, only the model for Bovonne open pasture transects showed a statistically significant relationship. In this case,

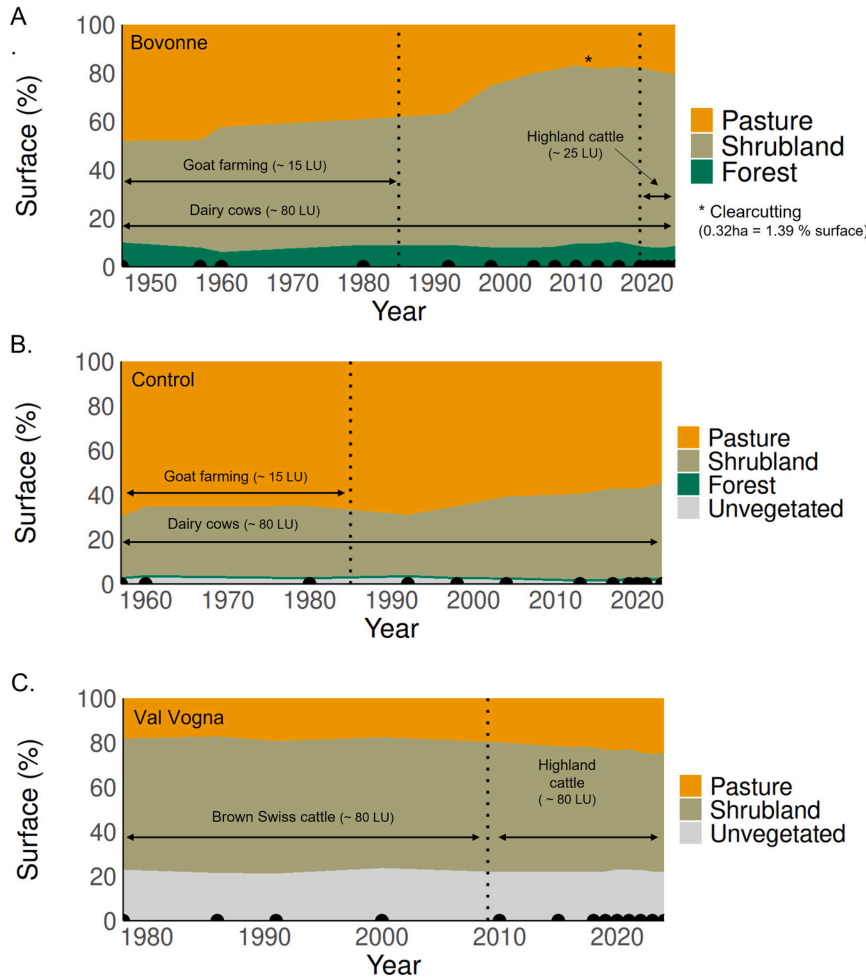

Fig. 1. Vegetation cover changes in relation to historical livestock management at both study sites (A and C) and on control paddocks (B) at Bovonne. Black dots on the x-axis indicate the years in which manual classifications were conducted (17 years for Bovonne, 13 for the control and 13 for Val Vogna). Manual classification years were selected based on the availability of high-resolution imagery at both sites (ortophotos). From 2019–2024, however, annual classifications were conducted, including Planet Labs mosaic data, to capture detailed vegetation changes even in years without orthophotos. Livestock stocking is expressed in Livestock Units (LU) following European standards, where one LU corresponds to a 500 kg animal.

species richness decreased with increasing stocking density ($p = 0.04$; Fig. 4A). Regarding changes in %SC, the cover of species associated with nutrient-rich pastures in the open pastures of Bovonne was positively associated with stocking density ($p < 0.01$; Fig. 4B). For the open pastures of Val Vogna, we found that the change in species cover associated with nutrient-poor pastures increased nonlinearly with stocking density, showing higher values at intermediate stocking densities ($p = 0.04$; Fig. 4C). Furthermore, changes in the cover of fringe-associated species remained relatively stable at low to intermediate stocking densities but exhibited a marked increase at moderately high densities , indicating a J-shaped response ($p < 0.01$; Fig. 4D).

Species turnover rates were, on average, 0.41 at Bovonne and 0.29 at Val Vogna. In general, no significant differences were found between open pastures and encroached areas. However, a higher species loss rate was observed in open pastures (0.14) compared to encroached areas (0.10) in Bovonne, mainly explained by the disappearance of some occasional species (Fig. S2).

3.2. Cattle movement patterns

The model for Bovonne indicated that all covariables considered significatively affected cattle spatial use. According to our results, cattle spent less time in forest or shrubland areas compared to open pastures (Fig. 5A). Livestock spatial distribution was also negatively affected by slope and distance to attractive points. The distance to the edge inside *A. viridis* stands also had a negative effect, meaning that cows tended to spend more time close to *A. viridis* stand edges rather than to their inner parts. We found a significant negative interaction between forest cover and year, which showed a temporal decrease in animal use of forest areas over time. Furthermore, significant positive interactions between the distance to attractive points and year, as well as between the distance to *A. viridis* stand edges and year were found (Fig. 5A). Therefore, although the effects of distance to attractive points and to *A. viridis* stand edges are negative, these effects have weakened over time. The map showing space use over the years represents a mosaic, with both positive and negative trends, spatially clustered within specific areas of the paddocks (Fig. S3).

At Val Vogna, livestock spent less time in zones covered by shrubs (both by dwarf shrubs and *A. viridis*) compared to open pastures. Unvegetated zones were also less visited than pasture zones (Fig. 5B). Similar to the pattern observed in Bovonne, the distance to attractive points had a negative effect on GPS fix density, while the distance to *A. viridis* stand edges had no significant effect. The interaction between dwarf shrub cover and time was negative, while the interaction between unvegetated cover and time was positive. Therefore, over time, the negative effect of unvegetated areas on livestock use became less

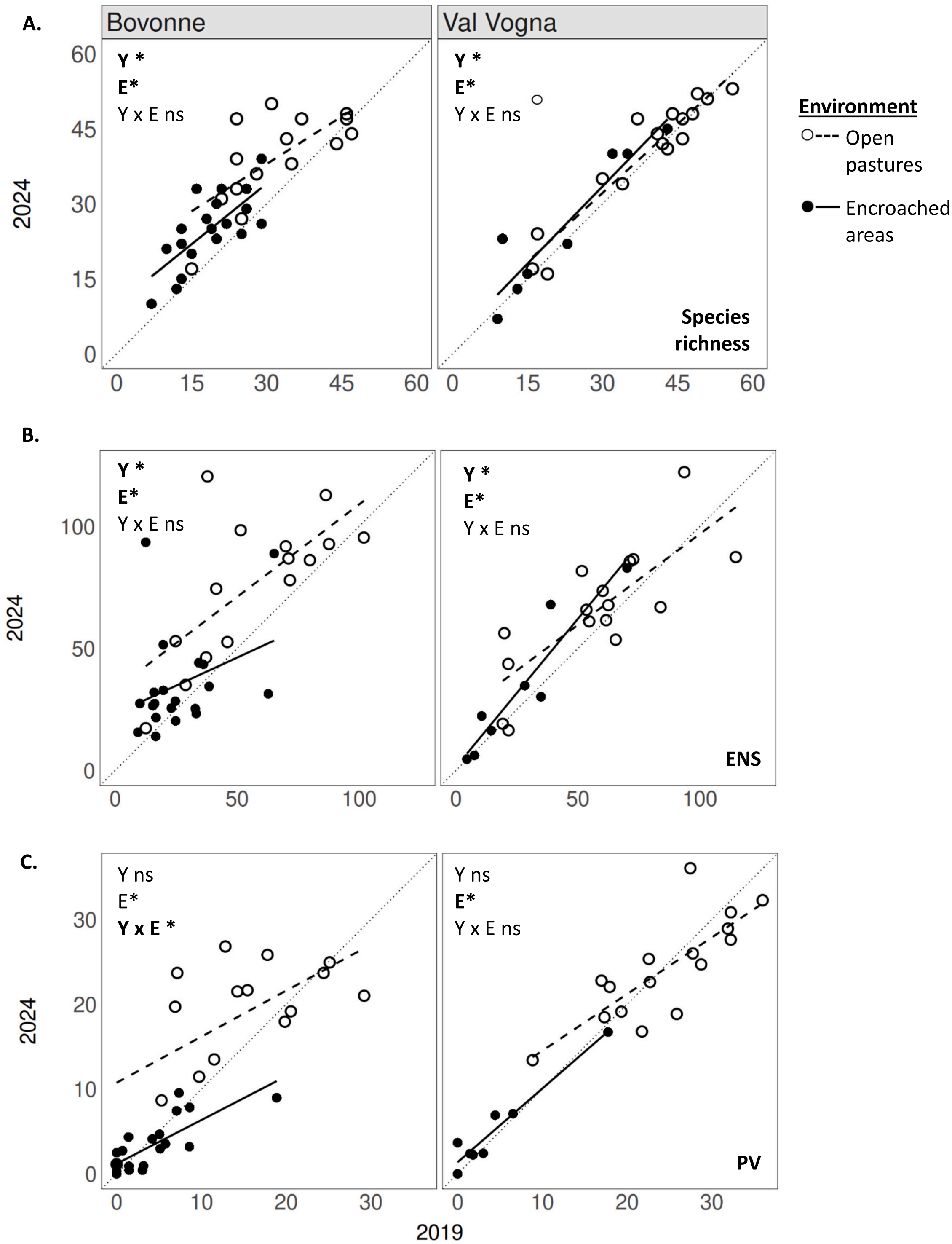

Fig. 2. a) Species richness, b) effective number of species (ENS), and c) pastoral value (PV) for paired data from each transect in 2019 and 2024 at both study sites. Transects were classified according to the environment in which they were placed as open pastures (open circles and dashed lines) or encroached areas (filled circles and solid lines). Fixed effects (Y = year, E = environment, and Y × E = interaction) are indicated with asterisks when their effect on species richness, effective number of species (ENS), or pastoral value (PV) is significant ($p < 0.05$).

intense, while the negative effect of dwarf shrub cover became more intense. All other interactions were not significant. The map showing space use over the years at Val Vogna, also showed both positive and negative trends in specific areas of the paddock (Fig. S4).

4. Discussion

4.1. Shrubland cover decreased following the introduction of Highland cattle

In accordance with our first hypothesis and in both study sites, shrubland cover decreased after the Highland cattle introduction.

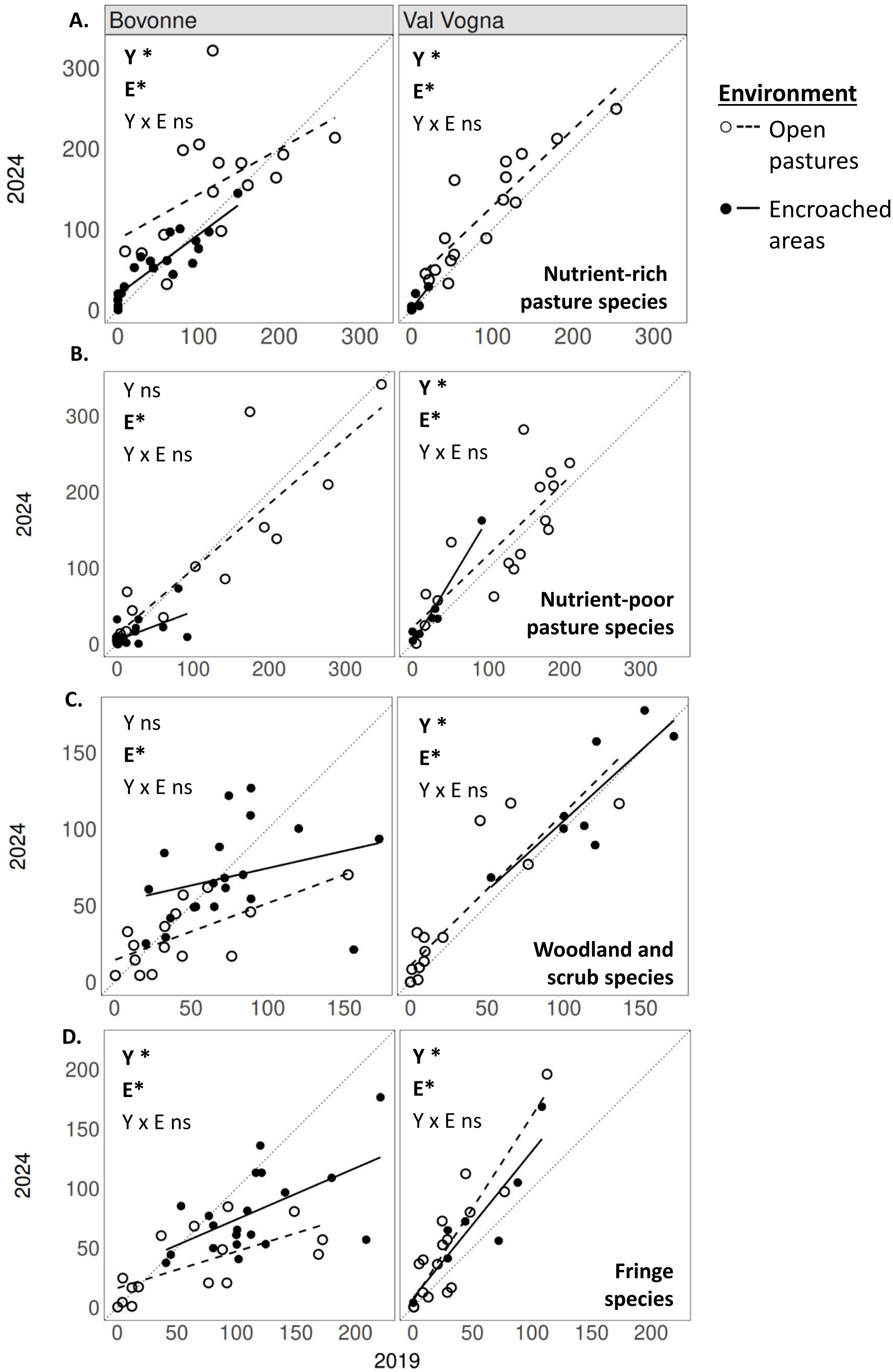

Fig. 3. Sum of species cover grouped according to Social Behaviour Types (SBTs), for paired data from each transect in 2019 and 2024 at both study sites. Transects were classified according to the environment in which they were placed as open pastures (open circles and dashed lines) or encroached areas (filled circles and solid lines).

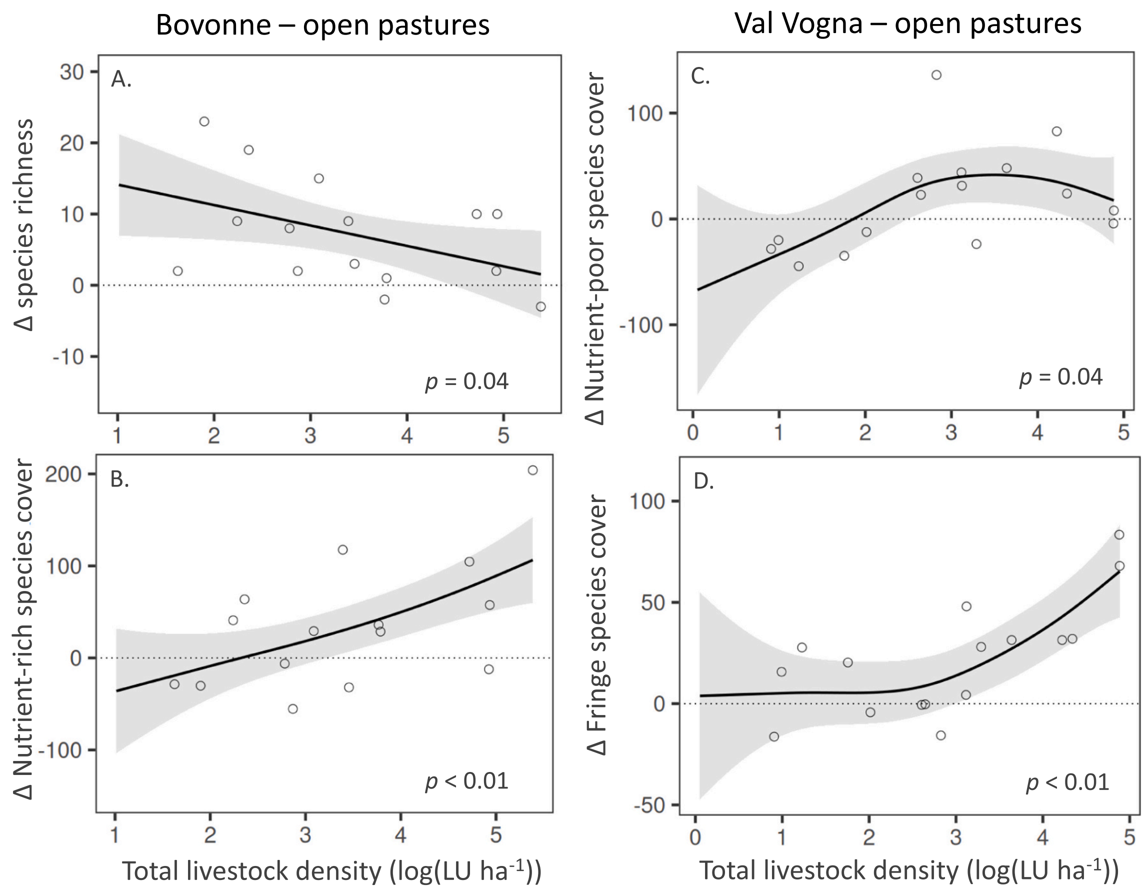

Fig. 4. Results of Generalized Additive Models (GAMs) that showed significant relationships between stocking density (LU ha^{-1}) and change in species richness over the years at Bovonne in open areas (A), in the %SC of nutrient-rich grassland species at Bovonne in open areas (B), in the %SC of nutrient-poor grassland species at Val Vogna in open areas (C), and in the %SC of fringe and tall herb species at Val Vogna in open areas (D). Only significant models ($p < 0.05$) are shown. Smooth functions represent predicted relationships, with shaded areas indicating 95 % confidence intervals.

Although livestock management has been reported by several studies as a possible tool for controlling woody encroachment processes, the potential of robust breeds is still largely underexplored (Gutman et al., 2000; Durigan et al., 2022; Yantes et al., 2025). The decrease of shrubland cover following the introduction of Highland cattle to our study sites may be explained by various direct impacts on woody plants by livestock (Vandenberghe, 2006; Vandenberghe et al., 2007). First, Highland cattle can significantly remove and damage *A. viridis* branches through trampling, scratching, their movement and trail generation (Svensk et al., 2021; 2022). Second, they can heavily defoliate woody species because their feeding behaviour and lower energy requirements allow them to forage on poor-quality, shrub-encroached pastures, resulting in a diet comprising a large share (up to 46 %) of shrub and tree foliage (Berry et al., 2002; Nota et al., 2024). In fact, Highland cattle select significantly more woody plants and fewer broad-leaved grasses compared to production-oriented cattle breeds (Pauler et al., 2020b). Indeed, recent studies have shown that *A. viridis* leaves can be a valuable forage resource due to their high content of crude protein as well as macro- and micro-elements (Svensk et al., 2024), accounting for up to 12 % of the diet of this breed (Nota et al., 2024). It has also been shown that robust breeds may consume the understorey vegetation of *A. viridis* without changes in animal growth performance (Zehnder et al., 2023).

The patterns of shrubland cover change may reflect the history of grazing management at the sites. Before the introduction of Highland cattle, vegetation trajectories differed between the two study areas, likely due to contrasting management regimes. On the one hand, the analysis at Bovonne highlighted that shrubland cover increased, especially for the period from 1990s to 2019 (Fig. 1A). During this period, the study paddocks were exclusively grazed by dairy cows, with highly productive breeds, such as Holstein, being introduced over the course of recent decades. These breeds are indeed less able to forage on steep and marginal sites, yielding insufficient grazing pressure to limit green alder encroachment (Koczura et al., 2019; Pauler et al., 2020b). Before that period, goats, which have been documented as capable of foraging on steep slopes and penetrating dense shrub patches (Pauler et al., 2022; Mochi et al., 2025), foraged on these areas and contributed to limiting *A. viridis* encroachment. Furthermore, the analysis of vegetation cover changes in control areas (*i.e.*, areas not grazed by Highlands but by production-oriented dairy cows) at Bovonne, reinforced this interpretation by showing that the cover of shrubland vegetation has continued to increase in these other neighboring paddocks (Fig. 1B). Although manual clearcutting management has also been performed at Bovonne, this was restricted to a very small area (1.39 % of the total surface) and occurred six years before Highland cattle introduction. In this regard, our results on shrubland cover decrease after 2019 indicates that grazing by Highland cattle played the dominant role.

On the other hand, at Val Vogna, shrubland cover remained more stable over time, likely because the area has been continuously grazed, without abrupt changes in livestock categories and grazing pressure. Before 2009, it was grazed by Brown Swiss cows—a dual purpose, productive yet rustic breed well adapted to the harsh alpine conditions—and, since 2009, by Highland cattle. The stocking rate of both herds was consistent and sufficient to prevent shrubland expansion into the pasture area; however, a trend of decreasing shrubland cover since the introduction of Highland cows was also detected (Fig. 1C). Nonetheless, our interpretation at this site is limited by the lack of a control

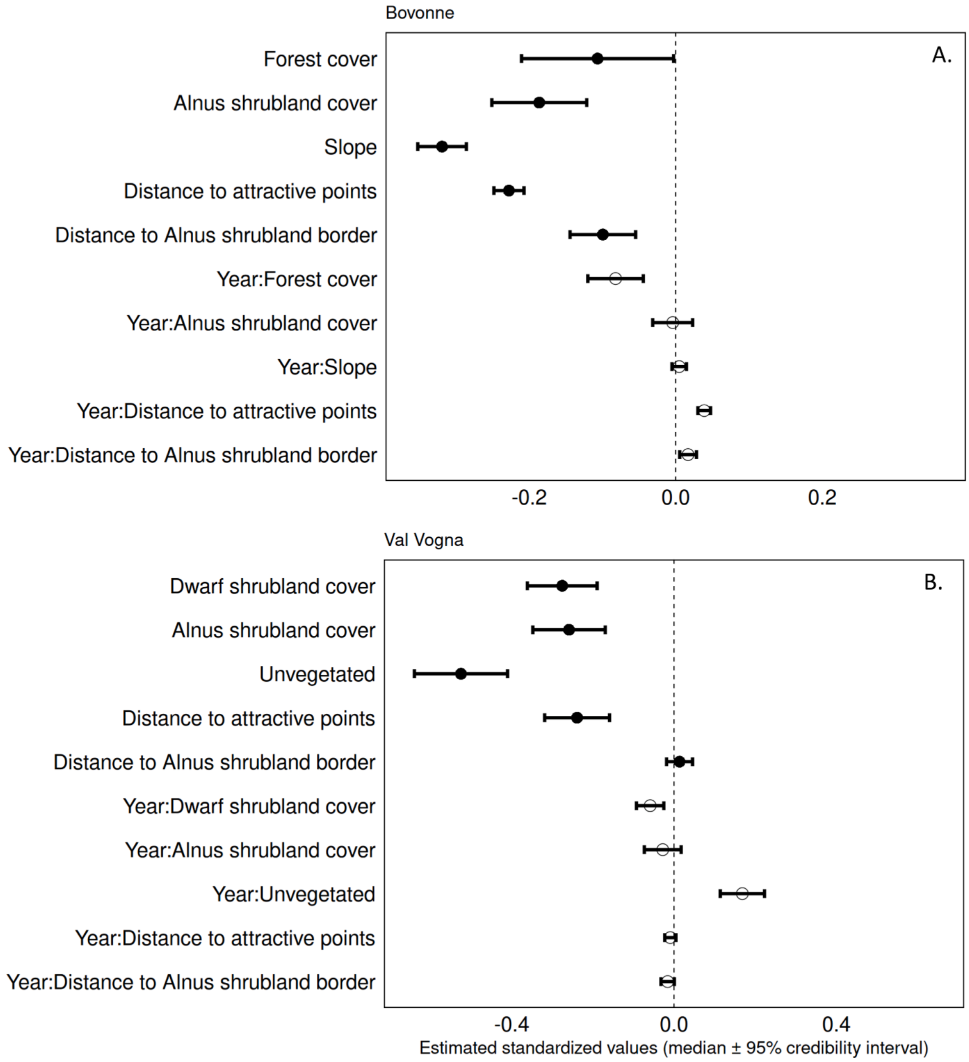

Fig. 5. Effects of covariates on livestock spatial use over years, in Bovonne (A), and Val Vogna (B) for the period 2019–2023. Open and filled dots show the median estimated effects of covariates and the interactions with year, respectively. Lines indicate the 95 % credibility intervals. The estimated values for vegetation cover types (forest and shrubland cover as well as unvegetated) indicated the effect of these covers in comparison with pasture cover.

area not grazed by Highland cattle, which constrains our ability to isolate the effects of this breed from other concurrent environmental or management changes. However, the continuity in stocking density and the absence of major shifts in management practices strengthen the inference that Highland cattle contributed to the observed reduction in shrubland. In this regard, a joint description of the evolution of vegetation cover and grazing management practices at both study sites allowed us to draw the conclusion about the positive role of Highland cattle in counteracting *A. viridis* encroachment.

4.2. Plant diversity increased after Highland cattle introduction

In agreement with our first hypothesis, our results concerning the plant diversity pointed out the potential of Highland cattle to restore encroached grasslands. However, our hypothesis was only partly confirmed, since the pastoral value only increased in open pastures at Bovonne. Both plant diversity and pastoral value are influenced by cattle management (Belsky, 1992; Parolo et al., 2011; Su et al., 2023), and Highland cattle may have the ability to increase plant diversity in encroached pastures by various direct and indirect mechanisms (Milchunas et al., 1988; Derner et al., 2009; Cipriotti and Aguiar, 2012). For instance, their impacts on shrub branches would generate canopy opening, increasing the light availability at the soil level (Olff and Ritchie, 1998; Kohler et al., 2006; Yantes et al., 2025). Grazing and trampling reduced understory species cover, such as ferns and tall herbs, which opened soil gaps recolonized by typical pasture species (Probo et al., 2016; Pauler et al., 2019; Durigan et al., 2022). Furthermore, Highland cattle can translocate seeds from pastures to encroached areas via both epi-zoochory, due to their long fur, and endo-zoochory, as seeds dispersed through dung can contribute to plant recolonisation (Traba et al., 2003; Gillet et al., 2010; Pauler et al., 2019; Svensk et al., 2021). Increases in plant diversity may also be explained by nitrogen translocation from *A. viridis*-encroached areas towards open areas, as has recently been shown (Svensk et al., 2024), which might reduce the competitive advantage of nitrophilous plant species in the understorey of green alder stands.

On transects in open pastures at Bovonne, the increase in species richness over time declined with higher stocking densities (Fig. 5A). This result suggests that, although species richness increased over the years, the magnitude of this change was smaller under higher livestock pressure compared to transects with more moderate stocking densities. In this regard, excessive grazing and trampling intensity may therefore limit the restoration potential of mountain pastures. This finding highlights the critical role of grazing pressure management in shaping pasture plant diversity (Milchunas et al., 1988; Piana and Marsden, 2014; Pizzio et al., 2016) and underscores the need to carefully manage grazing pressure to both promote plant diversity and effectively control woody vegetation cover, avoiding overgrazing.

Although both diversity measures—species richness and ENS—increased similarly in both sites and environments (open pasture and encroached areas; Fig. 3A and B), the increase in species richness in encroached areas in Bovonne showed a stronger positive trend than the increase in ENS. A similar pattern was found in open areas in Val Vogna. This result highlighted a marked species turnover, with an intense increase in the number of newly established species, which gradually led to improvements in species evenness within the vegetation community, although this latter change was less pronounced. In agreement, our results on species turnover indicate that over five years, 41 % of the species at Bovonne either newly appeared or disappeared (30 and 11 %, respectively), and 29 % at Val Vogna (17 and 12 %, respectively).

Moreover, the cover of nutrient-rich pasture species increased over time at both study sites, and in Bovonne it was positively correlated with grazing pressure, showing that intensive Highland cattle grazing could favour competitive and nutrient-demanding herbaceous species. In particular, this result was driven by increases in the cover of *Ranunculus aconitifolius* L., *Phleum rhaeticum* (Humphries) Rauschert, *Festuca pratensis* Huds. and *Deschampsia cespitosa* (L.) P. Beauv. at Bovonne, and by increases in the cover of *Poa alpina* L., *Poa pratensis* L., *P. rhaeticum* and *Trifolium pratense* L. at Val Vogna. Apart *R. aconitifolius* and *D. caespitosa*, these species are characterized by high forage yield and nutritional values (Cavallero et al., 2007; Peyraud et al., 2009; Gounden et al., 2018; Wild et al., 2023). Highland cattle grazing also increased the cover of nutrient-poor pasture species at Val Vogna, mainly driven by *F. nigrescens*, *R. montanus*, *Lotus alpinus* (DC.) Ramond, *Geum montanum* L., and *Pulsatilla alpina* (L.) Delarbre. However, even if classified as nutrient-poor species, some of these species (*e.g., F. nigrescens*) are typical of mesotrophic mountain grassland communities, and can thus benefit from a moderate grazing pressure (Cavallero et al., 2007). The cover of species typical of woodland and scrub communities did not change at Bovonne, while it increased at Val Vogna, where the cover of *V. biflora and V. myrtillus* and *R. ferrugineum*—typical species from dwarf-shrublands—increased. This result could be explained by the presence of areas within the paddock that are particularly difficult to access, where even Highland cattle rarely graze. Indeed, although the overall stocking rate was balanced with pasture carrying capacity, these inaccessible zones experienced low grazing pressure and were largely undergrazed. This underuse, even over just five years, has favoured the expansion of dwarf shrubs such as *Vaccinium myrtillus* and *Rhododendron ferrugineum*, highlighting the need for targeted pastoral management to optimize the distribution of grazing pressure. Finally, while the cover of tall herb species typical of fringe ecosystems decreased at Bovonne, it increased at Val Vogna. This is mainly due to decreases in *A. alliariae*; *C. hirsutum*, *G. sylvaticum* and *A. distentifolium*; and increases in *R. alpestris*, *C. hirsutum*, *P. ostruthium* and *P. chaixii,* respectively. This finding is in agreement with previous studies that have documented how Highland cattle graze or heavily trample species with particularly low forage quality, such as ferns (e.g., *A. distentifolium*) and tall herbs (*e.g., A. alliariae*; Svensk et al., 2022), which highlights the ability of this breed to impact unpalatable species in the *A. viridis* understory. Regarding the increase in fringe species cover at Val Vogna, *R. alpestris* and *P. chaixii* are commonly associated with nutrient-rich soils and tend to expand in grazed areas (Spatz et al., 1993; Pittarello et al., 2016), which could explain their increased cover in the last five years.

4.3. Cattle progressively adapted to the encroached environment

Our findings showed that the movement patterns of Highland cattle were influenced by several environmental factors, such as vegetation cover and distance to attractive points at both study sites. Confirming our second hypothesis and in accordance with previous studies, cattle preferred open pastures over shrublands (Jewell et al., 2005; Meisser et al., 2014; Homburger et al., 2015; Rivero et al., 2021). While some of the patterns remained relatively stable over the years, we also observed significant changes—highlighted by significant interactions between environmental variables and year—which suggested behavioural adaptation or shifts in spatial use within specific paddock areas (Thomas et al., 2011; Manning et al., 2017, Cibils et al., 2023). For instance, at Bovonne, where Highland cattle were introduced more recently, although the distance to the edges of *A. viridis* stands had a negative effect on GPS fix density, its interaction with time was positive, indicating that the animals increasingly used areas deeper within encroached stands (*i.e.,* further from the shrubland edge). This shift likely reflects a gradual behavioural adaptation over the years, characterized initially by cattle extensively exploring and roaming the paddocks immediately after introduction (Svensk et al., 2021), followed by a gradual increase in the spatial use of areas encroached by *A. viridis.* This pattern of initial exploration followed by adaptation aligns with previous findings showing that cattle can adjust their behaviour in response to environmental factors (Thomas et al., 2011; Lopes et al., 2013). Further support for this trend comes from field observations, where *A. viridis* shrubs further from stand edges (*e.g.,* along trails created by livestock within the shrubland) increasingly exhibited broken, defoliated, and even dead branches—evidence of growing grazing pressure over time in areas that were previously closed-canopy. In Val Vogna, on the other hand, a more stable grazing pattern had likely been established due to a longer presence of Highland cattle, since a longer familiarity with the paddock may influence livestock movement over time. So, historical grazing management plays an important role in how livestock uses space and affects vegetation. However, maps showing the use of space over the years, for both sites, represented both positive and negative values, suggesting that animal movement patterns have shifted over the years in specific areas within the paddocks. These localized changes imply a reconfiguration of habitat use, with some areas becoming more frequently used and others less.

In contrast to another short-term study on Highland cattle movement patterns (Svensk et al., 2021), in which no effect of slope was detected, our results showed that the animals tended to spend less time in areas with steeper slopes, as reported for other cattle breeds (Homburger et al., 2015; Raniolo et al., 2022). However, Highland cows have been described as more capable of grazing on steeper terrain than other production-oriented breeds, due to their lower weight (Pauler et al., 2020a, 2020b). In fact, although they spent more time in open pastures, our findings indicated that, at Bovonne, they increasingly entered *A. viridis* stands, which are typically associated with steep slopes (Skoczowski et al., 2021; Caviezel et al., 2017). Furthermore, at Val Vogna, the distance to *A.viridis* stand edges did not show an impact on cattle movements. Therefore, even though Highland cows spent more time in open areas compared to shrublands, they entered the *A. viridis* stands and did not just stay close to the edges. This was probably because at Val Vogna, the longer-term use of the area by Highland cattle determined a more stable use of *A. viridis* stands, even in their inner parts.

4.4. Grazing patterns evolved over time, reflecting grazing history

Regarding our third hypothesis, our results indicate that although some effects of Highland cattle grazing were consistent across both study sites, other outcomes differed between them. For instance, shrub cover—estimated through aerial and satellite imagery—decreased at both sites in the years following the introduction of Highland cattle, and species richness increased over the years. This result is particularly noteworthy, as it contrasts with previous studies suggesting that the positive impact of grazing on plant species richness is limited to the first five years following livestock introduction (Bokdam, Gleichman, 2000). Our findings, however, highlight the potential of grazing as a long-term restoration tool for enhancing plant diversity in mountain grasslands, with positive effects still detectable 15 years after the initial introduction of Highland cattle.

Conversely, pastoral value does not show a clear trend: it increased in the open grasslands of Bovonne, where Highland cattle were introduced five years ago, but this pattern was not observed in Val Vogna. Furthermore, the cover of species fringe and tall herbs significantly decreased at Bovonne, while it increased at Val Vogna. In addition, regarding animal movement patterns, in Bovonne we observed that the animals progressively spent more time within the *A. viridis* patches. This contrasted with Val Vogna, where the distance to the *A. viridis* stand edge had no significant effect on cattle movement, likely because the animals were already adapted to and familiar with the environment after 15 years of summer grazing within the same paddock.

5. Conclusion

Overall, our study demonstrates the potential of targeted grazing with Highland cattle as an effective management tool for restoring alpine pastures encroached by *A. viridis*. The inclusion of two sites with contrasting grazing histories enabled us to identify some consistent effects produced by livestock and others that changed over the years following cattle introduction. By combining long-term satellite-based analyses with GPS tracking and vegetation surveys, we showed that this robust cattle breed not only helps to reduce *A. viridis* cover, but also triggers broader shifts in the plant species composition. Notably, these changes are still ongoing 15 years after their introduction. It has also contributed to increasing the pastoral value in open pastures, particularly after their reintroduction. These findings highlight the value of Highland cattle grazing as a medium- to long-term restoration tool in mountain pastures encroached by *A. viridis*. However, our findings also pointed out the importance of targeted grazing management (*e.g.*, herding or use of attractive points) in the most marginal and roughest areas, where limited livestock pressure may hinder the expansion of dwarf shrub species. Therefore, complementary management measures may be required to fully ensure long-term success in restoring plant diversity across heterogeneous mountain landscapes.

CRediT authorship contribution statement

Ginevra Nota: Writing – review & editing, Investigation, Formal analysis. **Manuel K. Schneider:** Writing – review & editing, Methodology, Formal analysis. **Marco Pittarello:** Writing – review & editing, Investigation, Formal analysis. **Lucía S. Mochi:** Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Fabio Oriani:** Writing – review & editing, Methodology. **Jacopo Volpe:** Writing – review & editing, Formal analysis. **Massimiliano Probo:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Pierre Mariotte:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Lucia S. Mochi reports financial support was provided by Swiss National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.110070.

Data availability

Data is available online: https://doi.org/10.5281/zenodo.15675680

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