



Browsing intensity as an index of ungulate density across multiple spatial scales

Valerio Donini^{a,b,*}, Luca Corlatti^{b,d,1}, Francesco Ferretti^{a,e}, Giorgio Carmignola^f,
Luca Pedrotti^{b,c}

^a Department of Life Science, University of Siena, Siena, Italy

^b Stelvio National Park, Bormio, Italy

^c Stelvio National Park, Sustainable Development and Protected Areas Service, Autonomous Province of Trento, Cogolo di Pejo, Italy

^d Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany

^e NBFC, National Biodiversity Future Center, Palermo 90133, Italy

^f Alperia greenpower, Bolzano, Italy

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ABSTRACT

Large herbivores can profoundly influence terrestrial ecosystems. Through browsing, for example, they can impact forest regeneration with consequences for both plant and animal species. Understanding the drivers of ungulate browsing is therefore crucial from a conservation and management standpoint. Browsing is generally thought to be affected by ungulate density, such that increased density leads to greater browsing probability. As a result, browsing has been suggested as an indicator of ungulate density. While most studies investigated long-term browsing impact of ungulates in single study areas, few of them focused on different spatial scales using multiple replications in time and space. In this study we took advantage of 25 years of browsing data within the Stelvio National Park (central Italian Alps) derived from several populations of red deer and modelled the ratio of browsing on conifers (calculated as browsed conifers divided by total number of conifers) as a function of two different density indices at different spatial scales and a set of environmental covariates. Specifically, we investigated whether variations in red deer density at different spatial scales reflect variations in browsing probability. The results suggest that as deer density increased, the ratio of browsing increased at all spatial scales, at times mediated by shrub species diversity. Density was a consistent driver of browsing probability within all deer populations, while the effect of confounding variables was statistically unclear as they yielded conflicting results for the different populations, failing to find common patterns. This study highlights that density at different spatial scale is an important predictor of browsing probability, suggesting that browsing could be a reliable indicator of variations in ungulate density. In turn, as browsing can map small- and large-scale density variations, pattern of browsing impact may be a useful tool to investigate small- and large-scale changes in red deer densities due to disturbance factors such as human activities or the presence of large predators.

1. Introduction

Large herbivores have a great potential to influence other trophic levels, for example through their role in prey-predator and herbivore-plant interactions (e.g., Côté et al., 2004; Hebblewhite et al., 2005). However, the ecological interactions established by large herbivores can be complex and their outcome may vary in a context-dependent way depending on local environmental conditions or population characteristics (Kuijper et al., 2013; van Beeck Calkoen et al., 2018; Borowski

et al., 2021a). In forested habitats, large herbivores can impact forest renovation (Reimoser and Gossow, 1996; Renaud et al., 2003; Reimoser and Putman, 2011) through browsing main shoots and lateral shoots (Pépin et al., 2006) or bark stripping, affecting growth, survival and reproduction of shrubs and trees (Côté et al., 2004), thus habitat structure (Focardi and Tinelli, 2005), plant composition and development (Möst et al., 2015). In turn, browsing can impact human activities (Côté et al., 2004) by reducing species diversity and productivity of plants of commercial interest (Reimoser, 2003). Furthermore, it may

* Corresponding author.

E-mail address: v.donini@student.unisi.it (V. Donini).

¹ VD and LC contributed equally to this work.

have indirect effects on the abundance and distribution of birds, insects, and small mammals (Suominen and Danell, 2006; Cardinal et al., 2012), but also on other ungulate species, e.g., through exploitative competition (Putman, 1996; Dolman and Wäber, 2008). Because of these direct and indirect effects, understanding the drivers of ungulate browsing is of utmost importance from both the ecological and forestry management standpoint (Horsley et al., 2003).

Over the past decades, deer populations have increased both numerically and geographically worldwide (Côté et al., 2004; Apollonio, Andersen and Putman, 2011) for several reasons, such as lack of predators (Manning et al., 2009), new forestry practices, changes in land use (e.g., increase in wooded areas, in palatable crops plantations or decrease in livestock husbandry), reduced hunting pressure and direct conservation measures such as establishment of protected areas and translocation of individuals (Fuller and Gill, 2001; Carpio et al., 2021). Herbivore population density is expected to affect browsing impact (Gill, 1992; Partl et al., 2002; Kupferschmid and Bugmann, 2005); as such, spatial and temporal variation in browsing has been suggested as a useful indicator of changes in ungulates density (Morellet et al., 2001; 2007; Chevrier et al., 2012). Previous studies suggested a positive relationship between ungulate density and browsing pressure on forest ecosystems, which can significantly affect the regeneration of palatable species (Motta, 1996; Tremblay et al., 2007; Gill & Morgan, 2010; Nuttle et al., 2014; Borowski et al., 2021a). However, the density-dependent effect of browsing may be scale-dependent as variations in ungulate density at a spatial level in terms of distribution and over time in terms of variation in the number of individuals may have complementary effects upon browsing impact (Sample et al., 2023). At a broad scale, variation in ungulate abundance may lead to an increase or a decrease in the overall browsing pressure on vegetation. In turn, variation of browsing at a broad scale would reflect changes of population density in space and/or time. At a smaller scale, spatial variation of ungulate density, for example due to a redistribution of the individuals within the area, may lead to increased or decreased local impact on forest renewal. Consequently, spatial patterns in browsing pressure may be generated regardless of variations in total population density. Understanding the scale-dependent drivers underlying browsing impact would be important to predict ecological effects and investigating different scales can lead to understanding different ecological mechanisms. Furthermore, it might help to calibrate spatio-temporally explicit management actions to mitigate the impact, as and when necessary. However, the effects of ungulate densities at multiple spatial scales on browsing impacts have been relatively neglected.

Furthermore, the relationship between ungulate density and browsing impact is expected to be complex and affected by several biotic and abiotic factors. Beside the direct effect of population density, in mountainous areas browsing impact may be influenced by a number of abiotic factors, which indirectly affect local density, such as the topography of the terrain (Allen et al., 2014), elevation, due to a greater occurrence of individuals at higher altitudes during the summer period (Campbell et al., 2006; Fluri et al., 2023), snow depth and food availability, which force ungulates to migrate from higher altitudes to low elevations with consequent increasing in population densities (Mysterud et al., 2011; Bocci et al., 2012; Luccarini et al., 2006). Furthermore, slope exposure may play an important role, as southern-exposed slopes are preferred in winter, increasing browsing probability (Fluri et al., 2023, but see Campbell et al., 2006). Over the long-term, weather stochasticity and, in particular, winter severity may strongly affect ungulate density (Willisch et al., 2013; Bonardi et al., 2017), thus browsing pressure. Density may also be influenced by biotic factors (Horsley et al., 2003). Bottom-up processes stimulated by, e.g., species richness and vegetation composition and quality may mediate the effect of density leading to lower or higher pressure where plant species diversity is higher (Bergvall et al., 2006; Moser et al., 2006; Milligan and Koricheva, 2013; Borowski et al., 2021a). The effect of species diversity on browsing, however, is still not clear (Ohse et al., 2017). Highly species-

rich areas can attract herbivores resulting in increased browsing pressure (Bergvall et al., 2006). At the same time, an increase in species diversity may distribute browsing over a larger number of species and dilute the effect, resulting in a decrease in browsing impact on certain species (Ohse et al., 2017). The presence of large predators (Terborgh and Estes, 2010) or the establishment of management practices such as hunting and population control (Rao, 2017) can affect browsing through top-down mechanisms, by reducing the number of individuals or modifying their distribution, with cascading effects on forest regeneration (Laundre et al., 2010; Ripple and Beschta, 2012). To add further complexity, ungulate density may relate to browsing pressure non-linearly (Tremblay et al., 2006; Tremblay et al., 2007), and plant productivity and reproduction may increase only when ungulate density falls below a specific threshold (Tremblay et al., 2006), or there may be a delay in the plant recovery after the decrease in deer density (Horsley et al., 2003; Tremblay et al., 2006).

Although several studies investigated the impact of ungulate browsing on long time scales (Kuijper et al., 2010; D'Aprile et al., 2020; Fluri et al., 2023) to date only few have focused on large spatial scales by considering multiple deer populations (Jarnemo et al., 2014; Petersson et al., 2019; Brock et al., 2023). We considered several populations of red deer *Cervus elaphus* in a protected area where deer browsing has been assessed across 25 years (Stelvio National Park, central Italian Alps). Cervids are often responsible of browsing (Gill, 1992) and red deer, in particular, is widely considered an ecosystem engineer because of its ability to influence vegetation, soil structure and, in general, biodiversity (Reimoser and Putman, 2011; Côté et al., 2004; Reimoser and Gossow, 1996). We took advantage of different scales of variation in density in different populations of red deer within the study area to investigate whether deer density reflects browsing intensity, thus whether browsing probability can be considered as a reliable indicator of changes in deer density at multiple spatial scales. We anticipate that red deer density positively relates with browsing impact in all the study populations at both large and small scale. Furthermore, considering the contrasting results from the previous literature, we anticipate that the effect of density may have positive or negative relationship on browsing as species richness increases.

2. Material and methods

2.1. Study areas

The study areas lie within the Stelvio National Park (SNP, Central Italian Alps; Fig. 1A; 5147241 N, 621,805 E, EPSG: 32632). The SNP extends over 130,700 ha and is divided into three administrative sectors: Lombardy (LOM; 59,700 ha), Trento (TN; 17,500 ha), and Bolzano (BZ; 53,500 ha). Within each sector, the study areas where browsing was assessed were selected according to the yearly distribution of red deer, considered the main responsible for browsing (see section 2.2), and respectively extended over 8,900 ha in LOM, 8,100 ha in TN, and 31,200 ha in BZ (Fig. 1B). With respect to the BZ sector, information obtained from the GPS data suggested the presence of two distinct red deer populations (30 VHF collars from 2001 to 2012 and 6 GPS collars from 2015 to 2017). Therefore, the BZ sector was divided into two different study areas: BZ1 (18,200 ha) and BZ2 (13,000 ha) (Fig. 1B). Hereafter LOM, TN, BZ1 and BZ2 will be used as names to identify the 4 study areas. Over the entire Park, elevation ranges from 700 m a.s.l. to almost 4000 m a.s.l. The climate is alpine, with yearly mean precipitation of 690 mm in LOM, 518 mm in BZ, and 859 mm in TN (Carmignola, 2001). Temperatures vary significantly with elevation and season: mean temperatures in winter and summer are -1.8°C and 16.8°C in LOM (weather station: Bormio, 1225 m a.s.l.), -0.3°C and 14.6°C in TN (weather station: Peio, 1160 m a.s.l.), -1.2°C and 18.8°C in BZ (weather station: Lasa, 874 m a.s.l.; Carmignola, 2001). The three areas share similar orographic, vegetation, and faunistic features.

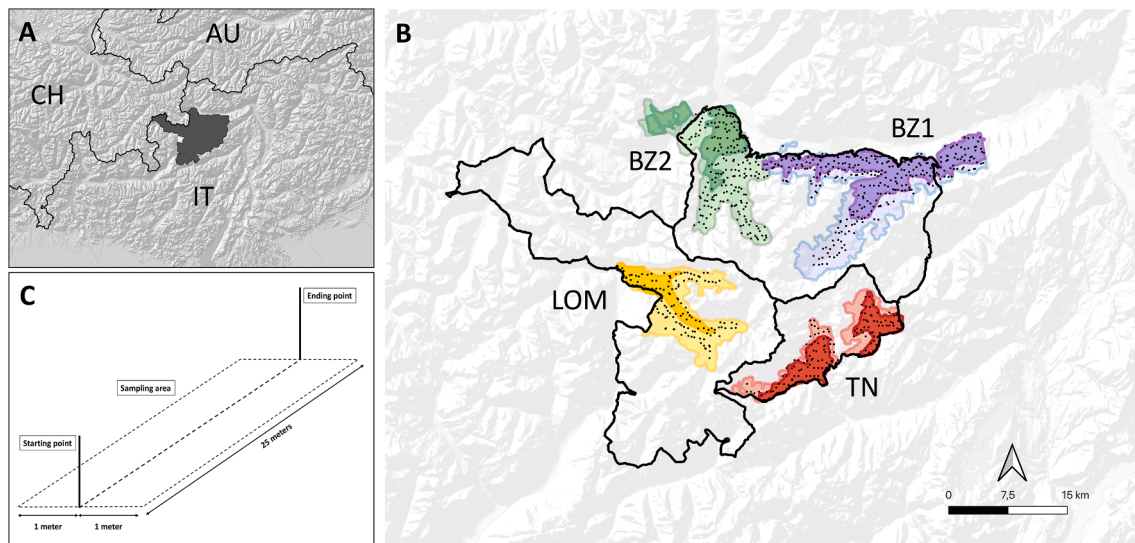


Fig. 1. Location of the Stelvio National Park (grey shaded area) in the Central Italian Alps (A). The park is divided into three administrative sectors in which four study areas were selected: LOM in yellow, TN in orange, BZ1 in light blue and BZ2 in green. The light colours represent the summer distribution of red deer, while the dark colours represent the winter distribution. (B). Within each study area, the location of the sampling areas is reported with black dots. Panel C shows the scheme of the control strip used during the field surveys. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Forest and wildlife in SNP

The relative extent of forest cover was similar among the sectors (20 % for LOM, 23 % for TN, and 33 % for BZ). The dominant tree species are spruce *Picea abies*, larch *Larix decidua*, Swiss stone pine *Pinus cembra*, and to a lesser extent mountain pine *Pinus mugo*. Broadleaf forests are almost absent. Above the treeline (>2100 m a.s.l.), vegetation is mainly composed of alpine and subalpine grasslands of *Carex curvula*, *Festuca halleri*, *Nardus stricta*, *Carex sempervirens*, *Carex firma*, and *Sesleria coerulea* (Carmignola, 2001). The forest management differs in the study areas. In BZ1 and BZ2, forest management aims at maintaining monospecific and monoplane forests, with large clearcuts and, consequently, abundant renovation. In contrast, group-selection harvesting is conducted in LOM and TN, where undergrowth is more widespread.

Within the SNP, 4 species of ungulates are present: red deer, chamois *Rupicapra rupicapra*, ibex *Capra ibex* and roe deer *Capreolus capreolus*. After near-extinction due to hunting pressure in the late 19th century, red deer recolonised the area, reaching very high densities. Within all study areas, red deer population size is monitored on a yearly basis using spring spotlight counts. In April, for at least three non-consecutive days, predefined routes are travelled by night by park rangers, and animals are counted using spotlights. Of the three surveys, the one with the highest number of counted individuals was used for the analysis. This method is a reliable index for tracking red deer abundance in the Park as it was validated using mark-resight, the least biased method for estimating deer abundance (Forsyth et al., 2022). Specifically, the results of 8 years of spring spotlight counts were compared with mark-resight data on 140 red deer marked during the same period (Corlatti et al., 2016). Raw counts from the spotlight surveys were adjusted for an underestimation of 48 % for LOM, 35 % for TN, 45 % for BZ1, and 35 % for BZ2, as defined by previous work (Corlatti et al., 2016, Bonardi et al., 2017). Chamois and ibex populations were monitored using block counts during summer (Corlatti et al., 2015). Within the LOM sector, the chamois population remained stable whereas it has strongly declined within the TN sector in recent years (Corlatti et al., 2019). Within BZ1 and BZ2, chamois counts were performed since 2010. Ibex is only present with a stable population within the LOM sector, while in TN and BZ, only about 50 individuals are estimated to be present. Roe deer densities in the three areas are unmeasured, but they are likely very low (the proportion between roe deer and red deer can be considered approximately 1:10,

based on spring spotlight counts, unpublished data), and the browsing effect of this species can be considered negligible. Likewise, owing to different density and different use of habitats, the effects of chamois and ibex on browsing can be considered negligible compared to that of red deer. The numerical trends in the population abundances of the three species (except for roe deer) are shown in Fig. 2. Within the SNP, hunting is not allowed, and the evolution of ungulate populations is left to natural regulation, except for red deer. Red deer management differs in timing in the three sectors: 1) in LOM, starting in 2011, a culling program was implemented with the aim of reducing impact on forest regeneration through the removal of a predefined number of individuals to lower red deer population density. From 2011 to 2019, 1,161 deer were culled (annual mean = 145 individuals; SD = ± 38). 2) Starting in 1998, a culling program was implemented in BZ for the same reason. In BZ1, 7863 red deer were culled from 1998 to 2021 (yearly mean = 328, SD = ± 57). In BZ2, from 2001 to 2021, 1504 red deer were culled (yearly mean = 72, SD = ± 34). 3) In TN no culling occurred until 2023.

2.3. Browsing sampling design

To investigate variation in browsing impact, information on the proportion of browsed saplings was collected. Browsing surveys were conducted in summer using the same sampling protocol in all three sectors of the SNP, in 1998, 2009, and 2021 in LOM; 1998, 2012, and 2023 in BZ1 and BZ2; and 1998 and 2021 in TN.

Before the survey started, the four areas were divided into 50 ha quadrants. Within each quadrant, a random point was identified, and starting from this point, the closest area of forest regeneration was identified, which represented the location of the transect (Fig. 1B). Where possible, the same sampling locations were used over the years within each sector. Overall, a total of 2112 surveys were conducted across the 4 areas, between 1998 and 2023 (LOM: 140 in 1998, 140 in 2009, 134 in 2021; TN: 150 in 1998, 150 in 2021; BZ1: 249 in 1998, 224 in 2012, 296 in 2023; BZ2: 211 in 1998, 211 in 2012, 207 in 2023). A total of 84,216 seedlings between 10 and 130 cm were sampled, 30,323 of which were browsed. Of all the seedlings sampled, in LOM 32 % were spruce, 28 % larch, 26 % stone pine, in TN 42 % were spruce, 43 % larch, and 11 % stone pine, in BZ1 27 % were spruce, 26 % larch, and 13 % stone pine, and BZ2 28 % were spruce, 27 % were larch, and 14 % stone pine. When no regeneration was found within each quadrant, a

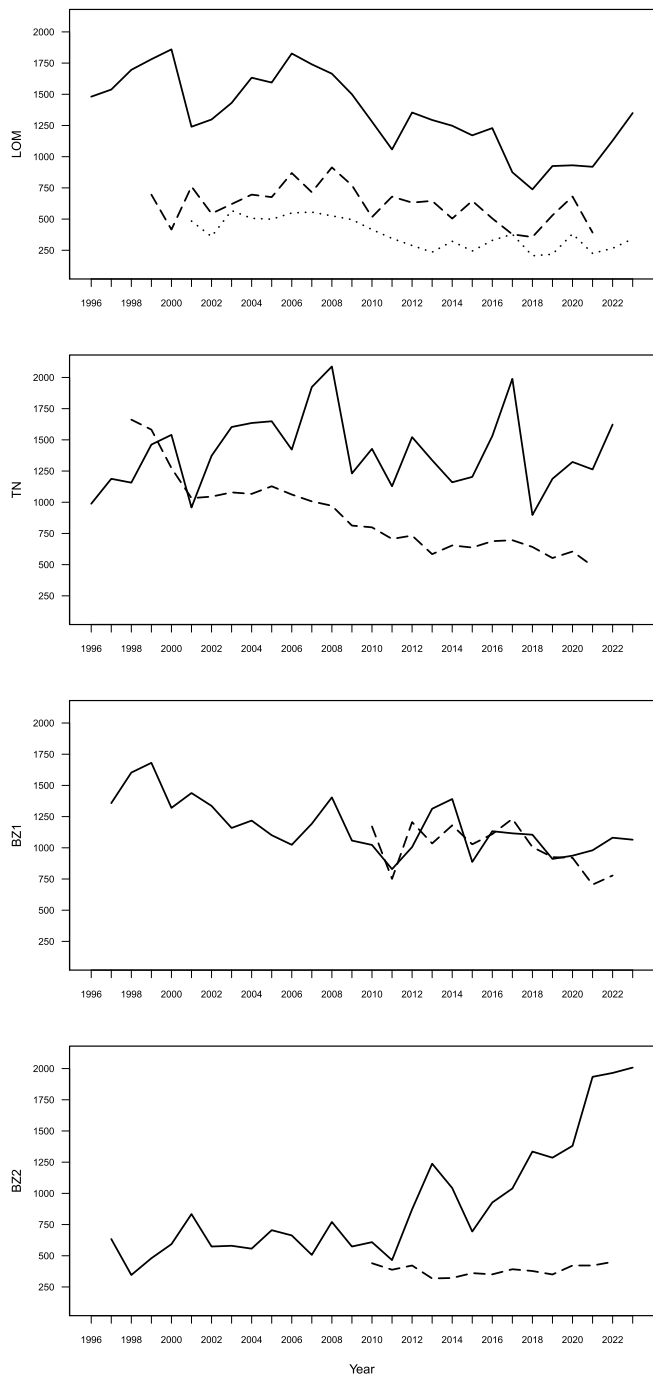


Fig. 2. Temporal trends of ungulate species within the Stelvio National Park divided by the study areas (LOM in panel A; TN in panel B; BZ1 in panel C; BZ2 in panel D) between 1996 and 2023 (straight lines: red deer; dashed lines: chamois; dotted line: ibex).

browsing probability of 1 was assumed. Preliminary analyses suggested there was no variation in the results even in the absence of these data. Events of no regeneration were 20 % of the total for LOM, 26 % for TN, 7 % for BZ1, and 8 % for BZ2. The browsing impact was assessed in a rectangular area that extended over 50 m² (25 m x 2 m: Fig. 1 C). For each shrub and tree up to 300 cm in height, within each transect, species and height class were identified (seedlings, < 10 cm, 10–25 cm, 25–40 cm, 40–70 cm, 70–100 cm, 100–130 cm, 130–300 cm) and the occurrence of bites on the terminal shoot was assessed.

As the aim was to investigate the relationship between browsing impact and ungulate density, assuming red deer as the main responsible

Table 1 Parameter estimates of the four models (LOM, TN, BZ1 and BZ2) built to explain variation in browsing ratio within the four studied red deer populations in Stelvio National Park.

Parameter	LOM				TN				BZ1				BZ2							
	Coefficient	SE	CI_low	CI_high	P-value	Coefficient	SE	CI_low	CI_high	P-value	Coefficient	SE	CI_low	CI_high	P-value	Coefficient	SE	CI_low	CI_high	P-value
Intercept	-0.014	0.046	-0.105	0.077	0.767	0.112	0.055	0.004	0.221	0.043	-0.163	0.044	-0.250	-0.076	<0.001	-0.027	0.030	-0.086	0.033	0.377
large scale density	0.139	0.050	0.041	0.236	0.005	0.618	0.053	0.513	0.723	<0.001	0.064	0.055	-0.043	0.171	0.241	0.391	0.029	0.334	0.448	<0.001
small scale density	0.289	0.046	0.199	0.378	<0.001	0.040	0.063	-0.084	0.164	0.526	0.169	0.034	0.103	0.235	<0.001	0.124	0.034	0.058	0.190	<0.001
shannon	-0.223	0.049	-0.320	-0.126	<0.001	-0.005	0.055	-0.113	0.103	0.924	-0.120	0.034	-0.187	-0.053	<0.001	-0.146	0.037	-0.220	-0.073	<0.001
northness	-0.033	0.033	-0.098	0.032	0.319	0.087	0.032	0.023	0.150	0.008	-0.028	0.028	-0.083	0.028	0.019	0.108	0.030	-0.077	0.040	0.528
elevation	-0.117	0.087	-0.287	0.054	0.179	0.104	0.072	-0.038	0.247	0.152	-0.048	0.066	-0.177	0.081	0.463	0.108	0.045	0.019	0.198	0.017
eastness	0.122	0.033	0.057	0.187	<0.001	-0.056	0.033	-0.121	0.009	0.091	-0.044	0.029	-0.100	0.012	0.123	0.050	0.029	-0.007	0.107	0.087
slope	-0.201	0.047	-0.293	-0.109	<0.001	0.024	0.035	-0.044	0.092	0.491	-0.003	0.033	-0.069	0.062	0.918	-0.020	0.033	-0.084	0.044	0.535
large scale density x shannon	0.153	0.059	0.038	0.269	0.009	0.141	0.050	0.042	0.240	>0.001	0.063	0.035	-0.006	0.132	0.074	-0.023	0.036	-0.094	0.048	0.522
small scale density x shannon	-0.022	0.043	-0.107	0.064	0.621	-0.042	0.058	-0.155	0.071	0.467	-0.004	0.034	-0.071	0.063	0.896	-0.078	0.037	-0.150	-0.006	0.035

Note: The table reports, for each model parameter, the coefficient estimates, the standard errors (SE), the lower 95% confidence intervals (CI_low), the upper 95% confidence intervals (CI_high) and the P-value. Statistically significant parameters are in bold.

of browsing, two different variables were used to assess the influence of density on forest renovation. On a small spatial scale, within each study area, red deer density was approximated using an index ranging from 0 to 3, based on the number of faecal pellet groups found within the transect (0: none; 1: from 1 to 3; 2: from 4 to 10; 3: more than 10), assuming this index maps the variation in red deer densities within the study areas (Forsyth et al., 2007). On a large spatial scale, the variation in red deer density was based on spring spotlight counts. For each area and year of survey, the mean of the previous three years of counts was calculated (under the assumption that the impact of density on browsing is cumulative) and divided by the extent of the winter red deer distribution area, to obtain a density value that is comparable among areas (LOM density on the winter surface of 23 km²: 1996–1998, 68.3 ind/km²; 2010–2012, 71.1 ind/km², 2019–2021, 40.2 ind/km². TN density on the winter surface of 46 km²: 1996:1998, 25.0 ind/km²; 2019–2021

$$\text{browsing ratio}_i \sim (\text{large scale red deer density}_i + \text{small scale red deer density}_i) \times \text{shannon index}_i + \text{northness}_i \\ + \text{eastness}_i + \text{elevation}_i + \text{slope}_i + s(x_i, y_i) + \text{transect}_i$$

28.3 ind/km². BZ1 density on the winter surface of 82 km²: 1997–1998: 18.1 ind/km²; 2010–2012, 11.6 ind/km²; 2021–2023, 12.7 ind/km². BZ2 density on the winter surface of 40 km²: 1997–1998: 12.2 ind/km²; 2010–2012, 16.2 ind/km²; 2021–2023, 49.2 ind/km²). Because the relationship of browsing impact with density may be confounded by other variables, additional information was collected. Using QGIS (v. 3.22.0-Białowieża; QGIS Development Team, 2021) and Digital Terrain Models (DTMs), information about altitude, exposure, and slope was collected from the transect location. Exposure, from 0° to 360°, was transformed into two distinct variables varying between 1 and -1: northness, calculated as the cosine of the aspect (northness = 1 slope exposed to the north and northness = -1 slope exposed to the south), and eastness, calculated as the sin of the aspect (eastness = 1 slope exposed to the east and eastness = -1 slope exposed to the west). To assess whether browsing pressure could vary as a function of shrub species diversity, the Shannon index (Shannon, 1948) was calculated as follows: $\text{Shannon} = -1 \times \sum (\text{coverage index} \times \log_2(\text{coverage index}))$, where the coverage index is the percentage of coverage of each shrub species calculated within each transect.

2.4. Data analysis

Data analysis was conducted using R v. 4.3.2 (R Core Team, 2023) in RStudio v. 2023.09.1 (RStudio Team, 2023). Browsing impact was calculated, for each sampling plot, as the ratio between the number of browsed conifers (pooling the most abundant species, spruce, larch, and stone pine with a height between 10 and 130 cm, as many studies have suggested that red deer prefer to browse at the height of their shoulder, cf. Renaud et al., 2003) to the total number of sampled trees with a height of 10–130 cm along each transect.

Variation in browsing ratio was assessed using a generalized linear modelling approach. The basic structure of the model assumed browsing ratio as the response variable. As this variable is intrinsically constrained between 0 and 1, a beta conditional distribution (Ferrari and Cribari-Neto, 2004) was initially assumed. However, given the large number of zeros and ones in the dataset, i.e., transects with no browsed seedlings or all browsed seedlings out of the total (10 % of zeros and 25 % of ones in LOM; 1 % of zeros and 28 % of ones in TN; 5 % of zeros and 10 % of ones in BZ1; 7 % of zeros and 12 % of ones in BZ2), a zero-one beta inflated approach (Ospina and Ferrari, 2007) was adopted, as it proved a better fit. Models were fitted using the package “gamlss” (Rigby and Stasinopoulos, 2005), which allows for both the beta inflation distribution and for the inclusion of a trend surface as a two-dimensional

spline on geographical coordinates of the sampling locations (Dorrmann et al., 2007). As the gamlss package does not allow for the direct inclusion of a trend surface, we used the “gamlss.add” package (Stasinopoulos et al., 2020), which allows for the inclusion of the smoothing term as in the “mgcv” package (Wood, 2011). Specifically, the surface trend was fitted as a grouped term, as spatial correlation in browsing probability in each area was assumed to occur only within each year. Furthermore, because sampling was repeated over the years at the same location, the transect id was used as a random factor within each model.

The following variables were included in the model: large-scale density (obtained from spring spotlight counts) and small-scale density (obtained from the number of pellets within each transect), both in interaction with Shannon index, plus the additive effect of northness, eastness, elevation and slope. Before fitting the models, the variables were standardized. The structure of the model was as follows:

where i is the i^{th} transect, and x_i and y_i are the coordinates of each transect location. Once the structure of the model was defined, four models were fitted, one for each area.

As we were explicitly interested in the relationship between browsing impact and deer density, after adjusting for potentially confounding factors, model selection was not performed. For each model, goodness of fit was assessed by visual inspection of residuals. Finally, to visualize the marginal effects, predictions were calculated using the package “gratia” (Simpson, 2023), and graphical outputs were obtained using the package “ggplot2” (Wickham, 2016).

3. Results

The inspection of model residuals did not show any systematic pattern, suggesting no violations of model assumptions. Model estimates (Table 1, Fig. 3, Fig. 4) show that overall, browsing probability increased as red deer density increased. In particular, large-scale density of red deer showed strong evidence for a positive relationship with browsing probability in LOM, TN and BZ2 (Table 1, Fig. 3, Fig. 4 Panel F). Small scale density of red deer also showed strong evidence for a positive relationship with browsing probability in LOM, BZ1 and BZ2 (Table 1, Fig. 3, Fig. 4 Panel B and Panel D). The effect of large-scale red deer density on browsing probability was mediated by the Shannon index in LOM and in TN. Specifically, in LOM as the diversity of shrub species increased, the probability of browsing decreased especially at low density, over the large scale (Table 1, Fig. 3, Fig. 4 Panel A). In TN a decreasing trend was present at low density, while at high density a positive relationship was found (Table 1, Fig. 3, Fig. 4 Panel C). Furthermore, in BZ2, the relationship between browsing probability and small-scale density was mediated by the Shannon index. As the diversity of shrub species diversity increased, the browsing probability decreased both at low and high density. Notably, the relationship was stronger at high density (Table 1, Fig. 3, Fig. 4 Panel E).

With respect to the other predictors, the probability of browsing was negatively related to the Shannon index in LOM, BZ1 and BZ2. An increase in the proportion of browsing was observed in north-exposed slopes in TN. Eastness had positive effect on browsing in LOM while elevation was positively related to the proportion of browsing in BZ2. Finally, slope showed a negative relationship with the proportion of browsing in LOM. The relationship between these variables and the browsing probability across the remaining study areas was statistically unclear. In particular, northness had a positive effect only in TN, while in the other study areas the relationship was negative but statistically

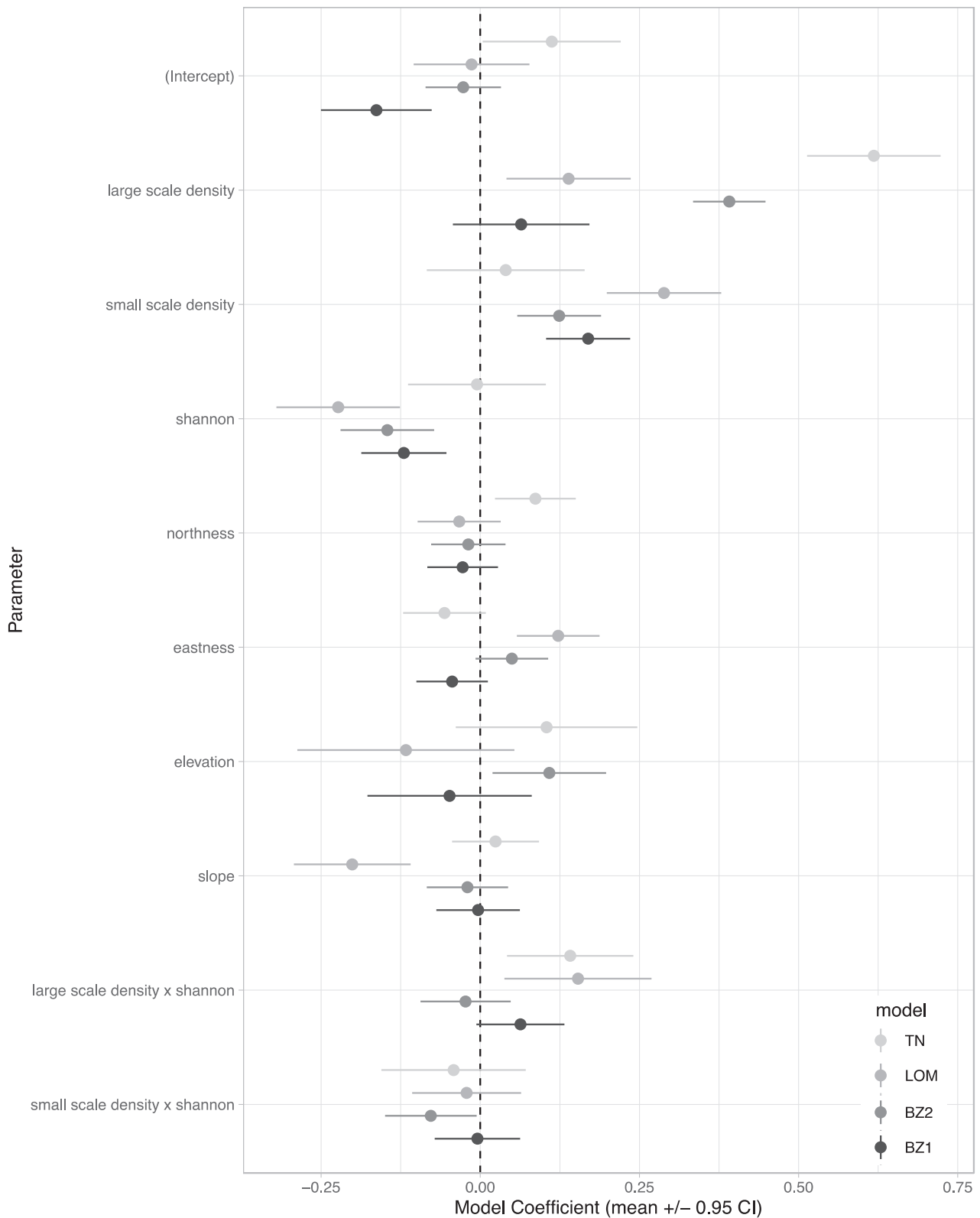


Fig.3. Visual representation of parameter coefficients (mean +/- 95% of confidence intervals) of the four models (LOM, TN, BZ1 and BZ2) built to explain the variation in browsing proportion within the Stelvio National Park.

non-significant. Elevation had a positive and statistically non-significant relationship with browsing probability in TN, while negative in LOM and in BZ2. Eastness was negatively related with browsing probability in TN and BZ1, while positively related in BZ2. Furthermore, the relationship between slope and browsing probability was non-significant

and negative in TN while positive in BZ1 and BZ2.

4. Discussion

This study assessed the relationship between deer density and

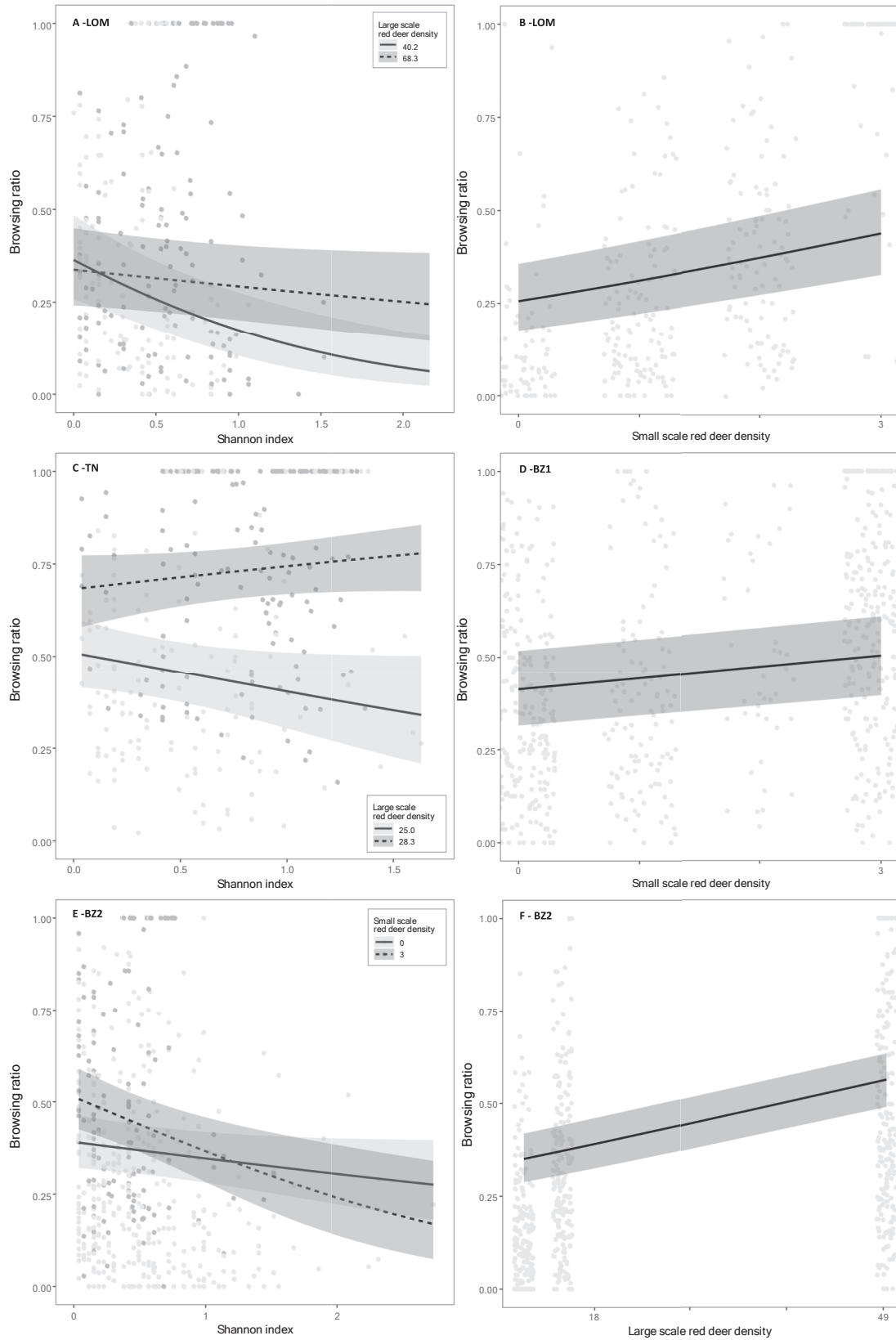


Fig.4. Marginal effects of the four models (LOM, TN, BZ1 and BZ2) built to explain browsing variation within the Stelvio National Park. Panel A and C: browsing ratio as a function of the interactive effect between the Shannon index and large scale red deer density expressed as low and high density in LOM and TN respectively. Panel B and D: browsing ratio as a function of small scale red deer density in LOM and TN. Panel E: browsing ratio as a function of the interactive effect of the Shannon index and small scale density expressed as low and high density in BZ2 study area. Panel F: browsing ratio as a function of large scale density in BZ2. Regression lines are reported with 95% confidence intervals (grey shaded area) and raw data are reported with grey dots.

browsing impact in an Alpine context at different spatial scales. Our results support the role of red deer density as mapper of browsing probability. In two out of our four study populations, browsing ratio positively associated with both large-scale and small-scale red deer density; for the other two populations, the positive effect of density on browsing was reported at either large or small scale. A greater richness of shrub species generally reduced browsing impact and attenuated the effect of red deer density. The role of other covariates was inconsistent across populations.

Several studies suggested that ungulates and, in particular, red deer play a key role in influencing forest regeneration (Tremblay et al., 2007; Gill and Morgan, 2010; Kuijper et al., 2010). Studies assessing the impact of ungulate density on vegetation can be broadly divided into two categories, those that use enclosure (or exclosure) fences under different levels of ungulate densities, and those that exploit natural variation in browsing impact without control conditions (Côté et al., 2004). Controlled browsing experiments allow to manipulate the density of ungulates and observe the effects on the vegetation community (Horsley et al., 2003; Pépin et al., 2006; Tremblay et al., 2006; Tremblay et al., 2007; Reimoser et al., 2024). However, the results of such experiments are often difficult to apply to natural environments since many other factors that are hard to investigate within enclosures, may affect browsing patterns, such as topography (Allen et al., 2014), elevation (Campbell et al., 2006) or distance to roads (Borowski et al., 2021b). On the other hand, studies exploiting natural variation in density without control conditions have been carried out in many areas yielding contrasting results (Motta, 2003; D'Aprile et al., 2020; Gill and Morgan, 2010; Kuijpers et al., 2010, Sample et al., 2023). In most cases an increase in browsing impact was found, as a consequence of high ungulate density. Consequently, overall browsing impact is considered an indicator of changes in ungulate abundance (Morellet et al., 2001; 2007; Chevrier et al., 2012). However, only few works investigated density-dependent effects on vegetation based on robust ungulate estimates (Morellet et al., 2007; Jarnemo et al., 2014; Borowski et al., 2021a). Although necessary, reliable population density data are difficult to obtain, mainly because they require many years of sampling and detection probability may vary from area to area (Morellet et al., 2007). As a result, in natural experiments is often difficult to replicate the study within different study areas or across different populations.

Results obtained using the same methodology of vegetation sampling and estimation of ungulate abundance are rare, but study replication is the cornerstone of scientific research. Our study, based on 4 replicates and using spatio-temporally explicit indices of deer density, supported the idea that density at both small and large scale is an important predictor of browsing probability. At a large spatial scale, red deer density was positively related with browsing in all study areas, except in BZ1. Similar results were also obtained in other studies (Ligot et al., 2011; Petersson et al., 2019; Brock et al., 2023) in which the role of ungulate density was investigated at large spatial scales, while in others no effects were found on browsing at a landscape level (Jarnemo et al., 2014). A possible explanation for the absence of a relationship between large scale density and browsing probability in BZ1 over the study period may be due to small variation in red deer abundance. Regarding the relationship between browsing and density at small scale, pellets are a widely used index for assessing ungulate densities (Forsyth et al., 2007) and other studies related them to browsing data with similar results (Janremo et al., 2014). In our study, except for TN study area, small scale density showed a consistently positive relationship with browsing across the other populations, suggesting an increasing browsing impact as density increased. The results in TN are difficult to explain as the coefficient of variation of density was similar across all study areas, suggesting similar patterns of local spatial distribution of individuals. It is possible that categorizing density into 4 levels reduced variability and thus the possibility to find relationships within the study area.

In addition to deer density, other variables can influence browsing (Carter and Fredericksen, 2007; Kuijper et al., 2010; Petersson et al.,

2020). Plant species diversity, i.e. the richness of species, may affect browsing pattern through, for example, the attraction of individuals to more species-rich areas (Borowski et al., 2021a) or, conversely, towards the dilution of grazing (Ohse et al., 2017). According to our initial hypothesis, Shannon index was negatively related with browsing ratio in all study areas except for TN, suggesting that as species diversity increased, the impact on vegetation decreased. Furthermore, the effect of red deer density mediated by the effect of species richness yielded contrasting results. In LOM and in BZ2, as the species diversity increased, the browsing ratio decreased, both at low and high red deer densities, supporting the dilution hypothesis. In contrast, in TN, the negative effect was only present at lower red deer densities, whereas at higher densities the browsing ratio increased. Areas of higher species diversity offer higher quality and quantity of palatable species for ungulates (Westoby, 1974). According to the optimal foraging theory (Krebs and Stephen, 1986), ungulate browsing would tend to increase because of an increasing occurrence in preferred and thus selected species (Borowski et al., 2021a). Moreover, it should be noted that in TN, red deer was present at very high densities for a long time, suggesting that, although an increase in species richness may decrease the browsing impact, this effect only applies when the densities are low, while conversely, at high densities browsing increased.

The increase in ungulate population density can have profound impacts on the ecosystem, both from an ecological and management point of view. For this reason, in some areas, active population managements are implemented. Hunting and culling have been widely used tools to reduce the impacts of ungulates on forests (Putman et al., 2005; Wright et al., 2012; Tanentzap et al., 2013; Rao, 2017) and in three of the four study areas analyzed in this study, a culling program is implemented to reduce red deer densities. As suggested by our study, numerical reductions on large scales can lead to reductions in the overall impacts of browsing on vegetation and this pattern was also found elsewhere (Rao, 2017). On the other hand, numerical reductions do not always correspond to positive effects on vegetation (Tanentzap et al., 2013), either because the effect may be delayed and only visible in the long term (Nuttall et al., 2014), or because it may depend on the spatial scale referred to (Ohse et al., 2017). While changes of density at a large scale should reflect variations in abundance at the population level, density variations at smaller scales would be expected to reflect spatial patterns in the distribution. Consequently, variation in browsing probability within area in different year largely owes to a redistribution of animals within the study areas. Ungulate density variations may also occur due to the presence of large predators which can alter both their abundance and their spatial distribution (Laundré et al., 2001; Beyer et al., 2007). Effects of large predators on ungulate abundance and behavior on the consequences on vegetation are still poorly studied, but some evidence in the European continent was found (Kuijpers et al., 2013). From a behavioral perspective, according to the "Landscape of Fear" concept (Laundré et al., 2010) the establishment of a landscape of higher or lower dangerous zones can alter the behavior of prey and consequently their use of the habitat to reduce the likelihood of being killed (cf. Bonnot et al., 2013). Within our four study areas, the wolf has arrived very recently (in TN and in LOM) or is absent (in BZ1 and BZ2), but the current trend in Europe (Chapron et al., 2014) and in particular in the Alps (Fabbri et al., 2007; Marucco et al., 2018) suggests that the establishment of packs within these areas is very likely. Based on our results, insofar as browsing variation can map small- and large-scale density variations, pattern of browsing impact may be a useful tool to investigate the ecosystem effects due to changes in red deer densities in response to the return of predators.

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CRediT authorship contribution statement

Valerio Donini: Writing – original draft, Formal analysis, Data curation. **Luca Corlatti:** Writing – original draft, Supervision, Data curation, Conceptualization, Formal analysis. **Francesco Ferretti:** Writing – original draft, Supervision, Conceptualization. **Giorgio Carmignola:** Methodology, Data curation. **Luca Pedrotti:** Writing – original draft, Supervision, Project administration, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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