



## Influence of wild ungulates on the secondary succession of an Apennine silver fir forest after windthrow

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### ABSTRACT

Windstorms are natural factors in vegetation dynamics, but their intensity is increasing and undermines the forest resilience. Post-event interventions depend on forest types and management purposes. To promote mixed stands that are less susceptible to windthrow than monocultures, natural tree regeneration is usually recommended. However, wild ungulates attracted by the increased food supply in the new clearings can influence the secondary succession and slow down vegetation recovery. The impact of ungulate pressure on secondary successions in blowdown areas is still poorly known, especially in Mediterranean areas, which is particularly vulnerable to climate stressors. We investigated this topic using a monospecific silver fir (*Abies alba*) forest of artificial origin in the Apennines as a model system. The forest was left to natural succession after a severe windthrow in 2015, offering the opportunity to establish an ungulate enclosure experiment to analyse vegetation changes over six years. For the whole plant community, cover and height,  $\alpha$ -diversity (species richness, Shannon and evenness indexes), and species composition were recorded yearly, together with tree seedling density, in open and fenced plots at increasing distances from the forest edge. Ecological and functional traits (proportion of light-demanding and forest specialists, endo-/epi-zoochorous species), and life-forms of the community samples were also analysed. Overall, we found that ungulates significantly influenced the dynamic trajectories of secondary succession. The effects on plant cover and diversity were negative and increased with distance from the forest edge. The presence of ungulates favoured generalist species and endozoochorous taxa. However, distance from the forest edge strongly reduced the latter effect. The average density of tree seedlings was overall high (ca. 10,000/ha), but it was strongly reduced by ungulates for three deciduous species and *A. alba*, the most browsed species. Natural recolonization after windthrow in Apennine pure silver fir stands may favour the formation of mixed, less susceptible forests, but the current ungulate pressure slows down this process, especially in the areas furthest from the forest edge.

### 1. Introduction

Disturbances affect the secondary successions of vegetation by altering species diversity and composition in ways that depend on their characteristics, particularly severity, extent, temporal and spatial scale (Viljur et al., 2022). Forests are currently exposed to an increasing number of disturbances mainly associated with climate changes and

anthropic pressure (Seidl et al., 2017; Gregow et al., 2017; Sommerfeld et al., 2018; Senf and Seidl, 2021; Romagnoli et al., 2023). Windstorms are well-known natural abiotic agents of forest disturbance (Fischer et al., 2013; Mitchell, 2013) affecting the structure and composition of the whole ecosystem (Gardiner et al., 2010). Compared to other forest types, coniferous stands, especially artificial ones, are highly susceptible to catastrophic windstorms (Seidl et al., 2011), while mixed stands are

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known to be more resistant and resilient (Bauhus et al., 2017). Therefore, after blowdown events in monospecific coniferous stands, natural regeneration is widely preferred over planting conifers, since it can provide great variability in both stand composition and structure, achieving more stable stands (Wohlgemuth et al., 2017; Motta et al., 2018; Senf et al., 2019).

In Europe, windthrow areas in coniferous forests are usually managed with salvage logging to reduce timber losses and protect neighbouring undisturbed stands from bark beetle outbreaks (Michalová et al., 2017; Sanginés de Cárcer et al., 2021). As a consequence, the sudden opening of clearings after windstorms and logging often attracts wild ungulates due to the increased amount of available forage (Storms et al., 2006). Ungulates are an integral part of forest ecosystems that use plant biomass as a food source: through browsing, as in the case of roe deer (mainly leaves and twigs of woody and herbaceous dicots), and by grazing, as in the case of red and fallow deer (mainly on grasses and sedges) (Gordon and Prins, 2008; Fischer et al., 2013). The interactions between plants and herbivores are complex and have mostly been analysed using enclosure experiments (Schmidt et al., 2011). Large herbivores are general drivers of vegetation dynamics worldwide and their impact increases heterogeneity in ecosystems and thus plant diversity via trophic cascades (e.g. Pringle et al., 2023). Ungulates can increase the species richness of herbaceous plants by improving light availability on the forest floor through the control of woody layers (Royo et al., 2010). However, this effect is not necessarily positive, as it mainly favours ruderal, hemerobic, epizoochorous and non-forest species and leads to biotic homogenization at the landscape level (Boulanger et al., 2018). Regarding tree regeneration, fauna pressure is detrimental to the formation and functioning of new forest stands (Landi et al., 2016; Ramirez et al., 2018; Nilar et al., 2019). The impact of herbivorous mammals on forest regeneration is particularly severe in Mediterranean environments (Zamora et al., 2001), where it is related to loss of tree diversity and lack of recruitment (Velamazán et al., 2018).

When different disturbances overlap, as in the case of ungulate pressure in blowdown or pest/pathogens outbreak areas, their effects are amplified, which can lead to unpredictable permanent changes in the functioning and composition of a community (Romme et al., 1998; Reyer et al., 2015; Williams et al., 2016; Andrus et al., 2020; Szwagrzyk et al., 2020; Marangon et al., 2022), both considering the woody and herbaceous vegetation. Indeed, most studies focused on tree regeneration, not considering the crucial role of the shrub and herb components regarding ecosystem stability and provision of services (Gilliam, 2007).

To date, studies on the combined effects of windthrow and ungulate pressure on the total plant succession were only conducted in a mixed conifer forest in the Swiss Alps (Senn et al., 2002; Rammig et al., 2007) and more recently in mixed deciduous forests in Pennsylvania (Spicer et al., 2023) and Japan (Morimoto et al., 2019), with contradictory results. This suggests that the effects of fauna on vegetation in windthrow areas are still incompletely understood and depend on different constraints of the studies, also at a local scale (Gill and Beardall, 2001). This problem may be related to a general difficulty in the study of disturbances since experiments cannot be planned with proper experimental designs (i.e. Szwagrzyk et al., 2018). Therefore, more case studies are needed (e.g. Ramirez et al., 2018), especially in the Mediterranean region where such an issue has not been investigated so far (Vacchiano et al., 2017; Champagne et al., 2021) and vegetation is also severely affected by increasing heat and drought (Barbeta et al., 2015).

Assessing the impact of wild ungulates on salvaged windthrow coniferous stands in Mediterranean areas can therefore help to understand the forest community resilience to the increasingly frequent combinations of disturbances and help to define the best options for management after such catastrophic events. Accordingly, we conducted a 6-year enclosure experiment in a blowdown area of a historical silver fir stand in the Italian Apennines of anthropic origin, in order to respond to the following questions:

- 1) What is the impact of ungulates on the early stages of the secondary succession after the logging of the fallen trees, in terms of growth, diversity, composition and ecological characteristics of the vegetation?
- 2) How do ungulates influence the success of tree recruitment and the composition of the developing new tree stand?

Overall, the responses to the above questions may provide hints that can help to define scientifically based solutions for the management of silver fir pure stands after windthrow in order to favour the formation of mixed, more natural and resilient forests in the Apennine region.

## 2. Material and methods

### 2.1. The windstorm event and the study area

The study was conducted in the forest of Vallombrosa (a Biogenetic Nature Reserve of the Apennines). The climate of the area is characterized by an average annual air temperature of 9.8 °C and an average annual precipitation of 1275 mm (thermo-pluviometric station of Vallombrosa, 980 m a.s.l.). The soils are formed on Oligocene siliceous sandstones and belong to the Inceptisols and Alfisols ([www.eusoils.jrc.ec.europa.eu](http://www.eusoils.jrc.ec.europa.eu)). The natural vegetation is a mixed deciduous stand dominated by oaks (mainly *Quercus cerris* L., *Carpinus betulus* L., *Ostrya carpinifolia* Scop., *Acer* sp.) and chestnut (*Castanea sativa* Mill.) stands. However, most of the reserve is covered by artificial silver fir stands (*Abies alba* Mill.). Silver fir is native to most of Italy (Pignatti, 2017-2019), but it was planted - especially along the Apennines - since the 11th century for timber production (Grossoni et al., 2018). Currently, stands dominated by this conifer cover about 70,000 ha in Italy (data from Italian National Forest Inventory of 2015) and management strategies are widely debated between those who support their conservation as a historical heritage and those who support their natural conversion into mixed and more resilient forest types (Borghetti et al., 2021).

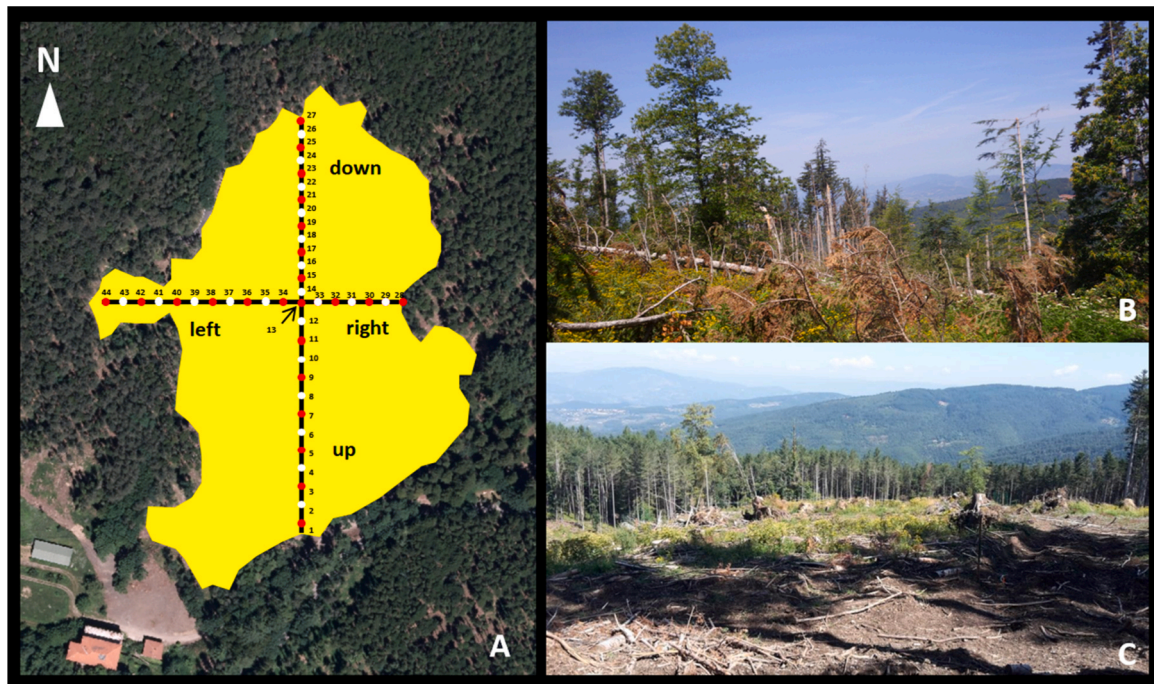
According to the last fauna census, the ungulate population of Vallombrosa forest consists mainly of *Dama dama* (300 animals) and *Sus scrofa* (230 animals), with a minor presence of *Capreolus capreolus* (Zanobetti, 2020). The main carnivores in the area are *Canis lupus* and *Felis silvestris* (Martini et al., 2021).

On 5th March 2015, a windstorm from the northeast with gusts of over 165 km/h hit several forests in Tuscany. The event caused extensive damage in the Vallombrosa forest, which was destroyed over a total area of 230 ha (Chirici et al., 2018). Our study area was located in a silver fir monoculture about 125-year-old called “Acquabella” (43°44'00.4 "N 11°32'40.8 "E). This stand showed the typical characteristics of pure artificial silver forests of the Italian Apennines, with a dense, even-aged and homogeneous structure. In the blowdown area, around 80 % of trees were snapped or uprooted (Fig. 1). The few isolated standing trees, in the summer of 2015, started to suffer of heatwaves showing symptoms such as leaf yellowing and shedding.

Logging was here carried out in June 2016 to remove the fallen trees from the forest floor and stressed standing trees. Traditional post-windthrow management in silver fir stands foresees artificial regeneration by planting silver fir saplings. In this case, for experimental purpose, the local administration left a blowdown area of 1.84 ha to its natural dynamics to favour the development of a conifer-broadleaf mixed forest. The area was homogeneous in terms of soil type (well-drained Alfisols of sandstone), aspect (north) and slope (20–25 %). Due to the uniqueness of the above management choice, compared to other damaged stands in the Vallombrosa forest area, it was not possible to replicate the study to other sites without introducing additional variables.

### 2.2. Experimental design and data collection

In spring 2016, 44 circular permanent observation plots of 1 m<sup>2</sup> were



**Fig. 1.** The study area of Acquabella as A) top view sampling design with location of open (white) and fenced (red) plots and uphill views of the area after the windthrow (July 2015, B) and after the salvage logging (July 2016, C).

established along the two main directions of the area (N-S, E-W), avoiding vehicle tracks. Although 1 m<sup>2</sup> plots are normally used for herbaceous vegetation (see Taylor and Zisheng, 1993, Liu, 1997, and Merriam and Feil, 2002), we considered this size acceptable as the regeneration of woody species is part of understory vegetation (Gilliam, 2007) during the first years of the secondary succession. Moreover, this design allowed us to take into account the distance from the forest edge as the main site variable.

To determine the influence of ungulates (especially fallow deer, hereafter referred to as “fauna effect”) on the secondary succession, half of the plots were closed with a 2 m high fence. The fence consisted of a square mesh with a large size (50 mm x 50 mm) to avoid any alteration in the ecological conditions (e.g. light availability, litter accumulation) or in plant development. The fenced and open plots were established alternately along the two plot orientations (Fig. 1). For six years after the logging, complete vegetation surveys were conducted in late spring of each year (at the time of maximum vegetation development), except for 2020 due to the Covid-19 pandemic restriction, i.e. 26 (spring 2017), 39 (spring 2018), 51 (spring 2019), 75 (spring 2021) months after the event. During each of the four spring surveys, the following variables were recorded considering the whole vegetation (e.g. trees, shrubs and herbs): 1) total ground cover and total maximum height; 2) identity and percentage of ground cover for each vascular plant species. In addition, tree regeneration was examined at 10 surveys between the 20th and 75th month after the event (dates are presented in Appendix A) by recording the total number and identity of tree seedlings per plot. Finally, during the last survey (75 months post-event), all species with signs of grazing/browsing in the open plots were recorded to identify those preferred by wild ungulates. Species identification was mainly conducted in field based on Pignatti (2017–2019).

### 2.3. Data analysis

Plant growth was estimated using the percentage of ground cover and maximum plant height, while community  $\alpha$ -diversity was quantified as species richness (SR), Shannon index (H') and evenness (J). Tree regeneration was assessed as the number of tree seedlings per species.

All analyses were performed in R version 4.0.3 (R CoreTeam, 2020).

A linear or generalised mixed model approach was applied to assess the effects of time, fauna and edge distance on plant growth,  $\alpha$ -diversity and tree regeneration variables. In each initial model, the effects of fauna (categorical variable; levels: open, fenced), time (categorical variable; 4 levels for the plant growth and diversity variables; 10 levels for the number of seedlings) and distance from the forest edge (continuous variable) were included along with the interactions fauna/time and fauna/edge distance. To remove variance from the models that may be due to spatial clustering in the four sections of the area, the variable “zone” (levels: up, low, right, and left, see Fig. 1) was included as a random factor (e.g. initial model: response variable  $\sim$  fauna + time + edge distance + fauna:edge distance + fauna:time + 1 | zone). For the continuous variables (cover, height, H' and J), linear mixed models with the *lmer* function and a Gaussian error distribution were fitted. For the count variables (SR and number of tree seedlings), the initial model was fitted with a generalized linear mixed model (*glmer*) with a Poisson error distribution. Most parsimonious models were selected following the protocol of Zuur et al. (2009) based on Akaike's Information Criterion (AIC; Akaike, 1973). The corresponding conditional (R<sup>2</sup>c) and marginal (R<sup>2</sup>m) R-squares (Nakagawa and Schielzeth, 2013; *MuMIn* package) were calculated for them. Parameter-specific p-values for each predictor level were determined using the Satterthwaite approximation (*lmerTest* package).

Differences in plant species composition between fenced and open plots were assessed using a multivariate approach. The cover-weighted Bray-Curtis distance was calculated among all plots over the entire monitoring period using the *vegdist* function in the *Vegan* R package (Oksanen et al., 2019). Non-metric multidimensional scaling (*metaMDS* function in *Vegan*) was then applied to summarize and display distances between i) different surveys (time effect) and ii) fenced and open plots (fauna effect). The significance of the compositional differences caused by the two factors was determined using PERMANOVA with 999 permutations (*adonis* function). We tested the multivariate homogeneity of dispersion within each plot group of plots using *betadisper* (Anderson et al., 2006; Warton et al., 2012). The Bray-Curtis distance was also calculated separately between plots for each survey, similarly, testing



the compositional differences determined by fauna. In addition, an Indicator species analysis (ISA) was performed to identify the species significantly associated with the fauna, using the function *multipatt* in *indicspecies* (Duf re and Legendre, 1997; Carrari et al., 2016).

Structural changes in vegetation were investigated based on the abundance (ground cover) of Raunkiaer life-forms, e.g. phanerophytes, nano-phanerophytes, chamaephytes, geophytes, hemicryptophytes, therophytes, and geophytes. Variations driven by time, fauna and their interactions were tested using the non-parametric Friedman test.

Differences in the relevant ecological and functional characteristics of the plant communities of open and fenced plots were examined using the following criteria: 1) light requirement based on the value of the Ellenberg Light index according to Pignatti et al. (2005); 2) proportion of epizoochorous species based on the Dispersal and Diaspore Database (Hintze et al., 2013) and endozoochorous species based on BROT 2.0 (Tav ano lu and Pausas, 2018); we considered as epizoochorous species those with an Epizoochory dispersal ranking index > 0.5; and 3) the forest guilds according to the classification of Heinken et al. (2019). The few species that were not included in the cited databases were classified using information from Pignatti (2017–2019). Linear mixed models were then applied to test the effects of fauna, time and edge distance and their interactions on the weighted mean value of light, the proportion of epi- and endo- zoochorous species and the proportion of forest specialists (categories 1.1 and 1.2 of Heinken et al., 2019) according to the model setting and steps explained above.

Finally, to assess the potential impact on future stand composition, the average number of seedlings per tree species for the entire period was compared between open and fenced plots using the non-parametric Wilcoxon test.

### 3. Results

#### 3.1. Effects of time, edge distance, and fauna on plant growth

Based on model results, vegetation cover was influenced by fauna, edge distance and their interaction (Table 1). In fenced plots, cover was higher than in open plots (121±48 % vs. 94±37 %, Fig. 2A;  $p < 0.05$ ; Table 1). As expected, cover was influenced by time, especially 75 months after the event ( $p < 0.001$ ; Table 1; Fig. 2B). Cover also increased with distance from the forest edge (+0.21; Fig. 2C;  $p < 0.05$ ; Table 1), and this increase was significantly greater in the fenced plots (+0.44;  $p < 0.001$ ) than in the open plots (Fig. 2D; Table 1).

The selected model for maximum plant height explained 60 % of the variance (Table 1). This variable was only weakly affected by fauna (Fig. 3A), but strongly influenced by edge distance, time and its interaction with fauna impact (Fig. 3B–C–D): at the last survey (75 months after the windthrow), height was three times higher than at the first survey (26 months after the windthrow) ( $p < 0.001$ ; Table 1). Until 51 months after the event, height was higher in the fenced plots, but the trend reversed in 2021 (Fig. 3D), when plants in the open plots were almost 27 % taller than in the fenced plots (2.33±0.52 m vs 1.83±0.76 m;  $p < 0.01$ ; Table 1).

#### 3.2. Effects of time, edge distance, and fauna on species diversity

A total of 151 vascular plant species were recorded on the plots. The total number was slightly higher in the fenced plots (133 compared to 117 in the open plots), but the mean S per plot was identical in both groups (12) (Fig. 4A). At months 51 and 75, SR was significantly lower than at the 26-month survey (Fig. 4B; Table 1) Again, the model revealed a strong interaction between edge distance and fauna ( $p < 0.001$ ; Table 1), showing that species richness increased in the fenced plots with edge distance, while it almost decreased towards the middle of the

**Table 1**

Linear mixed model structures showing the effect of time, fauna, distance to forest edge and zone (as random factor) on the response variables: plant cover, maximum vegetation height, Species Richness-SR, Shannon Index-H', Evenness-J, number of tree seedlings-no. trees); [R syntax of the starting model:  $y \sim$  fauna impact + time + edge distance + fauna impact: edge distance + fauna impact: time + 1|zone]. Values for the predictor variables: impact of fauna (level: "fenced" compared with "open"), time (levels: 75, 51, 39 compared with 26 months after the windthrow), edge distance, interactions between fauna impact and edge distance or time are parameter estimates.  $R^2$  m (marginal) refers to the fraction of the variation explained by the fixed model structure, while  $R^2$  c (conditional) accounts for the random factor. Significance level: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

	Cover <i>linear</i> <i>mixed-effects</i>	Height max <i>linear</i> <i>mixed-effects</i>	SR <i>generalized linear</i> <i>mixed-effects</i>	H' <i>linear</i> <i>mixed-effects</i>	J <i>linear</i> <i>mixed-effects</i>	no. trees <i>generalized linear</i> <i>mixed-effects</i>
Fauna (fenced)	3.019*	17.479*	-0.028	-0.049	-0.099**	0.384***
	-11.681	-16.095	-0.046	-0.065	-0.045	-0.125
Edge distance	0.210*	0.425***	-0.03	-0.218***	-0.002***	-0.010***
	-0.115	-0.113	-0.05	-0.048	-0.0004	-0.002
Edge distance:fenced	0.437***		0.145***	0.178***	0.001**	
	-0.158		-0.047	-0.065	-0.001	
Time (m39)	9.318	40.714**	0.062	0.124	0.036	
	-8.184	-16.431	-0.059	-0.091	-0.032	
Time (m51)	0.864	96.429***	-0.310***	-0.320***	-0.037	
	-8.232	-16.431	-0.066	-0.091	-0.032	
Time (m75)	25.321***	181.340***	-0.434***	-0.423***	-0.065**	
	-8.185	-16.436	-0.067	-0.091	-0.032	
Fenced:Time (m39)		19.851				
		-22.727				
Fenced:Time (m51)		17.702				
		-22.727				
Fenced:Time (m75)		-63.949***				
		-22.73				
Constant	71.669***	47.020**	2.562***	1.716***	0.668***	1.572***
	-10.968	-23.458	-0.079	-0.122	-0.033	-0.455
Observations	175	175	175	175	175	440
Log Likelihood	-873.965	-920.41	-442.146	-112.418	68.122	-753.021
Akaike Inf. Crit.	1765.93	1862.82	906.292	242.836	-126.243	1516.04
Bayesian Inf. Crit.	1794.41	1897.70	941.105	271.319	-110.419	1536.48
R2m	0.282	0.558	0.404	0.254	0.126	0.071
R2c	0.316	0.57	0.493	0.383	0.192	0.354

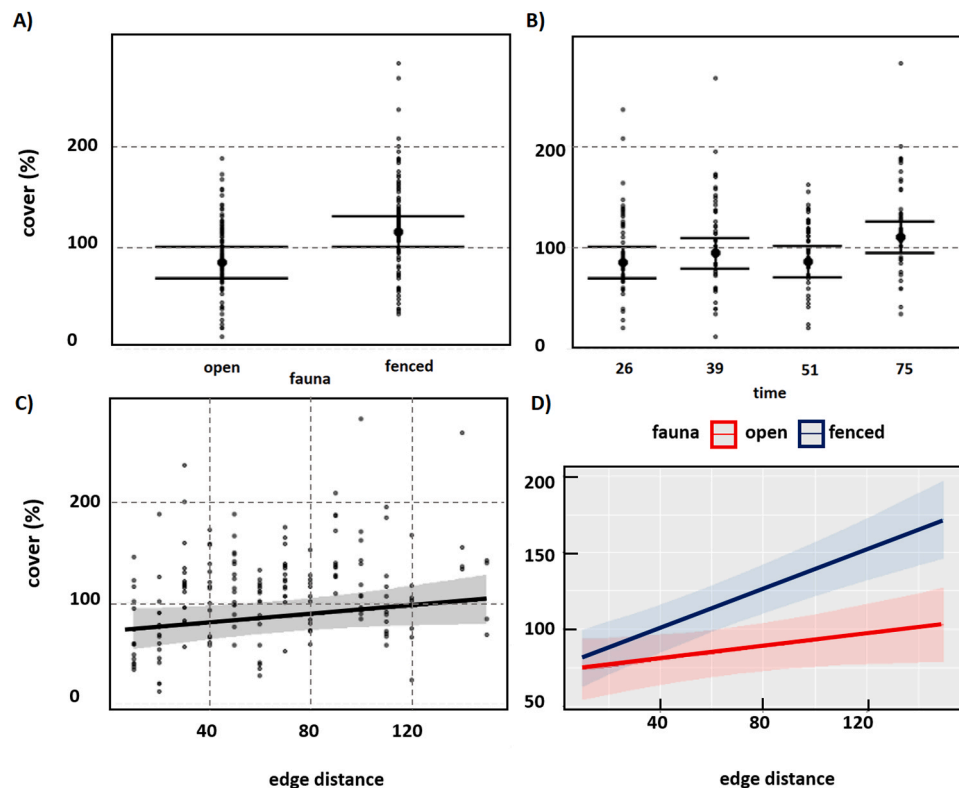


Fig. 2. Variables affecting ground cover. Regression estimates for total plant cover driven by factors selected in the best model (see Table 1): fauna impact (A), time (B), edge distance (C), and interaction between edge distance and fauna (D).

gap in the open plots (+14 % in fenced compared to open plots; Fig. 4D; Table 1). The Shannon index was not influenced by fauna presence ( $1.55 \pm 0.54$  in open plots VS  $1.52 \pm 0.52$  in fenced plots; Appendix B; Table 1), while it was negatively affected by edge distance and time ( $p < 0.001$ ; Table 1); 75 months after the event, diversity was significantly lower than in 2017 and 2018 (Appendix B). The significant interaction between edge distance and fauna ( $p < 0.001$ ; Table 1) led to a decrease in Shannon diversity with increasing distance from the edge, which was stronger in the open than in fenced plots (-18 %; Appendix B). This was associated with a sharp decrease in evenness in the open plots far from the edge (Appendix C).

### 3.3. Effects of time, edge distance, and fauna on species composition

The floristic differences between the open and fenced plots in the yearly surveys were not significant (data not shown). When all surveys were pooled, differences in composition between fenced and open plots resulted weakly significant ( $p_{\text{perm}} = 0.027$ ; Appendix D), due to differences between survey years ( $p_{\text{perm}} = 0.001$ ; Appendix E). In contrast, the ISA distinguished between open and fenced plots (Table 2): open plots had a higher number of indicator species (9), 4 of which were more typical of open habitats (category 2.2), while only one was a forest specialist (*Physospermum cornubiense*); in fenced plots, 3 of the 5 indicator species were forest specialists (category 1.1) (Table 2).

In terms of life-forms, time caused a significant increase in phanerophytes ( $p < 0.001$ ; Fig. 5A) and a decrease in hemicryptophytes ( $p < 0.001$ ; Fig. 5D). The exclusion of ungulates was positively associated with the cover of phanerophytes and geophytes (+35 % and +68 % respectively in fenced plots compared to open plots; Fig. 5A, F). The interaction between time and fauna was not significant for all life forms (Fig. 5).

There were no clear effects of ungulates on the mean Ellenberg L value, which was positively affected only by the edge distance. Remarkably, endozoochorous species were significantly more abundant

in the open plots, but their proportion decreased with time and distance from the edge (Table 3). For endozoochorous species, interactions of fauna with edge distance and time were significant, the latter also in case of epizoochorous but with opposite direction. Despite a higher proportion of forest specialists in the fenced plots ( $19.3 \pm 2.6$  % vs  $14 \pm 4.1$  %), the effect of fauna was not significant; model results showed a significant decrease in these species with time and, to a lesser extent, with edge distance (Table 3).

Seventy months after windthrow, 10 graminoid species (mainly of the genus *Carex*), one tree (*Abies alba*) and one perennial clover species (*Trifolium repens*) were among the most browsed species (Appendix F).

### 3.4. Effects of time, edge distance, and fauna on tree regeneration

A total of 14 tree species were recorded in the plots during the study period, 12 in the open and 11 in the fenced plots. The highest seedling density was observed 28 months after the event (16,136 seedlings/ha) and decreased until the 39th month, reaching an average of approximately 10,227 seedlings/ha (data not shown). Regardless of time, average seedling density was greatly increased by fauna exclusion and was on average twice as high in fenced plots as in open plots (Table 4). At the plot level, the model results showed a higher average number of tree seedlings in the fenced plots than in the open plots ( $p < 0.001$ ; Table 1; Fig. 6A) and their slight but significant decrease with distance from the forest edge ( $p < 0.001$ ; Table 1; Fig. 6B). The most frequent tree species was *Abies alba* in both the open and fenced plots, with the number of seedlings being significantly higher in the latter (2.4 times higher than in the open plots; Table 4). The number of seedlings of *Ostrya carpinifolia* and *Castanea sativa* was also significantly higher in the fenced plots, while the seedlings of *Pinus nigra* were more numerous in the open plots (Table 4).

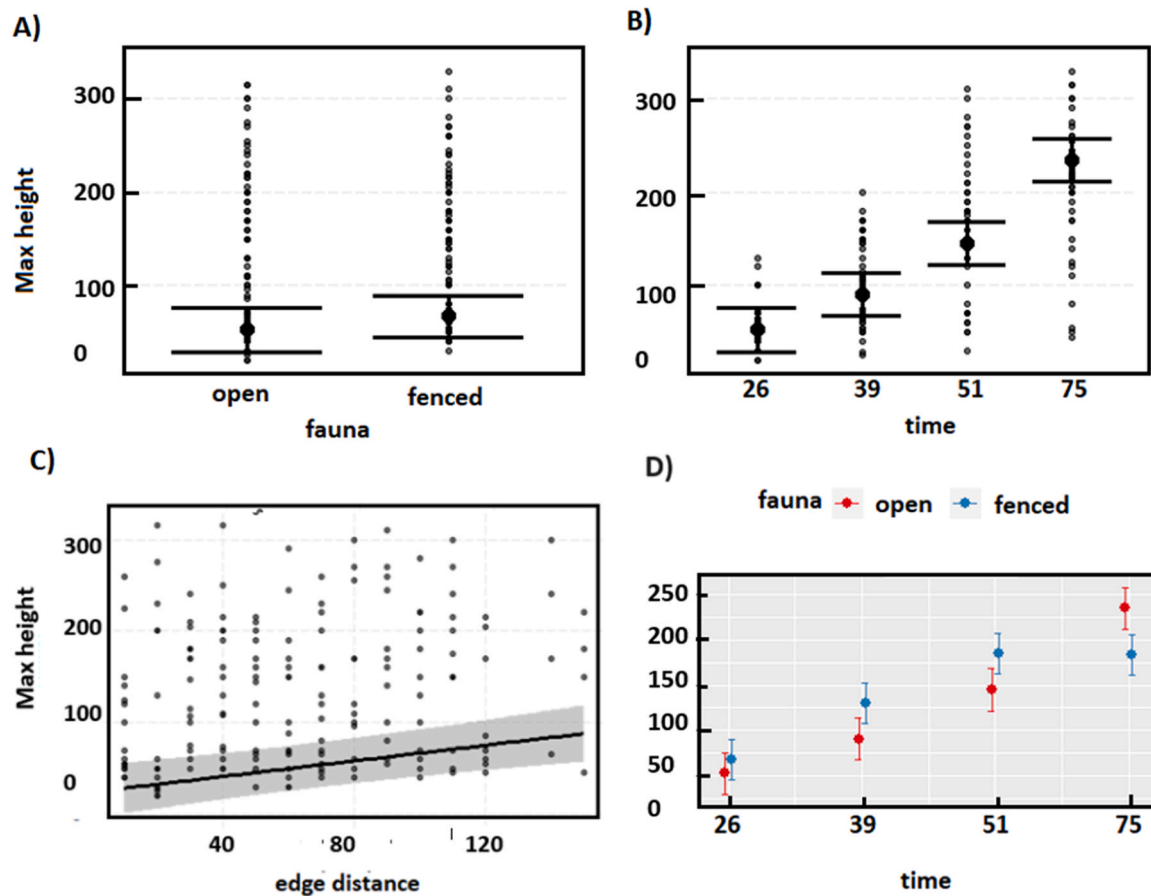


Fig. 3. Variables affecting maximum vegetation height. Regression estimates for maximum vegetation height driven by factors selected in the best model (see Table 1): fauna impact (A), time (B), edge distance (C), and the interaction between time with fauna (D).

#### 4. Discussion

Although the small size of the study area does not allow to generalize our findings to other European silver fir forests, our findings provide first evidence about the effects of wild ungulates on the natural vegetation dynamics of silver fir forests in Southern Europe after blowdown and salvage logging. In addition, the study area is representative of a widespread and historically relevant forest type in the Apennines, with artificial origin, simplified structure and low diversity of woody species. Results on plant growth, diversity, composition and tree regeneration, discussed below are useful for its management.

##### 4.1. Effects on plant growth

During the monitoring period, total vegetation cover increased on average by 21 %, reaching 124 % at the last survey six years after the event. This is consistent with the results of a similar study in a mixed forest in Switzerland, where the average vegetation cover was almost 120 % seven years after the storm (Senn et al., 2002). However, we found that cover was negatively affected by ungulates at this early stage of succession, indicating a stronger impact in our area than in the Swiss forest. A negative effect of fauna on vegetation cover was found in similar experiments in clear-cut areas of deciduous forests in Japan (Suzuki and Ito, 2014) and in undisturbed forest stands in Europe (Boulangier et al., 2018).

Not surprisingly, cover increased with the distance from the forest edge, due to higher light availability towards the centre of the gap (confirmed by the higher mean Ellenberg value; Table 3). Remarkably, however, the cover increase with distance from the edge was stronger in the fenced plots, demonstrating the influence of ungulates in limiting the

positive effect of higher light availability towards the centre of the gap. This finding suggests that ungulates prefer to forage in the centre of wide gaps, possibly due to the higher abundance of grasses and brambles (Storms et al., 2006). This result supports, also for silver fir forests of the present biogeographic region, the role of herbivores in maintaining gaps and edges after windthrows (Royo et al., 2010), with potential implications for plant diversity and composition (Erdős et al., 2023).

In parallel with cover, vegetation height increased rapidly in the six years following the logging due to the growth of nano-phanerophytes and phanerophytes such as *Cytisus scoparius* (L.) Link, a pioneer broom that reaches 3 m in height in the Italian regions (Pignatti, 2017-2019). Over the entire period, vegetation was slightly higher in the fenced plots, which is consistent with previous enclosure experiments (Fiorentini et al., 2015; Rammig et al., 2007). In the present study, however, vegetation was higher in the open plots than in the fenced plots between 51 and 75 months after the event. Although stochastic or concomitant factors unrelated to animal pressure may have played a role here - such as the influence of the fence on plant growth - some phanerophytes (especially *Cytisus scoparius*) were able to reach an average height of > 150 cm after 51 months in the open plots, becoming taller than the browsing limit for fallow deer (ca. 120 cm; Vila et al., 2003).

##### 4.2. Effects on $\alpha$ -diversity and species composition

Overall, the presence of ungulates in our model system was not associated with higher species diversity, despite the higher light availability that they cause by controlling the woody layers (Royo et al., 2010). This finding is consistent with previous studies on secondary successions after clearcutting in temperate forests (Ramirez et al., 2019; Suzuki et al., 2021), which suggested that the interaction between fauna

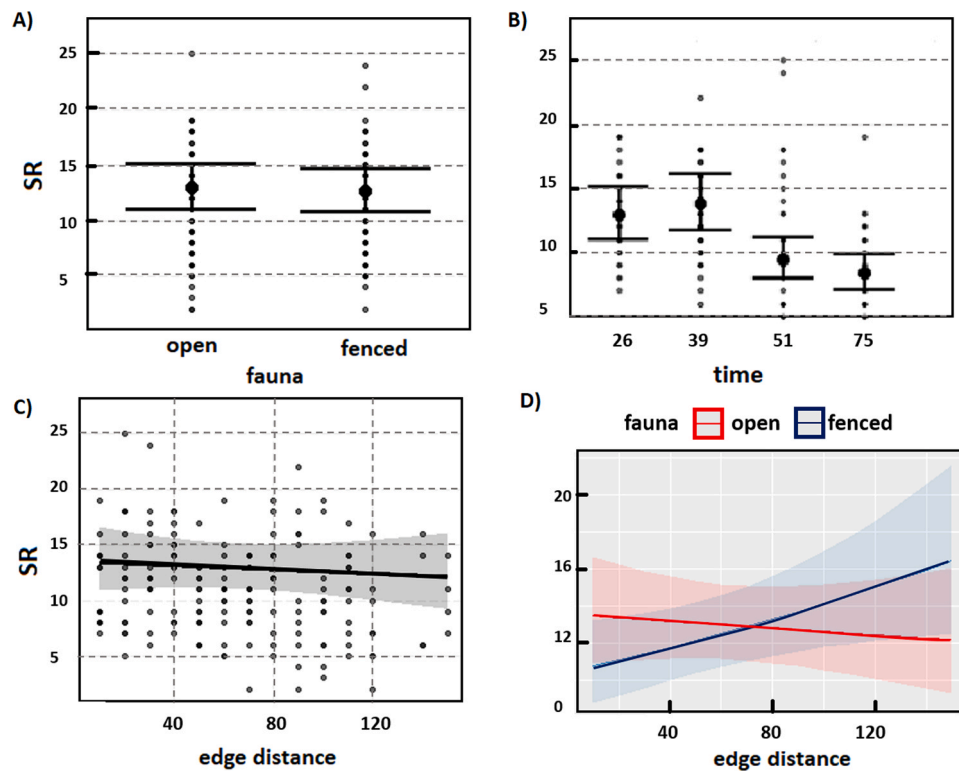


Fig. 4. Variables affecting species richness. Regression estimates for plant species richness (SR driven by factors selected in the best model (see Table 1): fauna impact (A), time (B), edge distance (C), and the interaction between impact of fauna with edge distance (D).

Table 2

Indicator species analysis (ISA) in open and fenced plots. Species significantly associated with open (fauna effect) and fenced plots (without fauna effect) are listed with forest guild (HC, Heinken et al. 2019) and Raunkiaer life-form.

Open	HC	Life form	p	Fenced	HC	Life form	p
<i>Carex divulsa</i>	1.2	H	0.017	<i>Luzula nivea</i>	1.1	H	0.034
<i>Rubus idaeus</i>	1.2	NP	0.045	<i>Hieracium racemosum</i>	1.2	H	0.041
<i>Cirsium arvense</i>	2.2	G	0.034	<i>Anemonoides trifolia</i>	1.1	G	0.016
<i>Stachys sylvatica</i>	1.2	H	0.024	<i>Vicia tenuissima</i>	2.2	T	0.035
<i>Cirsium vulgare</i>	2.2	H	0.048	<i>Salvia glutinosa</i>	1.1	H	0.022
<i>Pinus nigra</i>	2.1	P	0.006				
<i>Brachypodium rupestre</i>	2.2	H	0.042				
<i>Clinopodium vulgare</i>	2.2	H	0.039				
<i>Physospermum cornubiense</i>	1.1	H	0.05				

pressure and other disturbances leads to detrimental effects on diversity, in line with the intermediate disturbance hypothesis (Grime, 1973; Horn, 1975).

Moreover, the impact of fauna on plant diversity resulted strongly associated with the distance from the forest edge. Especially at a distance > 80 m (Fig. 4D) we observed a significant decrease in SR in the open plots, but an opposite trend in the fenced plots. Circumstantial support for a much stronger impact of ungulates towards the centre of the windthrow area was provided by the decreasing vegetation cover with increasing distance from the edge, suggesting that the centre of the gap is a preferred area for foraging. Hence, in the present case study, ungulates can reverse the normal increase in SR by keeping it higher at the edge of the gap than in its centre. This could be partly due to lower seed dispersal by animals and/or greater species selection in the central parts of the open area than at the edge. Shannon diversity in the open plots also decreased with increasing distance from the edge, due to a loss of species evenness. Selective feeding by ungulates in the centre of the area has likely increased the dominance of poorly palatable species such as *C. scoparius* over more palatable species, thus increasing the imbalance in their abundance. Moreover, the non-significant interactions

between time and fauna for diversity variables supported, for Apennine silver fir forests, that ungulates do not change the trend of diversity variation over time, which is consistent with the results of Ramirez et al. (2019) in a mixed forest in the Netherlands.

Regarding differences in composition, life form analysis showed a reduction in the cover of phanerophytes, geophytes and, to a lesser extent, hemicryptophytes; a similar result was also found by Spicer et al. (2023) after one-year enclosure experiment in a blowdown and logged area. In our model system, despite a higher frequency and abundance of generalist species such as *Cirsium arvense*, *Cirsium vulgare* and *Clinopodium vulgare*, we did not observe an effect on forest specialists and light-demanding species in the open versus fenced plots, as observed in undisturbed forests (Boulanger et al., 2018). In our study area, disturbance was caused by windthrow but also by salvage logging. Such a practice after windthrow might have contributed to alter the composition by favoring pioneer species, in line with previous observations (Fischer et al., 2013; Michalová et al., 2017; Oldfield and Peterson, 2019; Carrari et al., 2022). Many studies showed that species composition is more disturbed in cleared than in uncleared areas (Michalová et al., 2017; Oldfield and Peterson, 2019; Taerøe et al., 2019; Szwagrzyk

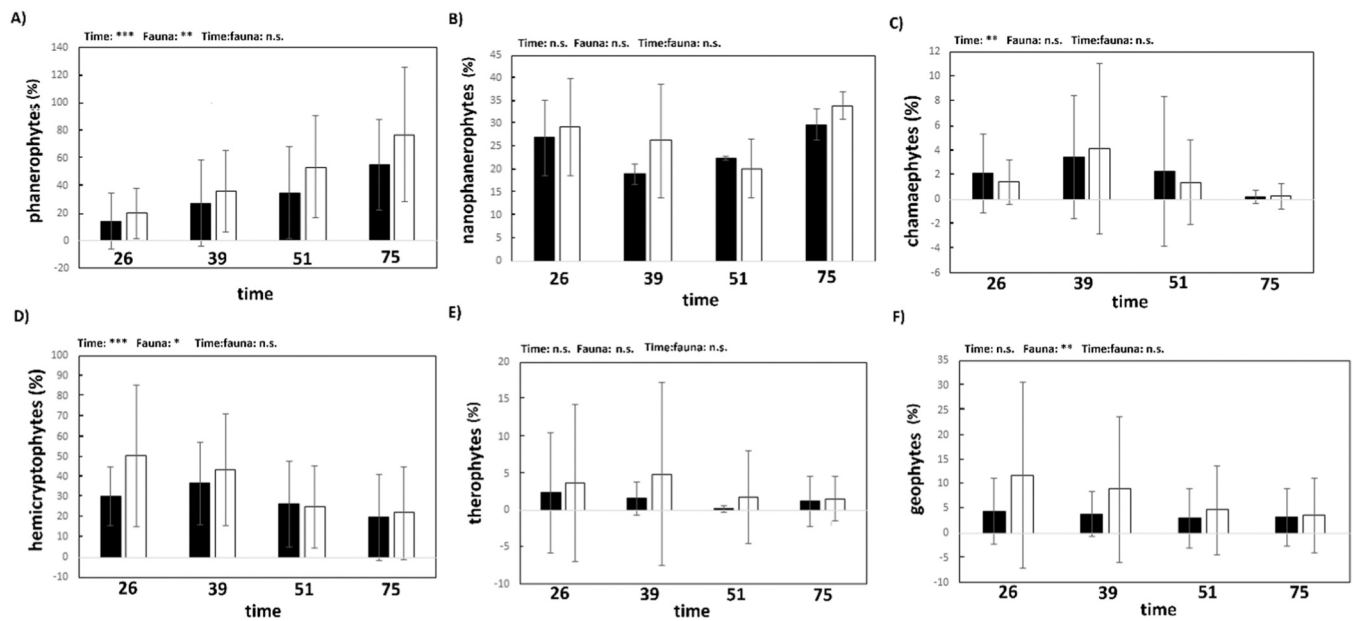


Fig. 5. Temporal cover variations of life-forms (A) phanerophytes, B) nano-phanerophytes, C) chamaephytes, D) hemicryptophytes, E) therophytes and F) geophytes) in open (black) and fenced (white) plots, at 26, 39, 51, 75 months after the windthrow. Differences by time and fauna impact were tested by Friedman. Error bars represent the standard deviation for each measure.

Table 3

Linear mixed model results showing the effect of fauna, time, and edge distance on the mean light (L) value (weighted by species cover), percentage of epi- and endo-zoochorous species, and forest specialists. See Table 1 for details in model settings.

	Light Ellenberg	Endozoochorous (%)	Epizoochorous (%)	Forest specialists (%)
Fauna (fenced)	-0.112 (0.100)	-111.188*** (25.953)	7.111 (3.839)	-0.015 (0.072)
Edge distance	0.012*** (0.001)	-0.836*** (0.195)		-0.002*** (0.001)
Fenced:edge distance		0.589** (0.267)		-0.001 (0.001)
Time (39)		-32.148 (19.999)	1.719 (3.926)	-0.034 (0.056)
Time (51)		-56.891*** (20.252)	2.676 (3.975)	-0.112** (0.056)
Time (75)		-51.237** (20.007)	19.691*** (3.926)	-0.144*** (0.056)
Fenced:Time (39)		38.801 (27.661)	-5.512 (5.430)	0.057 (0.077)
Fenced:Time (51)		59.425** (27.845)	-6.435 (5.465)	0.075 (0.078)
Fenced:Time (75)		60.160** (27.667)	-21.027*** (5.430)	0.076 (0.077)
Constant	5.554*** (0.220)	143.807*** (21.132)	0.806 (2.776)	0.403*** (0.068)
Observations	175	175	175	175
Log Likelihood	-187.012	-948.499	-674.020	20.796
Akaike Inf. Crit.	384.024	1920.998	1368.040	-17.592
Bayesian Inf. Crit.	399.848	1958.975	1399.688	20.385
R2m	0.251	0.178	0.166	0.15
R2c	0.431	0.235	0.166	0.302

Table 4

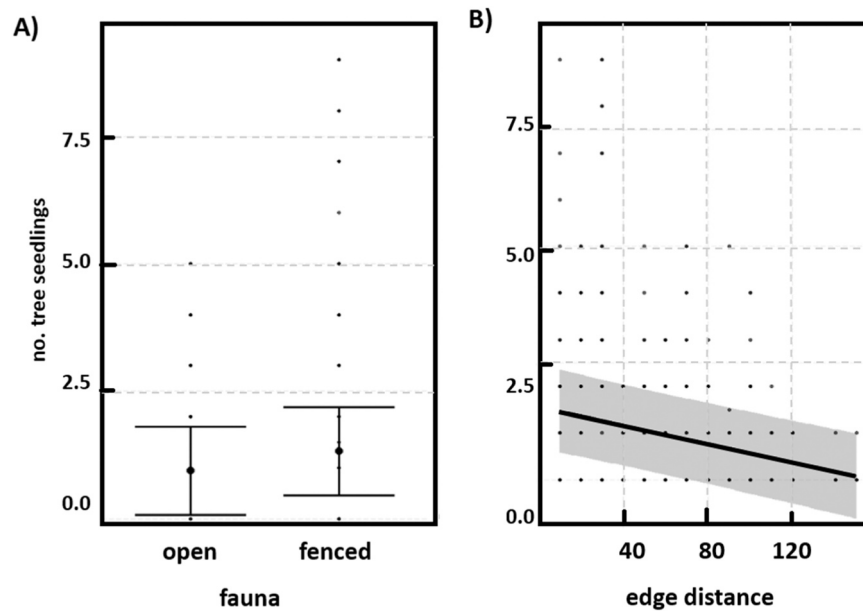
Number of tree seedlings per species at plot level and their total density in the area averaged for the ten surveys, with standard errors. Differences between open and fenced plots are based on the Wilcoxon test.

	open	fenced	p-value
<i>Abies alba</i>	0.26 ± 0.04	0.62 ± 0.08	<0.001
<i>Pinus nigra</i>	0.13 ± 0.03	0.01 ± 0.01	<0.001
<i>Acer pseudoplatanus</i>	0.11 ± 0.03	0.07 ± 0.02	n.s.
<i>Salix caprea</i>	0.09 ± 0.03	0.18 ± 0.04	n.s.
<i>Ulmus minor</i>	0.03 ± 0.01	0	0.01
<i>Pseudotsuga menziesii</i>	0.02 ± 0.00	0.03 ± 0.02	n.s.
<i>Acer campestre</i>	0.01 ± 0.01	0.03 ± 0.01	n.s.
<i>Ostrya carpinifolia</i>	0.01 ± 0.00	0.08 ± 0.02	<0.001
<i>Castanea sativa</i>	0.01 ± 0.00	0.09 ± 0.03	0.006
<i>Quercus cerris</i>	0.01 ± 0.00	0	n.s.
<i>Salix apennina</i>	0.01 ± 0.00	0	n.s.
<i>Populus nigra</i>	0.01 ± 0.00	0.05 ± 0.01	0.005
<i>Populus alba</i>	0	0.01 ± 0.01	n.s.
<i>Populus tremula</i>	0	0.01 ± 0.10	n.s.
TOTAL DENSITY (no. seedlings/ha)	6863.7 ± 790.6	13454.5 ± 1193.0	<0.001

et al., 2020; Marangon et al., 2022). Although the combination of the disturbances windthrow+logging+fauna cannot be tested in our study because there are no unlogged parts of the windthrow area, this could explain the weak effect of fencing on the proportion of forest specialists.

On the other hand, there was a significant difference in the frequency of endozoochorous species, which sharply decreased when ungulates were excluded. Previous works provided similar results, indicating that persistent shifts in plant community composition by fauna are related to endozoochory (Gill and Beardall, 2001; Boulanger et al., 2018) and nitrogen pulses resulting from concentrated foraging and defecation in canopy gaps (Tahtinen et al., 2014). Deer are effective seed dispersers of several plant species, particularly those with small, hard seeds (grasses and small herbs) that are most likely to survive digestion (Gill and Beardall, 2001). Our results indicate a strong edge distance effect, which is shown, for the present model system, to be negatively related to the frequency of endozoochorous plants in the plots, whereas no effect was found for epizoochorous species. This apparent contrast with the higher





**Fig. 6.** Variables affecting number of tree seedlings. Regression estimates for trees (number of seedlings recorded in the whole period per plot) driven by factors selected in the best model (see Table 1): fauna (A) and edge distance (B).

influence of ungulates in the centre of the area can be explained by two possible, not mutually exclusive, reasons: i) different preferences of ungulates for foraging and defecation sites and/or ii) the role of birds in the dispersal of endozoochorous plants, which is more effective at the edge (McClanahan and Wolfe, 1987).

Finally, the observed shifts in the proportion of forest specialists and species with different light requirements driven by edge distance support, also for blowdown areas, the role of forest edges in shaping the ecological and functional profiles of vegetation (Govaert et al., 2020; Gasperini et al., 2021, 2022; Erdős et al., 2023).

#### 4.3. Effects on tree regeneration

Ramirez et al. (2008) emphasised the importance of abundant potential tree regeneration in blowdown areas in the first years after clearing to overcome competition from tall herbs. Overall, the average total tree seedling density (> 10,000/ha) in our study area at each survey was likely enough to ensure regeneration and, potentially, the formation of a mixed forest with *A. alba* (45%) and broadleaf species. On the other hand, we found a significant influence of wild ungulates that reduced the average number of seedlings per plot and their overall density. The reduction in density was consistent with the model of Rammig et al. (2007) and showed a delayed regeneration of trees due to ungulate pressure. The negative effects of fauna on tree regeneration are also known both from recent studies observing browsing signs in windthrow areas (Szwagrzyk et al., 2020; Marangon et al., 2022) and enclosure experiments in standing forests (Ramirez et al., 2019; Gill and Beardall, 2001). Ungulates impaired forest regeneration, structure and functioning in 70% of the cases studied and defined a sigmoidal dose-response curve for the interaction between fauna density and forest regeneration, where ungulates started to impede forest regeneration from a density of 10 deer/km<sup>2</sup> (Ramirez et al., 2018). Based on the last census in the Vallombrosa Forest (13 Km<sup>2</sup>), the average fallow deer density is 2.3 times higher than the above threshold (Zanobetti, 2020); our results on tree regeneration confirm the elevated ungulate density in this area, even considering only the fallow deer.

In the present study, edge distance also caused a decrease in the number of seedlings, independently of interaction with fauna. Factors such as lower seed input and higher competition from tall shrubs in the centre of the gap could be responsible for this effect (Ramirez et al.,

2018; Walters et al., 2020). The influence of shrubs on tree regeneration on ungulate presence is likely not unidirectional: Salek et al. (2019) found that thorny shrubs largely protected tree seedlings from browsing, although this depended on shrub species, while Kern et al. (2012) reported that browsing and shrub competition lead to poor tree growth and survival, possibly limiting the extent of potential tree seedling responses to gap size. Our results are therefore more in line with the latter findings.

At the species level, regeneration of *A. alba*, *O. carpinifolia* and *C. sativa* was positively affected by fauna exclusion, while *Pinus nigra* seedlings from neighbouring plantations were more numerous in the open plots. The generally denser vegetation in the fenced plots probably favoured the three more shade-tolerant, deciduous trees, while the more light-demanding and less palatable pine species benefited from the lower vegetation cover in the open plots. Silver fir was the most browsed tree species, confirming, also within this enclosure experiment, the strong impact of ungulates on seedlings and saplings of this species reported from undisturbed forests in southern (Gonnelli et al., 2014; Fiorentini et al., 2015; Landi et al., 2016) and central Europe (Motta, 1996; Klopčic et al., 2010; Senn and Suter, 2003; Häsler and Senn, 2012; Unkule et al., 2022).

## 5. Conclusions

Overall, in the present monitoring study of a blowdown area in an Apennine silver forest, ungulates (i) prolong the gap by slowing down the timing of plant growth, (ii) do not favour tree, shrub and herb diversity but only slightly influence their composition by increasing endozoochorous and generalist species and reducing the abundance of geophytes, phanerophytes and hemicyptophytes, (iii) reduce the density of tree regeneration, especially of *Abies alba*, and favour pioneer tree species such as *Pinus nigra* rather than broadleaf species. The latter effect may be detrimental to the formation of more stable and wind-resistant stands when Apennine silver fir forests are damaged. In most cases, however, the intensity and direction of fauna impacts depended on the distance to the forest edge. In particular, the negative effects on diversity were lower at the edges of the gap, while they became much stronger towards the centre. This suggests that fencing parts of the windthrow gap towards the centre could be an effective strategy for the present Apennine forest type, to promote species diversity and tree regeneration,

where the positive effect of the forest edge disappears (about 80 m from the edge for gap of similar size). Overall, in this model system, the combination of the two disturbances leads to community reordering, decreasing species diversity and hindering the formation of a mixed stand with deciduous trees and silver fir. However, the dense and taxonomically rich seedling assemblage in the fenced plots, and to a lesser extent also in the open plots, argues in favour of natural tree regeneration as a viable strategy towards mixed and less vulnerable silver fir forests in the Apennines. Although our conclusions are valid for the studied biogeographic area, they contribute to reduce the knowledge gap on the comprehension of the interacting impacts of windstorms and ungulates on secondary successions in the Mediterranean area. Finally, this case study provides essential information to elaborate scientifically based solutions for the post-windthrow management of Apennine silver fir forests with elevated ungulate density.

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## CRedit authorship contribution statement

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## 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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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122200](https://doi.org/10.1016/j.foreco.2024.122200).

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