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# Comparative Understory Development in Fenced and Unfenced Beech Forest Stands in the Southern Alps

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**Abstract:** This study examines the impact of ungulate browsing on the understory dynamics of the Cansiglio Forest, the only European beech high forest in the Southern Limestone Alps. Utilizing seven pairs of fenced versus unfenced forest stands established over two decades, we assessed how fencing affects understory structure and tree regeneration. Significant differences were found in cover, height and vascular species composition in both tree regeneration and shrub layers. Fenced areas showed a significantly higher number and greater average height of young trees, supporting the hypothesis that ungulate browsing negatively impacts tree regeneration. Despite previous studies attributing the lack of silver fir (*Abies alba* Mill.) regeneration primarily to red deer (*Cervus elaphus* Linnaeus, 1758) browsing, our findings did not show a significant association of this species with fenced conditions. While *Rubus* abundance was higher inside fenced areas, overall vascular species richness did not differ. Our results highlight the evident effects of ungulate browsing and suggest the need to consider other factors influencing forest regeneration and understory development. Future research should establish additional study replicates, balanced across diverse site and stand structure conditions, to further explore these dynamics.

**Keywords:** browsing; deer; fencing; *Rubus*; beech; Norway spruce; silver fir

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**Citation:** Bovio, E.R.; Richard, J.; Iacopino, S.; Campagnaro, T.; Sitzia, T. Comparative Understory Development in Fenced and Unfenced Beech Forest Stands in the Southern Alps. *Forests* **2024**, *15*, 1088. https://doi.org/10.3390/f15071088

Academic Editors: Jan Cukor and Jakub Drimaj

Received: 6 May 2024
Revised: 10 June 2024
Accepted: 14 June 2024
Published: 23 June 2024



## 1. Introduction

The relationship between deer populations and the structure, including composition, of forest understories, has been extensively explored globally [1–4], including the alpine biogeographic regions of Europe [3,5–7] due to the significant effect that deer can have on the provisioning of ecosystem services [8]. One common method to study the effects of deer on forests is by excluding them by fencing, which has been shown to result in a range of outcomes. Positive effects include protection from grazing and trampling [3], whereas negative consequences may involve excessive litter accumulation that impedes tree regeneration [4,9]. Research has shown that excluding large herbivores significantly increases shrub cover in forests [10]. In the conifer forests of the Southern Alps, fenced areas used to keep deer out have revealed a significant impact of deer browsing on understory vegetation and tree regeneration [11]. However, the effects of fencing are not solely related to the cover of tree regeneration and understory vegetation but can also result in a change in species composition, with certain species being particularly associated with the fenced condition in contrast to an unfenced area [3,7], such as an increase in nitrogen-demanding species when ungulate browsing is prevented [12,13].

An Interesting example of the Interaction between ungulate browsing and the development and structure of the understory and tree regeneration can be seen in Cansiglio Forest, the only beech high forest on the Southern Limestone Alps. In this forest, the population of red deer (*Cervus elaphus* Linnaeus, 1758) has notably increased due to factors including hunting bans [14–16]. This trend is said to put significant pressure on the regeneration of silver fir (*Abies alba* Mill.), potentially leading to a long-term shift in forest composition to more European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.), depending on site conditions [14].

The present study focuses on identifying differences in cover, height and number of individuals within the shrub and tree regeneration layers, comparing areas inside and outside the fences. According to the cited literature, we hypothesized that fenced areas will have a higher presence of silver fir saplings [14] and a greater number of individuals in the shrub and tree regeneration layers [10,11]. Additionally, we predict taller growth within these layers in the fenced areas [1]. The study also examines specific vascular species linked to fenced and unfenced conditions and expects significant differences in species richness [3,7,12,13]. The findings of this study aim to deepen our understanding of forest understory development in European beech forests in relation to deer presence and the associated ecosystem services.

## 2. Materials and Methods

### *2.1. Study Area*

The Cansiglio Forest (7776 ha), located on a karstic plateau shared by the Veneto and Friuli–Venezia Giulia regions in Northern Italy, has been recognized for its unique characteristics since medieval times. It is a relatively remote, marginal area in the Alps. Today, it is managed with a shelterwood system, with a focus on preserving and increasing its growing stock. The area is well known for hosting a large number of red deer, with an average of 540 individuals observed per year through spotlight surveys from 2001 to 2021. In 2012, the Regional Government of Veneto approved a deer management plan that also reported the increasing population dynamics of the species over the previous 10 years, with estimated densities ranging from 24.1 to 33.9 individuals/km$^2$ between 2006 and 2008 [16].

Because of this consistent presence of the species, over the past two decades, seven fenced areas with similar vegetational and canopy cover conditions have been established to study the impact of ungulates on the regeneration of forest tree species by Veneto Agricoltura, the management entity of the Venetian portion of the Cansiglio Forest [16,17]. Fence installation in the study area started in 2004 with the placement of the first five fences, with three (ID3, ID4, and ID5) still in operation. Each is square-shaped, measuring 8 m by 8 m. In 2010, four additional fences (ID1, ID6, ID7, and ID9) were constructed, with the same characteristics as the first five [16,17]. These areas have understory species typical of the *Asperulo-Fagetum sylvaticae* plant association, classified as habitat type 9130 under the Annex I Habitats Directive [18]. The coordinates for these fenced areas are detailed in Table 1, utilizing the WGS 84/UTM zone 32N coordinate system (EPSG: 32632). Additionally, Figure 1 provides a map illustrating the spatial location of all the designated areas. The minimum distance between 2 different areas is 800 m.

**Table 1.** A table reporting the coordinates of each sampling area (EPSG: 32632).

| Fenced Area ID | Locality Name | X | Y |
|---|---|---|---|
| ID1 | Valbella | 767,685 | 5,112,551 |
| ID3 | Tiriton | 763,659 | 5,111,239 |
| ID4 | Lama del Porzel | 761,350 | 5,110,147 |
| ID5 | Val Piccola | 761,543 | 5,109,364 |
| ID6 | Taffarel | 761,548 | 5,108,018 |
| ID7 | Orto Botanico | 764,453 | 5,107,658 |
| ID9 | Vallorch | 761,742 | 5,106,639 |

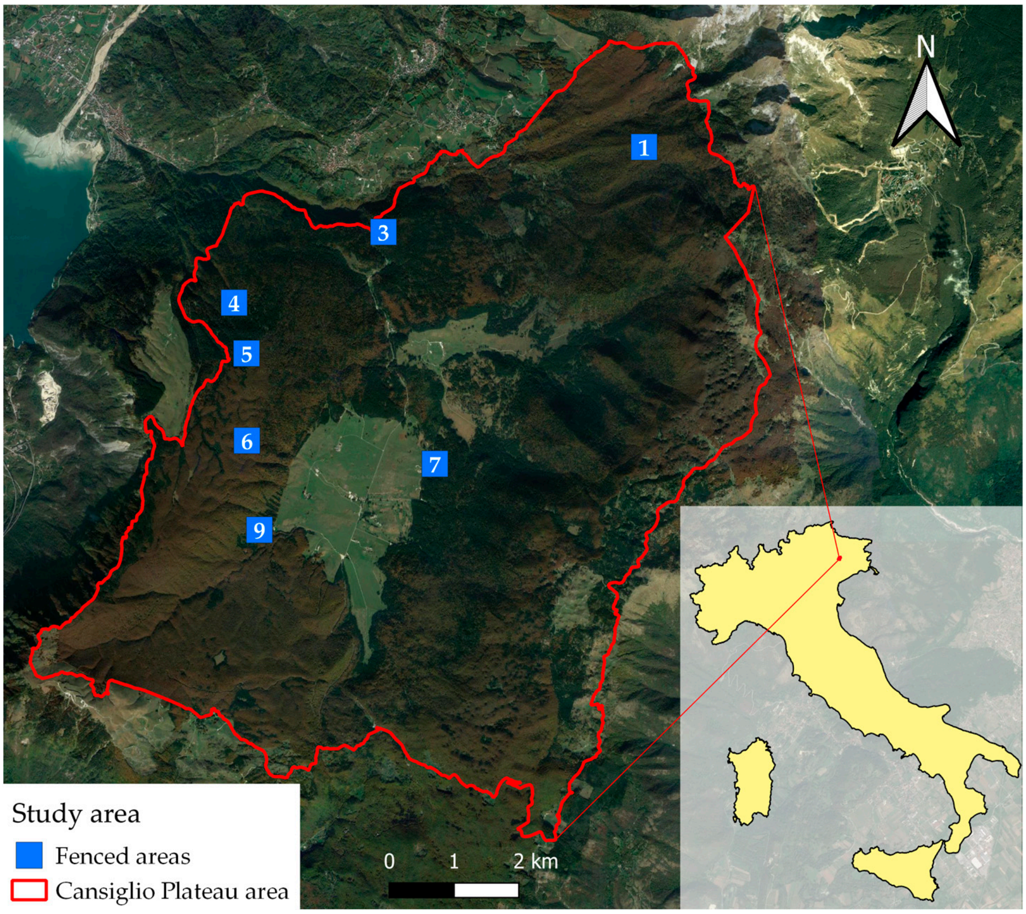



**Figure 1.** Location of the seven fenced areas within the Cansiglio Forest, in northern Italy. Each blue square represents a fenced area and displays its assigned ID number (Map data ©2024 Google, Satellite image https://www.google.it/maps accessed on 16 March 2024).

We can summarize the initial information on the undergrowth at the time of fencing for one of the first five pairs of fences. Although this pair is no longer operational, it provides useful insights indicating that the initial conditions of the undergrowth were similar across each pair. Between 2004 and 2009, the height growth rate in three initial height classes (50 cm, 70 cm and 90 cm) was consistently higher in the unfenced areas. By 2009, the mean heights in the initial classes were 50 cm, 85 cm and 114 cm in the unfenced areas, compared to 100 cm, 136 cm and 176 cm in the fenced areas [16]. This clearly indicates that the initial conditions were similar and that the fences had a significant effect on growth rate, so the difference might be attributed to the fence.

### 2.2. Sampling Approach

The study began with an observational and qualitative description of the areas of interest. This was followed by establishing transects for collecting vegetation data. Transects were marked along the diagonals of the square-shaped fenced areas using two plastic tape measures, as in another study conducted to evaluate the impact of ungulates on vascular plant species [19]. For comparative purposes, adjacent control areas identical in size and shape to the fenced areas were utilized [17]. These control areas were marked on the ground with wooden stakes at the vertices to allow for continuation of the study in the future. The layout of the transects is shown in Figure 2, where measure tapes are represented by blue dotted lines.

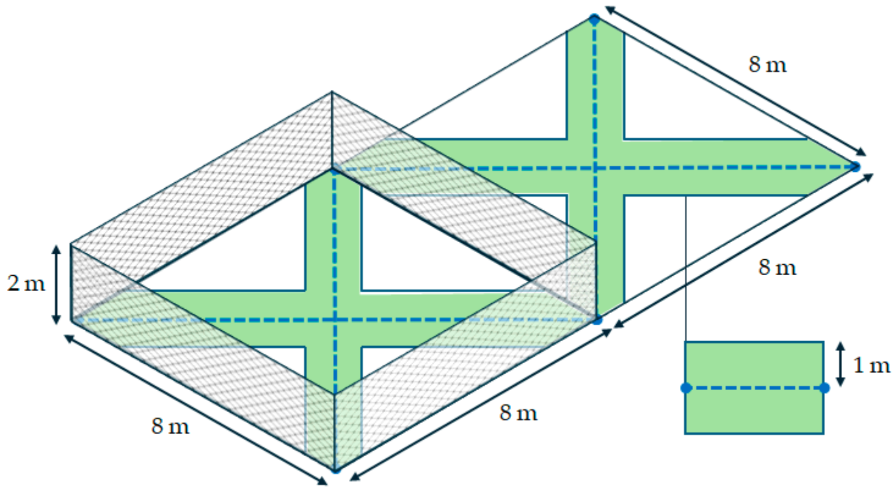



**Figure 2.** Example of a fenced plot with an unfenced replica, where blue dotted lines indicate transects for observing herbaceous and shrub individuals at 10 cm intervals. A green depicted 1 m buffer includes all tree saplings with heights between 20 cm to 250 cm, identified and measured for height.

Surveys recorded the scientific names of vascular species at 10 cm intervals along the 11.3 m diagonal transects, with a total of 113 points per diagonal of the 8 m by 8 m square plots. At each point, up to four vascular species were recorded, up to a maximum height of 250 cm. The maximum height was set at 250 cm due to the possibility of deer browsing during the winter season, when the snow cover on the ground can allow the animals to reach higher levels [20]. Where vascular plants intersected the perpendicular projection of the reading points on the tape measure, they were recorded. The tallest individuals' height in the shrub layers was measured at each reading point to estimate average height inside and outside the fenced areas.

Tree species regeneration data were collected within a one-meter buffer as indicated in Figure 2, using methods from earlier studies [17]. The total surface area of this buffer is 37.25 $m^2$ for each sampling plot. Within this buffer, all tree regeneration individuals with heights ranging from 20 to 250 cm were identified and measured. The presence of ungulate browsing traces on tree regeneration individuals was also recorded. Data collection occurred in July 2022.

*2.3. Data Analysis*

Data were analyzed using R software (version 4.2.2). A generalized linear mixed model implemented in the glmmTMB package [21] was used to investigate significant differences in shrub height and tree regeneration inside and outside the fenced areas. Due to positively skewed data, a gamma distribution was implemented for the shrub height analysis [22,23]. Shrub layer cover was analyzed by calculating the cover percentage at all shrub-present reading points along the transects, employing a glmmTMB model with a beta distribution suitable for proportion data [24]. Tree regeneration density was analyzed using a Poisson distribution glmmTMB model, appropriate given the nature of the data [25]. Each model included plot pairs by their ID numbers as a random factor to account for potential variations across different locations [26].

Further analyses searched for significant differences in Ellenberg indicator values for light (L), soil moisture (U) and soil nutrients (N) [27] inside and outside the fenced areas. These numerical values are assigned to plant species based on their preference for specific environmental conditions, such as, in this case, light, moisture and nutrient availability, and must be calibrated by correcting for regional deviation of each species [27]. In order to account for these differences, the values were estimated using the dataset of Italian vascular flora, applying a weighted approach based on species abundance along the transects to calculate average indicators across plots, considering plot IDs as random factors [28,29].

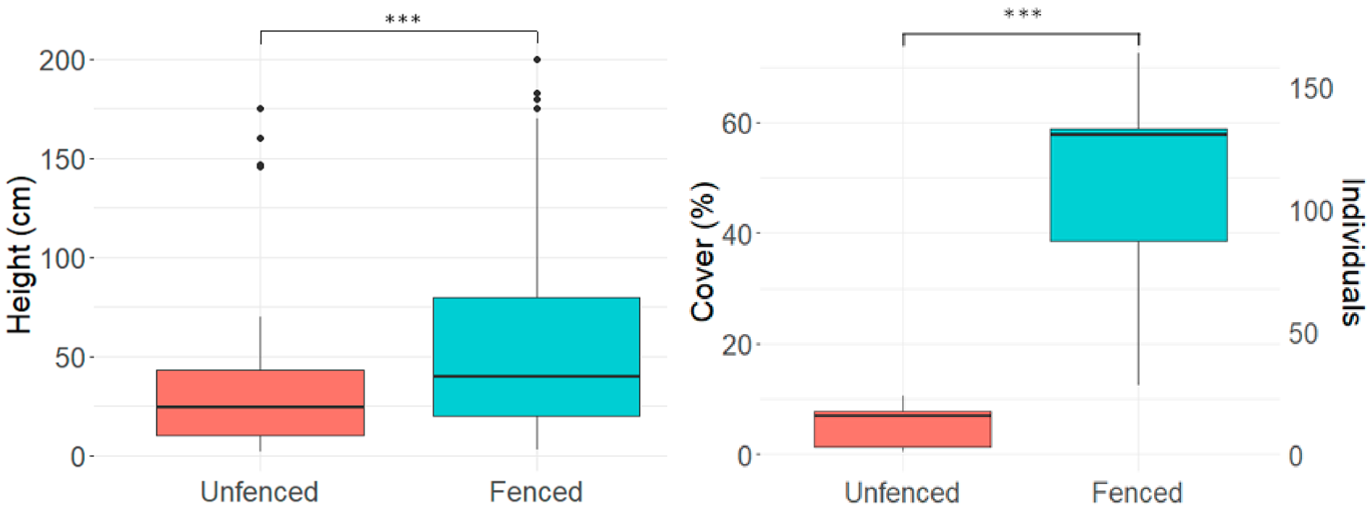
A linear mixed-effects model was used due to the normal distribution of residuals [30]. The same linear mixed-effects model was also used to search for significant differences in number of species found inside and outside the fenced areas. The statistical assumptions were checked using the DHARMa package [31].

Lastly, the presence of species associated with the fenced condition was investigated using a multi-level pattern analysis (multipatt) algorithm from the indicspecies package [32]. This method calculates the indicator value (IndVal) of species, which combines species abundance and frequency data to identify species strongly associated with specific site conditions and tests its significance using permutation tests to determine if the observed associations are statistically significant [32,33].

## 3. Results

### 3.1. The Shrub Layer

The statistical analysis of the data revealed significant differences in the structure of the shrub layer between these conditions. Figure 3 visually illustrates these differences through boxplots that depict shrub layer height and cover in both fenced and unfenced areas.



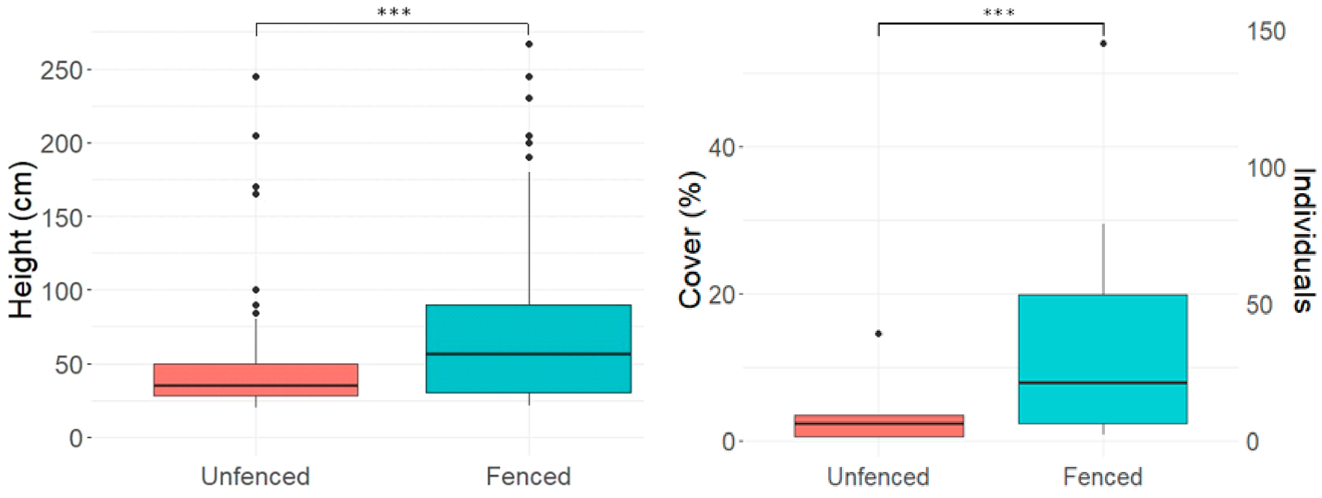

(**a**) (**b**)

**Figure 3.** The shrub layer: (**a**) Shrub height (cm) in unfenced and fenced areas; (**b**) shrub cover (%) and average number of individuals in unfenced and fenced areas (***: significant differences with $p < 0.001$).

The results indicate that the shrub layer height in fenced areas was 1.74 times higher than in unfenced areas, with an average height of 51.3 cm within the fences compared to 29.6 cm outside ($p < 0.001$). Additionally, the shrub layer cover was significantly greater in fenced areas: 11.3 times higher than in unfenced areas. Specifically, the estimated cover within fenced areas was 47.23%, compared to only 4.18% in unfenced conditions ($p < 0.001$). A total of 1582 reading points were analyzed in both the fenced and unfenced areas. In fenced areas, understory presence was observed at 761 reading points, significantly higher than the 84 reading points in unfenced areas.

### 3.2. The Tree Regeneration

The statistical analysis of the data revealed significant differences in the structure of the tree regeneration layer between these conditions. Figure 4 visually illustrates these differences through boxplots that depict both tree sapling heights and number of individuals in fenced and unfenced conditions.




(**a**) (**b**)

**Figure 4.** The tree regeneration: (**a**) Tree regeneration height (cm) in unfenced and fenced areas; (**b**) tree regeneration cover (%) and average number of individuals in unfenced and fenced areas (***: significant differences with $p < 0.001$).

The results indicate that the height of the tree regeneration layer was 1.76 times higher in fenced areas compared to unfenced ones, with an average height of 77.9 cm inside the fences versus 44.1 cm outside ($p < 0.001$). A total of 351 tree seedlings were observed, with 286 found within fenced areas and 65 in unfenced areas. Additionally, the average number of individuals within the fenced areas was 4.28 times higher than outside, with an estimated 20.18 individuals in fenced areas compared to 4.72 individuals in unfenced areas ($p < 0.001$). The estimated average density was 5418 individuals per hectare in fenced conditions and 1267 individuals per hectare in unfenced conditions. In addition, all tree regeneration individuals observed outside the fenced areas were at least partially browsed by ungulates.

### *3.3. The Vascular Plant Species Richness*

As for the comparative analysis of the number of vascular species found inside and outside the fenced areas, Figure 5 provides a visual representation of the findings through boxplots.

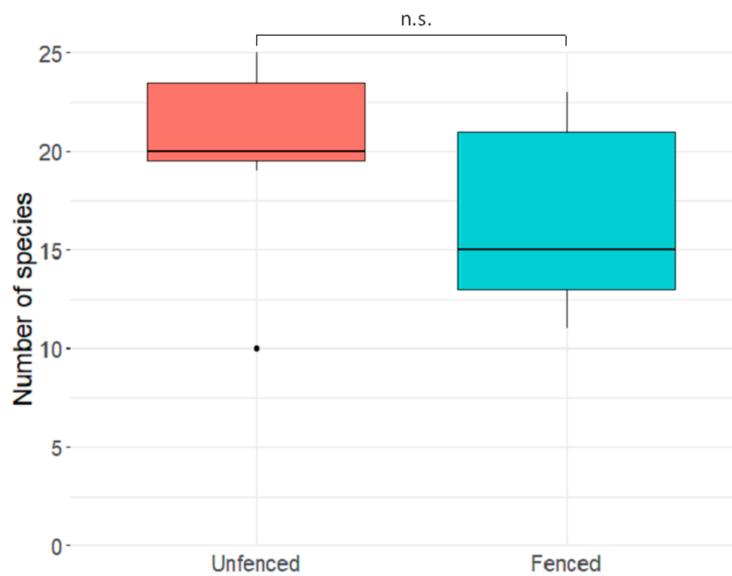



**Figure 5.** Comparison of species number in fenced and unfenced areas (n.s.: not significant differences).

In total, 72 vascular plant species were identified. The analysis revealed that the difference in number of vascular species between fenced and unfenced areas was not statistically significant ($p = 0.154$), with an average of 20 species found outside the fenced areas and 17 within.

### *3.4. The Ellenberg Indicator Values*

Regarding the Ellenberg indicator values estimated in both fenced and unfenced areas, Figure 6 uses radar charts to visually represent these values, highlighting significant differences only for the soil nutrients indicator.

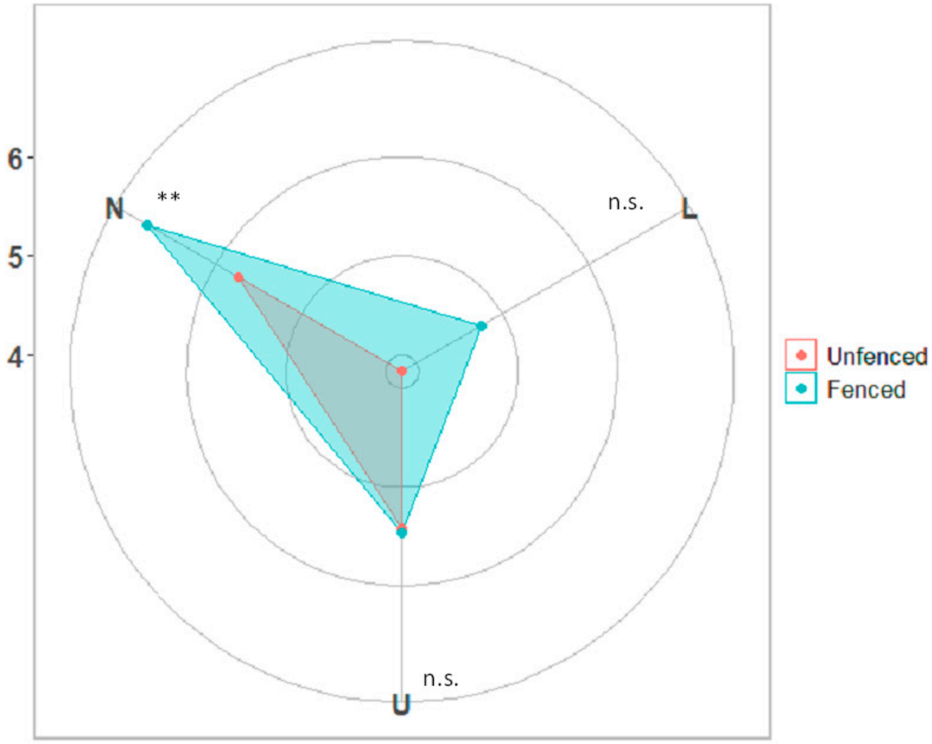



**Figure 6.** Comparison of average Ellenberg indicators in fenced and unfenced areas, soil nutrient (N), moisture (U) and light (L) indicators are reported (n.s.: not significant differences, **: significant differences with $p < 0.01$).

The analysis showed no significant differences in light availability (L indicator) between the fenced and unfenced areas, with estimated mean L values of 3.99 and 3.24, respectively ($p = 0.144$). Soil moisture (U indicator) also showed no significant differences, with mean values of 6.46 in fenced areas versus 6.19 in unfenced areas ($p = 0.766$). In contrast, the soil nutrient (N) indicator showed a statistically significant difference, with a mean value of 5.67 inside fenced areas compared to 4.58 outside ($p < 0.01$). This significant variation is attributed to the different distribution of *Rubus* spp. within the fenced areas.

### *3.5. The IndVal Indicator Values*

The analysis of species associations between fenced and unfenced areas revealed significant relationships with certain species. *Rubus caesius* L. and *R. idaeus* L. showed strong associations with the fenced condition, with indicator values of 0.923 and 0.951, respectively ($p = 0.005$ for both). Conversely, *Galium odoratum* (L.) Scop. displayed a slightly significant association with the unfenced condition ($p = 0.067$), with an indicator value of 0.756. Similarly, *Fragaria vesca* L. demonstrated a moderate association with the unfenced condition, sharing the same indicator value of 0.756 as *G. odoratum*, although its *p*-value was slightly higher ($p = 0.074$).

## 4. Discussion

As observed in previous studies [3–5,7,11], significant differences were found in the composition and structure of the understory between fenced and unfenced areas. Notably, fenced areas contained a higher number of individuals and demonstrated greater average heights compared to the unfenced areas.

The 1.74 times greater height and 11.3 times greater cover within fenced areas suggest that browsing pressure not only limits shrub growth but also affects the spatial distribution and density of shrub species. This aligns with studies by Boulanger et al. [2] and Meier et al. [3], which found that ungulate browsing can suppress shrub layer development, leading to significant ecological shifts in forest structure. These findings also align with those reported by Pedrotti et al. [11] in an adjacent region, who noted a substantial increase in tree regeneration and understory individuals within fenced areas after 30 years.

The non-significant difference in overall vascular species richness between fenced and unfenced areas ($p = 0.154$) suggests that while fencing alters the structure of the understory, it does not necessarily increase the number of species. This finding is consistent with studies by Bucher et al. [4] which observed that fencing primarily affects species composition and abundance rather than species count. Meier et al. [3] even observed a significant decrease in the diversity of the undergrowth vegetation within fenced ungulate exclosures.

Despite no significant differences in the total number of species between the two conditions, IndVal analysis supported the hypothesis of specific species associations with both fenced and unfenced areas. The high palatability of *Rubus* [34,35] and strong preference by deer, especially in winter [2], has already been confirmed by its strong association with the fenced condition [7]. Furthermore, the slight association of *G. odoratum* with the unfenced condition suggests selective browsing effects on the undergrowth, given the species' lower palatability to deer [36]. Although *F. vesca* is highly palatable to deer [34], its moderate association with the unfenced condition, as observed by Simončič et al. [7], could be due to reduced ground cover in these areas where the understory is more heavily browsed by ungulates. This study found significantly lower shrub layer cover in unfenced areas, suggesting that while ungulate browsing detrimentally impacts certain species, it may favor the establishment of others [3,7].

Ellenberg indicator values showed no significant differences in environmental conditions between the fenced and unfenced areas, except for the soil nutrients (N) indicator. The disparity in N values can be attributed to the higher presence of *Rubus* within fenced areas, known for their higher N indicator values [28]. These results are consistent with those of Dufresne et al. [13], where the authors found a reduction of nitrogen demanding species with an increased population of ungulates. This serves as further evidence of the impact of deer on the area's flora.

The substantial increase in tree sapling height and density within fenced areas, with heights averaging 77.9 cm compared to 44.1 cm in unfenced areas, indicates that browsing effectively impedes tree regeneration. The observed differences in tree regeneration densities, 5418 individuals per hectare in fenced conditions versus 1267 in unfenced, highlight the critical role of physical barriers in mitigating browsing impacts. However, regarding tree regeneration composition, despite previous studies attributing the lack of silver fir regeneration in the Cansiglio Forest primarily to deer browsing [14,17], this study did not find a significant association of the species with the fenced condition. Contrary to the hypothesis, this result suggests that browsing might not be the sole cause of the phenomenon. In fact, other studies [37,38] have indicated that factors like seed consumption by birds and rodents and potential fungal attacks, along with forest management practices, also influence the regeneration dynamics of silver fir [6,39]. Additionally, climate change can impact the growth of silver fir [40], but results are not consistent [41]. Several factors other than climate might affect regeneration of silver fir, including stand composition, free space availability and improper silviculture [42]. These findings call for a broader consideration of factors affecting forest regeneration and understory development and composition. We did not collect specific information to answer this question.

## 5. Conclusions

This study underscores the significant impact of fencing on the composition and structure of understory vegetation in the Cansiglio Forest. Fenced areas exhibited a higher number of individuals and greater average heights, supporting the hypothesis that shrub and tree regeneration layers thrive better in the absence of ungulate browsing. The results corroborate findings from previous research, such as Pedrotti et al. [11], which documented increased tree regeneration in fenced areas.

Future research should aim to establish additional study replicates, ensuring that their number is balanced across diverse site and stand structure conditions, including areas with reduced tree cover. This approach will help assess the impact of ungulate browsing on tree layer development in clearings as well as the effect on the provisioning of ecosystem services. This focus is driven by the significant effects of disturbances such as storm Vaia [43] and the recent return of wolves to the area [44], which may influence ungulate dynamics and, consequently, forest species regeneration, especially under these changing conditions. Also, there is no doubt that future studies in the area should combine the study of fenced areas, with data collected to complete the understanding of the dynamics of coexistence of beech and silver fir in the area and the interplay between biotic, abiotic and management factors, mechanisms driving forest regeneration. These studies must be integrated into forest management plans to ensure their coupling with practical sustainability.

**Author Contributions:** Conceptualization, T.S., J.R. and E.R.B.; methodology, T.S., J.R. and E.R.B.; investigation, T.S. and E.R.B.; formal analysis, T.S., S.I. and E.R.B.; resources, T.S. and T.C.; writing—original draft, E.R.B. and T.S.; visualization, E.R.B. and T.S.; supervision, T.S.; project administration, T.S. and J.R.; funding acquisition, T.S., J.R. and T.C. All authors have reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** S.I., T.C. and T.S. acknowledge that this study was, in part, carried out within the Agritech National Research Center and received funding from the European Union Next-GenerationEU (PIANO NAZIONALE DI RIPRESA E RESILIENZA (PNRR)—MISSIONE 4 COMPONENTE 2, INVESTIMENTO 1.4—D.D. 1032 17/06/2022, CN00000022). This manuscript reflects only the authors' views and opinions, neither the European Union nor the European Commission can be considered responsible for them.

**Data Availability Statement:** The original data presented in the study are openly available in [Research Data Unipd] at [https://doi.org/10.25430/researchdata.cab.unipd.it.00001314 (accessed on 13 June 2024)].

**Acknowledgments:** We would like to thank the staff of the 'Agenzia veneta per l'innovazione nel Settore primario—Veneto Agricoltura' for their assistance during the data collection phase and for granting permission to access the study sites. We also deeply appreciate the suggestions provided by Michele Bottazzo and the assistance of Marco Cunico during the data collection phase.

**Conflicts of Interest:** The authors declare no conflicts of interest.

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