

Article

Interspecific Growth Reductions Caused by Wild Ungulates on Tree Seedlings and Their Implications for Temperate *Quercus-Fagus* Forests

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Abstract: Ungulate impacts on forest understory alter tree species composition, with cascading effects on forest functions and resilience against future climate conditions. Indeed, the ungulate browsing pressure on tree seedlings is species-specific and causes contrasted growth reductions that alter tree recruitment rates. Untangling the effects of browsing from the effects of the other factors driving regeneration success is required to guide the forest and ungulate management. In particular, *Fagus sylvatica* L. strongly dominates temperate *Quercus-Fagus* forests close to their climax, and it remains unclear if controlling ungulate populations can maintain tree species diversity in naturally regenerated forests. We addressed this question by monitoring 734 pairs of fenced and unfenced 6-m² plots across a broad gradient of *Cervus elaphus* L. abundance in Belgian *Quercus-Fagus* forests managed by continuous cover forestry. Seedling height, density, and vegetation cover were monitored from 2016 to 2021. Species diversity and ecological affinity for light, temperature, and atmospheric humidity conditions were computed from these measures. With ungulates, the mean growth of *Betula pendula* Roth. and *Sorbus aucuparia* L. was negligible, whereas, without ungulates, their growth was higher than the growth of other species. With ungulates, the growth of *Fagus sylvatica* L. and *Picea abies* (L.) H. Karst was higher than other species. *Quercus* (*Quercus petraea* (Matt.) Liebl and *Quercus robur* L.) growth was the lowest in all conditions. Finally, *Carpinus betulus* L. was heavily browsed but still grew higher than its competitors with ungulates. Ungulate browsing can then severely affect seedling growth and likely reduce the diversity of future recruited trees. In the study area, browsing unfavored the regeneration of the species that are less shade tolerant, more-drought tolerant, and more-heat tolerant. It thus accelerates the natural succession and reduces forest resilience to heat and drought events. Such an observation was found valid over a wide study area encompassing contrasting levels of *Cervus elaphus* L. abundance. Combining further reductions of ungulate populations with foodscape improvement is likely required to maintain species diversity in these forests.



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1. Introduction

Wild ungulates alter forest understory, including tree regeneration, causing direct and cascading effects on numerous biological groups and forest functions [1,2]. As ungulates consume herbaceous vegetation, they affect seedling establishment, density, and growth. Recruitment bottlenecks can occur for the most palatable and the least resistant species, causing shifts in the long-term forest structure and composition [3–7].

A recent literature review documented that the majority of studies addressing ungulate impacts on forest climate adaptation strategies considered ungulates as a threat [8]. Ungulates indeed most strongly alter the regeneration of those species with the best potential for adaptation to future climate in several contexts [9,10]. The altered succession may also lead to a less diversified tree composition. However, interspecific interactions increase the resilience and resistance of trees to disturbances, especially extreme heat and drought events [11–18].

Maintaining admixed tree species in the widespread European *Quercus-Fagus* forests is essential to foster their resilience and resistance to climate change [19], especially since *Fagus sylvatica* L. vitality losses have been reported throughout Europe [20]. However, *Fagus sylvatica* L. has a strong competitive advantage over most early succession species both in the canopy and the understory [21–23]. The share of early succession species, which regeneration has been lacking these last decades (Figure S7), may thus shrink further as forests may get closer to their climax, largely dominated by *Fagus sylvatica* L. [24].

Forest managers need methods to quantify ungulate impacts on regeneration, as it could be one of the most determinant drivers of the undergoing succession process [24,25]. These impacts are density-dependent [26], and both the environmental and the socioeconomic contexts have favored a steady increase of the ungulate abundances in numerous regions of Europe and northern America in the late 20th and early 21st centuries [27–31]. Recreational hunting is the main factor limiting ungulate populations [28,32–34], but hunting pressure is unlikely to meet societal and sylvicultural optima without science-based quantification of ungulate impacts [35]. To date, large-scale scientific monitoring of vegetation remains limited [36]. Ungulate impacts have rarely been conducted or else have yielded only limited direct information on the true impact of ungulate populations on regeneration success at a large scale.

Bio-indicators have been used to detect the variations of ungulate impact on forest regeneration. Monitoring bio-indicators at a large scale has been considered a cost-effective solution [37] to follow changes in ungulate impacts on forest ecosystems. Such indicators can serve to set annual ungulate culling targets and adapt them to the observed changes. Nevertheless, the suggested bio-indicators (e.g., browsing rates, [38]) do not per se give indications for achieving regeneration goals [39] because their relation to regeneration success remains unknown or limited to a few tree species and forest contexts [40]. Seedling growth rates vary with browsing intensity and may be positively affected by moderate browsing [41].

Enclosure–exclosure experiments, based on the comparison of vegetation protected from ungulates with a reference situation, have provided information about achievable regeneration goals and how ungulates prevent them from being reached locally. Unfortunately, reported experiments are based on small numbers of sampling plots (usually fewer than 30, [2]) that are often of large size (up to 20 ha). Considering the high heterogeneity of regeneration and ungulate pressure in space and time and the number of influencing variables, their outcomes are thus hardly generalizable to a whole region or management district [42–44].

To gain a better understanding of ungulate impacts on forest regeneration at a large scale, we monitored a large set of fenced and unfenced small plots ($n = 734$, area = 6 m²) installed in secondary *Quercus-Fagus* forests managed by continuous cover forestry [45,46]. Seedling height and density were monitored for 5 years. The results were used to infer how ungulates might affect future forest composition and adaptation to climate conditions across a wide range of ungulate abundance.

We hypothesized (i) that ungulates would reduce herbaceous and seedling height, cover, and density with possible positive effects on the seedling growth; (ii) that the seedling growth reductions would be species-specific; and (iii) that it would (a) promote the regeneration of *Fagus sylvatica* L. and *Picea abies* over the other admixed species by altering the mean growth ranks of the seedling species (b) erode species diversity, (c) and alter the ecological aptitudes of seedling communities.

2. Materials and Methods

2.1. Study Area

The study area encompassed 3085 km² of forest in Wallonia (Figure 1). The climate is warm and temperate without a dry season and with a mild summer (Cfb in the Köppen-Geiger classification system or continental in the Metzger climate classification of Europe [47]).

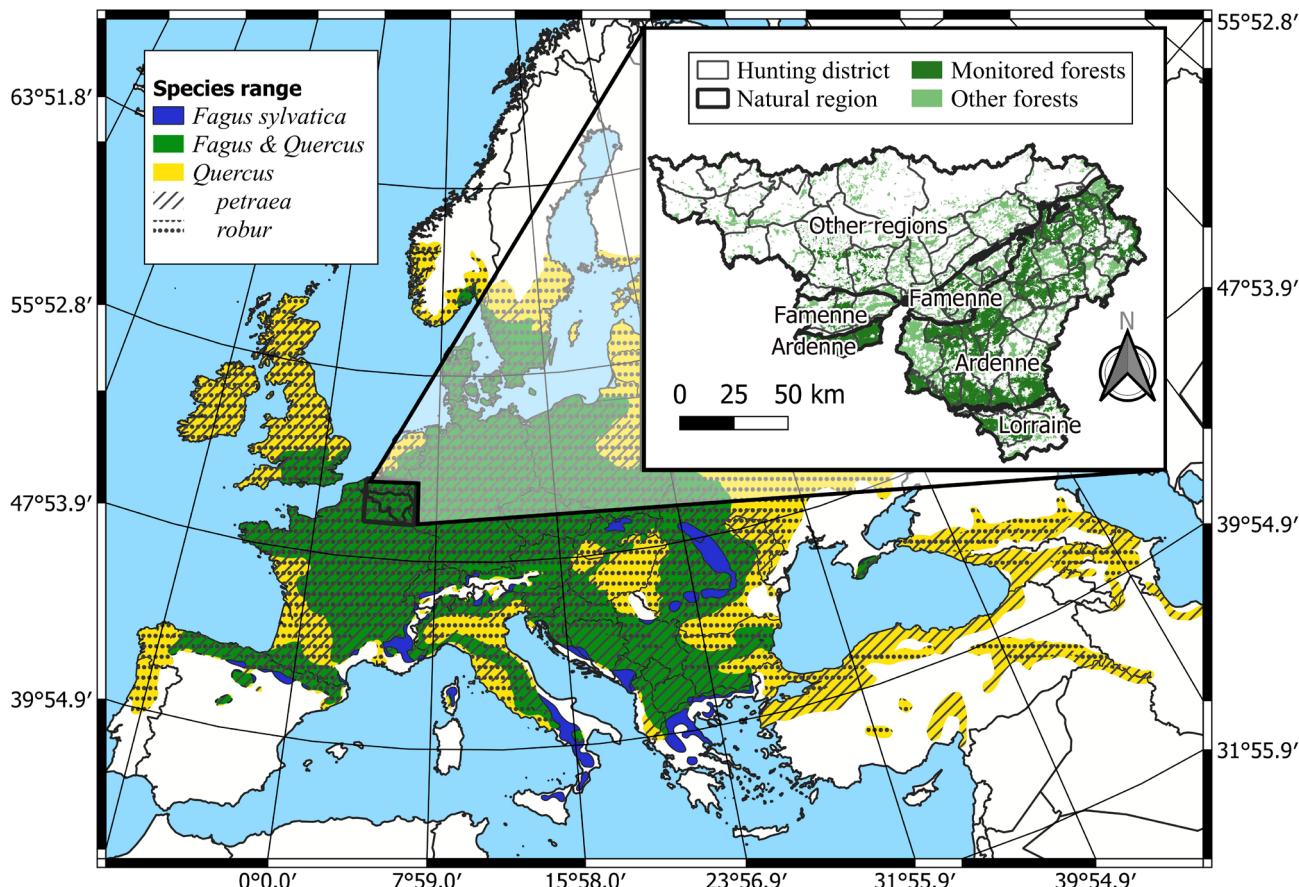


Figure 1. Study area within the distribution range of *Fagus sylvatica* and *Quercus petraea* & *robur* in Europe (adapted from [48]). Inset map: forest areas are displayed with the regional forest mask of Wallonia [49]. Monitored forests are the forest areas in the hunting districts where enclosure-exclosure network was installed.

Fagus sylvatica L. is the main climax species in most of the area, but alternative climax vegetation occurs depending on particular climatic and soil constraints, which differ between the three main natural regions, Ardenne, Famenne, and Lorraine (Figure 1). In particular, Sphagnum-rich *Betula pubescens* wood and Western Hercynian woodrush-hawksbeard *Quercus* forests are the climax vegetation in the highest parts of Ardenne, where the mean temperature is lower and precipitations more abundant. The Famenian *Quercus-Carpinus betulus* forests are the climax vegetation in Famenne, where soils are clayey (Table A1).

Forests are managed in our study area and can be qualified as secondary forests. Tree composition often differs from those of the climax vegetation. Coniferous and broadleaved forests cover respectively 55% and 45% of the forest area; 76% of the coniferous area is dominated by *Picea abies*. These stands are mainly even-aged plantations. *Quercus* and *Fagus sylvatica* L. are the main deciduous species. Altogether, they cover 32% of the forest area. Of the broadleaved forests, 85% have been naturally regenerated, 52% are uneven-aged, and 40% are coppice-with-standards. The stands are generally harvested every 12 years with

selective felling. *Fagus sylvatica* L. regeneration is abundant, whereas *Quercus* regeneration has been lacking for several decades [50]; (Figure S7).

The *Cervus elaphus*, the *Capreolus capreolus* L. and the *Sus scrofa* are the three native ungulate species living in the study area. Their abundance has risen sharply since 1980 [27]. Ungulate population management is coordinated at the level of hunting districts. These districts cover forest areas ranging between 18.1 km² and 258.5 km². At the district level, the *Cervus elaphus* populations ranged between 0 and 16.5 animals per km² in 2017. No accurate estimations of *Capreolus capreolus* or *Sus scrofa* densities are available. The mean number of culled animals per km² of forest ranged between 0 and 6.7 *Cervus elaphus*, between 0.8 and 6.3 *Capreolus capreolus*, and between 1.4 and 21.6 *Sus scrofa*. *Ovis gmelini* and *Dama dama* are also present sporadically in the study area.

2.2. Data Collection

Systematic sampling of the forest regeneration was conducted. In all, 930 pairs of plots were set up across the study area in 2016, 734 of which were measured until 2021. Their location was randomly selected among the intersections of a 400 × 400 m grid. The field operators selected the closest location to the grid intersection where regeneration was expected to thrive. The plots were installed only where light availability was judged sufficient, where the competing herbaceous vegetation (e.g., *Rubus fruticosus* L. or ferns) was not abundant, and where seed trees were present nearby. Areas with advanced regeneration (seedlings taller than 50 cm) were avoided.

The selected sampling points measured until 2021 were mainly located in broadleaved stands ($n = 539$ pairs of plots) of *Quercus* and *Fagus sylvatica* L. and less frequently in coniferous or mixed stands ($n = 192$) of *Picea abies* and *Pseudotsuga menziesii* (Mirb.) Franco. The type of the stand was not registered for the three plots. Most of the sampling points ($n = 690$) were in forests managed by continuous cover forestry [45] and where selective felling had been carried out in the two previous years. A total of 30 plots were set up in forest clear-cuts, and the regeneration method was not registered for 14 plots.

The plot pairs were composed of two 6 m² circular plots set 4 m apart from center to center. One plot was fenced with a 1.6 m high wooden lattice (Figure A1). The second plot remained unfenced and accessible to ungulates. The operators endeavored to set up the two plots in closely similar environmental conditions.

Vegetation and regeneration development were assessed in 2016, 2017, 2018, 2020, and 2021. Data were collected during the vegetation season, mostly in July and August. Species identity and height of the five tallest seedlings (dominant seedlings) were collected. In addition, the number of seedlings per species was monitored using classes (0, 1–2, 3–6, 7–9, 10–20, 21–50, >50 seedlings). The total cover (%) of all the understory woody species (seedlings of tree species including admixed species such as *Sambucus* sp. *Cytisus scoparius* and *Rubus fruticosus* L. L., *Rubus idaeus*, *Calluna vulgaris*), the total cover of all non-woody species except *Pteridium aquilinum* (e.g., *Deschampsia* sp., *Luzulla* sp., etc.), and the total cover of all bryophyte species were estimated visually on the Braun-Blanquet scale. Additionally, the cover of five understory species (*Rubus fruticosus*, *Rubus idaeus*, *Calluna vulgaris*, *Pteridium aquilinum*, and *Cytisus scoparius*) was estimated separately. These five species are known to frequently affect regeneration development and/or are important food items for ungulates [51,52].

2.3. Data Analysis

We compared the temporal dynamics of understory growth and composition in the fenced and unfenced plots. The plot-level observations were the height of the tallest seedling of each species, the mid-class value of seedling density, and the mid-class value of cover. These values were averaged by treatment and by species. Analyses were performed using R Statistical Software (v4.1.2; R Core Team 2021).

Max-*t* tests were used to compare the species means across years successively in the fenced and in the unfenced plots. This test is robust for unbalanced and heteroscedastic

datasets [53]. Max-*t* tests were performed with the R package multcomp 1.4–17 [54] and sandwich 3.0–1 [55,56].

The effect of the treatment (fencing) on the response variables was tested yearly and by species with paired Student *t*-tests when the differences were normally distributed or with the Wilcoxon rank sum test otherwise [57]. Mixed linear models were adjusted to estimate the effect of ungulate abundance and species-specific growth reductions. However, all available ungulate abundance variables had a negligible contribution, both when predicting the differences between fenced and unfenced plots and when predicting the growth in unfenced plots using fenced plots growth among predictive variables (Figures S8–S11).

Zero counts had to be allowed for the tests, as not every studied species was observed in all plots. For a given species, only the plots where that species was present were taken when computing a specific average of seedling height, density, and cover for the entire study area. However, to assess the treatment effect with the paired *t*-test (or its non-parametric substitute), a zero value was assigned to the plots with a zero count when the species was recorded in the other paired plot.

We went on to investigate how ungulates affected regeneration diversity and the tolerance of successful seedlings to future climate conditions. We computed the species richness of the dominant seedlings (*S*) and ecological affinity indices (EAI_S). The species richness of the dominant seedlings was defined as the number of species present in each plot. EAI were estimated for temperature (EAI_T), atmospheric humidity (EAI_H), and light EAI_L following a methodology adapted from [58]. The (EAI_S) were computed as the mean species aptitude score (SAS) for temperature, humidity, and light weighted by the seedling height (Equation (1)). The species aptitude scores were extracted from the baseflor database [59]. The species aptitude scores are bounded between 0 and 9, with maximum value corresponding to the most thermophilous, hygrophilous, and light-demanding species.

$$EAI_v = \frac{\sum_{i=1}^5 SAS_i \times H_i}{\sum_{i=1}^5 H_i} \quad (1)$$

where EAI_v is the ecological affinity index of the variable v (temperature, atmospheric humidity, or light), and SAS_i and H_i are respectively the species aptitude score and the height of seedling i , one of the five tallest seedlings in the plot. The seedlings smaller than 50 cm were discarded to compute *S* and EAI since small seedlings have lower survival probability and are less influenced by ungulates than taller seedlings [2]. The plots without observed seedlings counted for zero in the computation of *S* and were discarded to compute EAI . Similarly to the other variables, the indexes were computed per plot and treatment. The differences were tested with Student *t*-test or Wilcoxon rank sum test.

3. Results

3.1. Species Frequency

The six most frequently occurring species were *Fagus sylvatica* L., *Quercus*, and *Picea abies* (observed in >300 plots) and, to a lesser extent, *Carpinus betulus* L., *Betula pendula* Roth., and *Sorbus aucuparia* L. (observed in 100–150 plots) (Figure 2). When present in a plot, these species generally had at least one dominant seedling among the five dominant seedlings. The only exception was *Quercus*, for which dominant seedlings were found in only 60% of the plots with *Quercus* seedlings (Figure 2). Other species were all present in less than 100 plots (Figure S1).

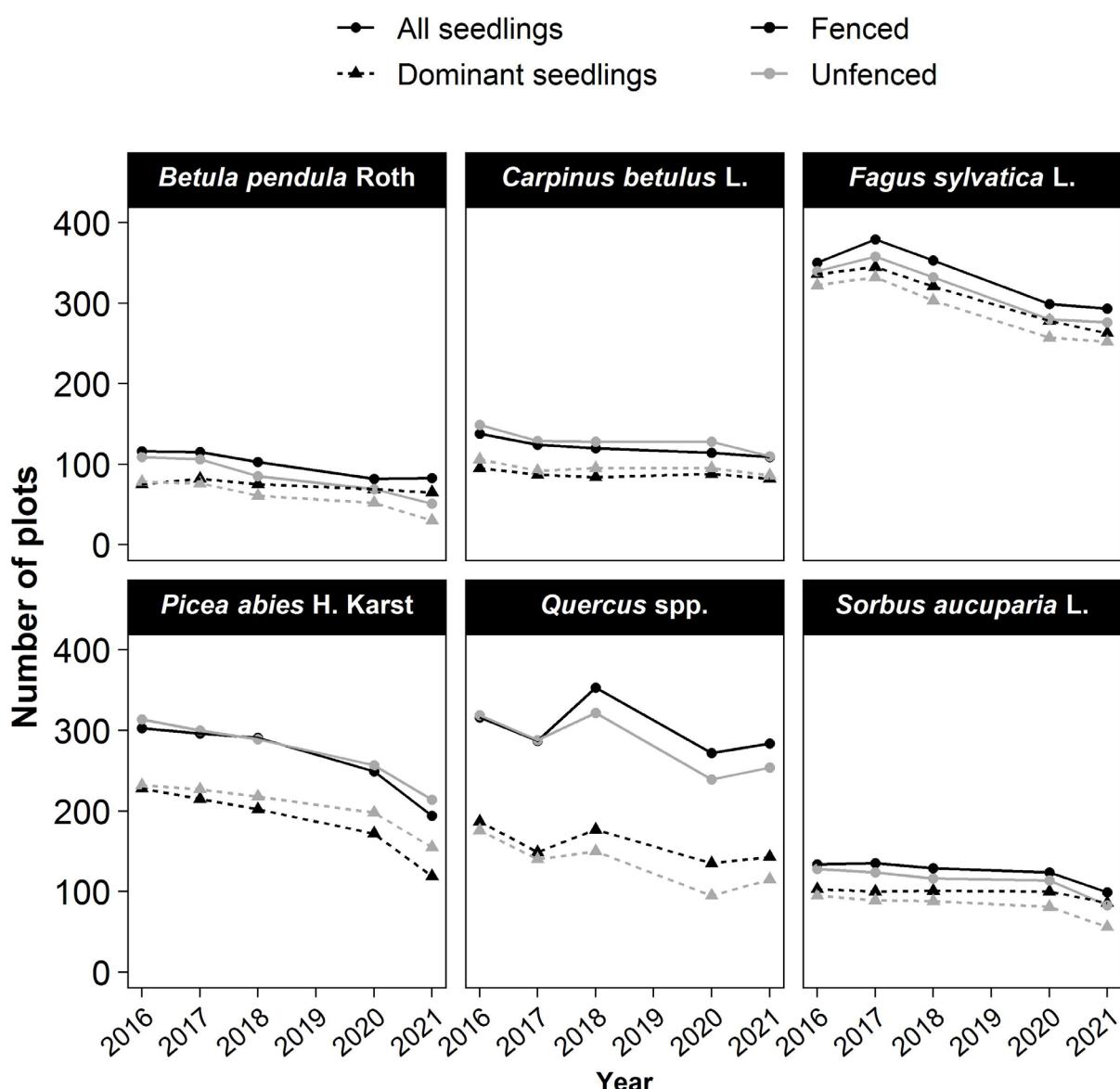


Figure 2. Changes of species occurrence over time. The number of occurrences for a species is the number of plots where a seedling of the species was present among all seedlings or only among the five tallest in the plot (dominant seedlings) of 734 plots. Symbol (dot or triangle) are used to represent the seedlings. (Dot for all seedlings, Triangle for dominant seedlings.) Colors for the treatment (dark grey: fenced—light grey: unfenced).

The occurrence of every species declined with time in both fenced and unfenced plots (Figure 2 and Figure S2). In the fenced plots, the decline in the number of plots where the species was present was moderate for most species (dominant: 10%–21%; all seedlings: 10%–30%) but substantial for *Picea abies* (dominant: –48%; all seedlings: –36%). In the unfenced plots, the decline in plot number was moderate only for *Fagus sylvatica* L. and *Carpinus betulus* L. (~–20%), whereas it was greater for *Picea abies* (–33%), *Quercus* (–35%), *Sorbus aucuparia* L. (–41%), and especially, birch (–62%). The differences between treatments in the proportion of plots with the occurrence of a species were the highest for *Sorbus aucuparia* L. (fenced: –17%; unfenced: –41%) and birch (fenced: –13%; unfenced: –62%). *Picea abies* was the only species for which the plot number decreased more in the fenced than in the unfenced plots.

3.2. Vegetation Cover

In 2016, woody and nonwoody cover and seedlings' heights were low (cover < 16.72% and height < 32 cm). No significant treatment differences of woody cover were observed in 2016, except for higher bryophytes cover in fenced plots and *Calluna vulgaris* L. (Figure 3). Woody cover (Figure 3) increased significantly over time. This increase was stronger in the fenced plots (Figure 3). In 2021, it reached 19.21% (± 2.03) in the fenced plots against only 13.62 (± 1.69) in the unfenced plots. In contrast, the total cover of non-woody species was slightly lower in 2021 than in 2016 and did not differ between treatments (Figure 3).

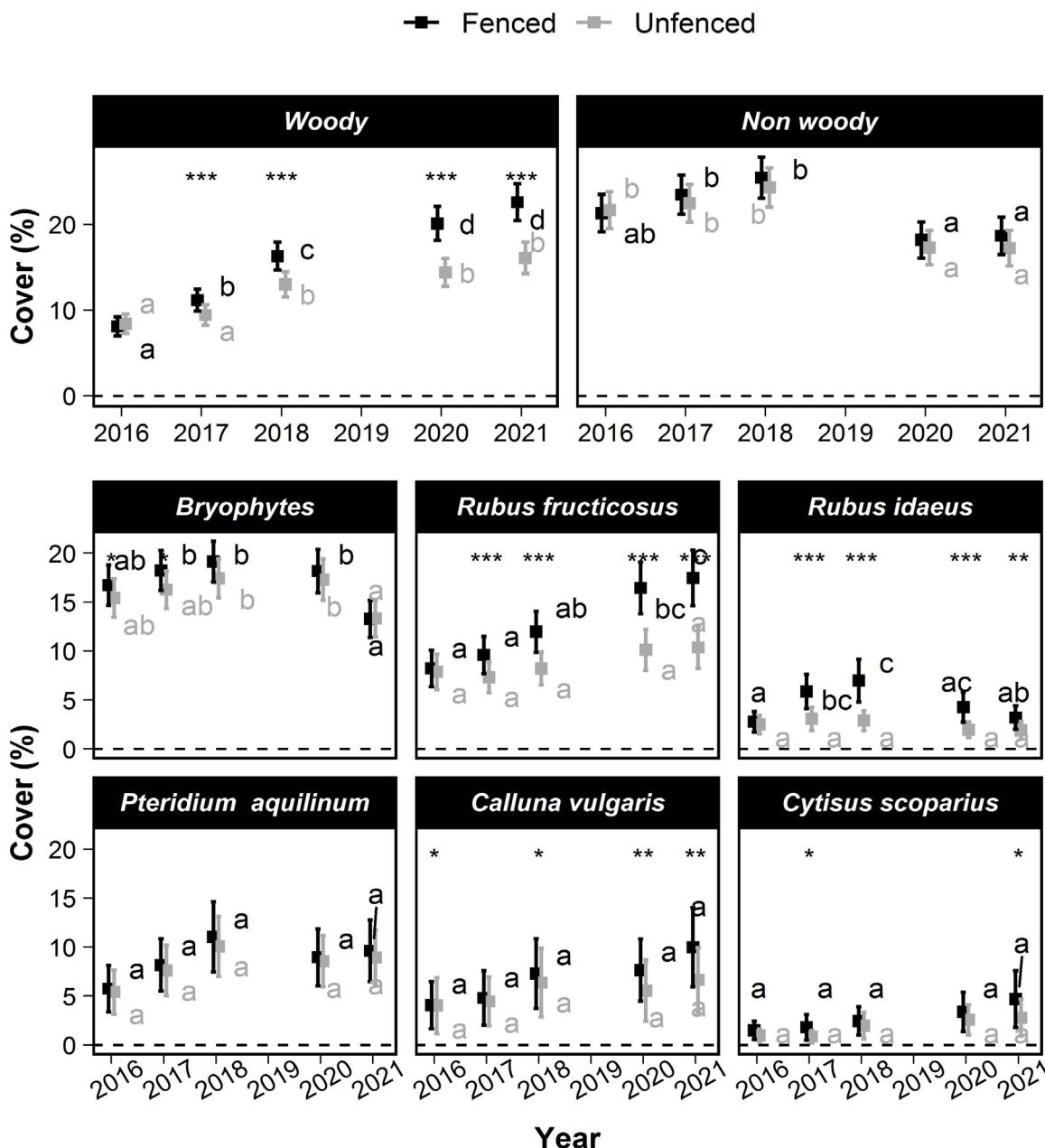


Figure 3. Changes over time of the mean cover of various taxa in the understory vegetation. The squares show the mean cover values, and the error bars show the 95% confidence intervals. Within a treatment, means that are not significantly different are labeled with a common letter according to the max-t test. Significant treatment effects are symbolized with stars depending on the degree of significance (*: $0.01 < p \leq 0.05$; **: $0.001 < p \leq 0.01$; ***: $p < 0.0001$).

Taking species individually, the cover of *Rubus fructicosus* L. increased significantly between 2016 and 2021. The *Rubus fructicosus* L. cover was 8.22% (± 1.87) in 2016 and reached only 10.36% ($\pm 2.15\%$) in unfenced plots versus 17.46% ($\pm 2.83\%$) in the fenced plots. *Rubus idaeus* L. cover did not increase between 2016 (2.76% $\pm 1.04\%$) and 2021 (3.2% $\pm 1.2\%$). However, the *Rubus idaeus* L. cover temporarily reached a higher value in the fenced plots only (6.98% $\pm 2.2\%$ in 2018). The cover of *Calluna vulgaris* L., *Cytisus scoparius* (L.) Link and *Rubus idaeus* L. remained approximately constant, but their mean cover became significantly higher in the fenced than in the unfenced plots in 2021.

3.3. Seedling Height

In 2016, the *Quercus* seedlings were significantly shorter than the other species (14 cm \pm 2 cm in fenced plots), and *Fagus sylvatica* L. was significantly taller than the other species (32 cm \pm 3 cm) (Figure 4). No significant differences were observed between treatments, except for *Carpinus betulus* L., which was significantly higher in the unfenced plots ($p = 2.6 \times 10^{-4}$). In 2021, seedlings of all species except *Picea abies* were significantly taller in the fenced than in the unfenced plots. The fenced-unfenced difference in the mean height ranged from more than 59 cm for birch and *Sorbus aucuparia* L. (corresponding to 54% of the mean height in fenced plots) and only –3 cm for *Picea abies*.

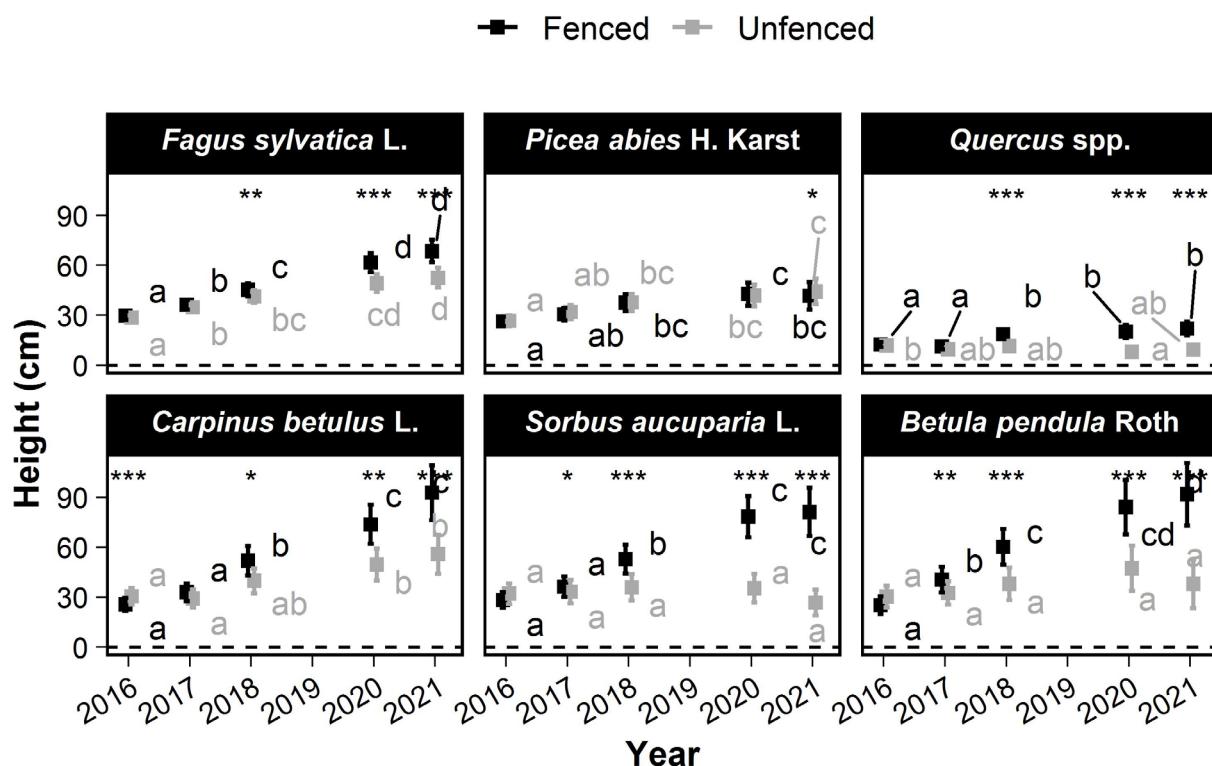


Figure 4. Changes over time in the mean height of the six most frequently occurring tree species. The squares show the mean height. Error bars show the 95% confidence intervals. Within a treatment, the means without a common letter are significantly different according to the max-t test. Significant treatment effects have stars depending on the level of significance (*: $0.01 < p \leq 0.05$; **: $0.001 < p \leq 0.01$; ***: $p < 0.0001$).

Compared with the fenced plots, height was reduced for all species, and the rank of species height growth was altered in the unfenced plots (Figure S4). In fenced plots, *Carpinus betulus* L., *Sorbus aucuparia* L., and birch grew fastest ($>11 \text{ cm} \cdot \text{year}^{-1}$), while *Quercus* and *Picea abies* grew slowest ($<1.4 \text{ cm} \cdot \text{year}^{-1}$). *Fagus sylvatica* L. growth was intermediate ($8 \text{ cm} \cdot \text{year}^{-1} \pm 1.1 \text{ cm}$). In the unfenced plots, *Fagus sylvatica* L. grew fastest ($5 \text{ cm} \cdot \text{year}^{-1} \pm 1 \text{ cm} \cdot \text{year}^{-1}$), followed by *Carpinus betulus* L. and *Picea abies* ($>2.3 \text{ cm} \cdot \text{year}^{-1}$),

and *Sorbus aucuparia* L. and *Quercus* grew most slowly ($<0.6 \text{ cm} \cdot \text{year}^{-1}$). The growth rate of birch was $2 \text{ cm} \cdot \text{year}^{-1}$ (± 2.8), which was intermediate (but with no significant difference) between those of *Sorbus aucuparia* L. and *Picea abies*.

3.4. Seedling Density

No significant differences were observed between treatments in 2016 (Figure 4). Between 2016 and 2021, seedling density varied little except for some species and treatments. Seedling density significantly increased only for *Quercus* in the fenced plots ($1.4 \pm 0.2 \text{ seedlings m}^{-2}$ in 2016 vs. $2.1 \pm 0.3 \text{ seedlings m}^{-2}$ in 2021). Seedling density decreased for *Picea abies* ($2.2 \pm 0.3 \text{ seedlings m}^{-2}$ in 2016 vs. $1 \pm 0.2 \text{ seedlings m}^{-2}$ in 2021) and for *Fagus sylvatica* L. only in the unfenced plots ($1.9 \pm 0.2 \text{ seedlings m}^{-2}$ in 2016 vs. $1.2 \pm 0.2 \text{ seedlings m}^{-2}$ in 2021). No other significant changes occurred between 2016 and 2021.

The treatment effect on seedling density was significant mostly for *Fagus sylvatica* L. and after masts (*Quercus* in 2018: $2.6 \pm 0.3 \text{ seedlings m}^{-2}$ in fenced vs. $2.1 \pm 0.3 \text{ seedlings m}^{-2}$ in unfenced plots; *Fagus sylvatica* L. in 2017: $2.9 \pm 0.3 \text{ seedlings m}^{-2}$ in fenced vs. $2.2 \pm 0.2 \text{ seedlings m}^{-2}$ in unfenced plots). The density increases were mitigated, and the drops were accentuated in unfenced plots in comparison with that in fenced plots (Figure 5). The treatment effect on seedling densities was tiny or insignificant for all other species (less than $0.2 \text{ seedling} \cdot \text{m}^{-2}$). Nevertheless, this decrease was marked relative to the low densities of *Sorbus aucuparia* L. and birch seedlings: in the fenced plots, their density was twice that observed in the unfenced plots. The treatment effect was insignificant for *Picea abies*. *Carpinus betulus* L. was the only species with more seedlings in the unfenced plots in 2021.

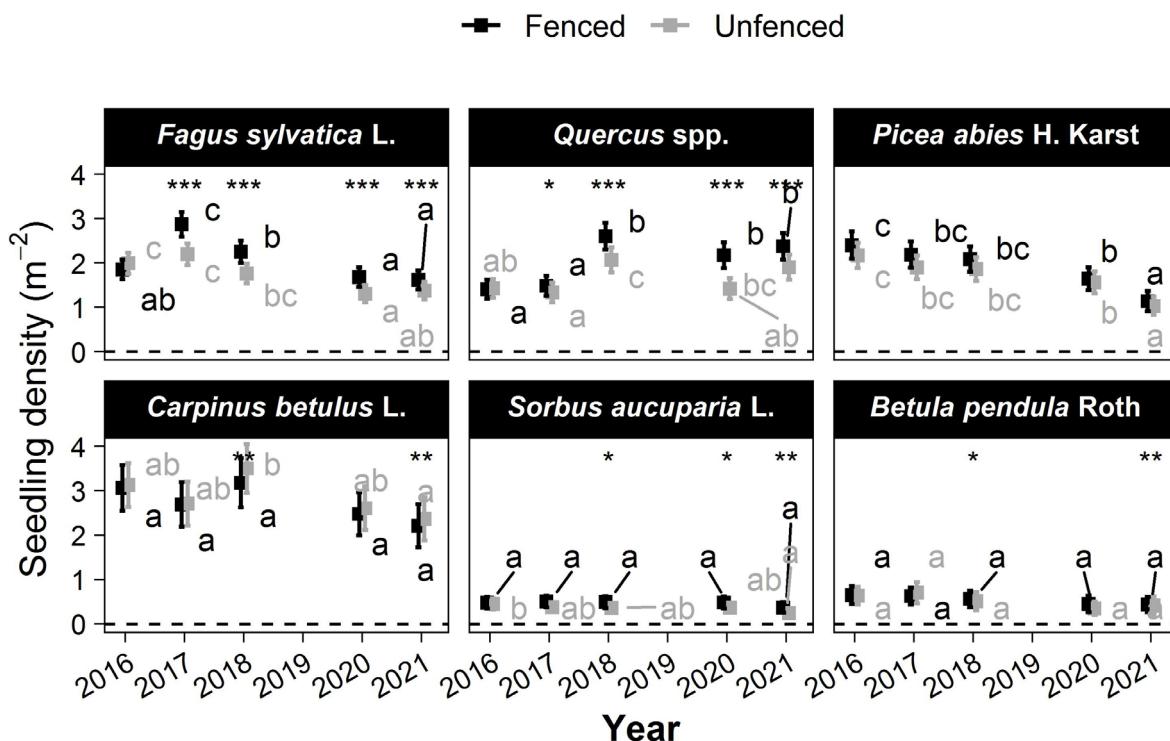


Figure 5. Changes over time in the mean seedling density of the six most frequently occurring tree species. The squares show the mean height. Error bars show the 95% confidence intervals. Within a treatment, the means without a common letter are significantly different according to the max-t test. Significant treatment effects have stars depending on the level of significance (*: $0.01 < p \leq 0.05$; **: $0.001 < p \leq 0.01$; ***: $p < 0.0001$).

3.5. Species Richness and Ecological Aptitudes

The treatment modified the composition of the species richness (S) and ecological aptitude indexes (EAI) of the seedlings higher than 50 cm. At the end of the study period, more species were present in the fenced plots than in the unfenced plots. Fenced plot communities were also less shade tolerant, more drought, and more heat tolerant in the fenced plots than in the unfenced plots (Figure 6).

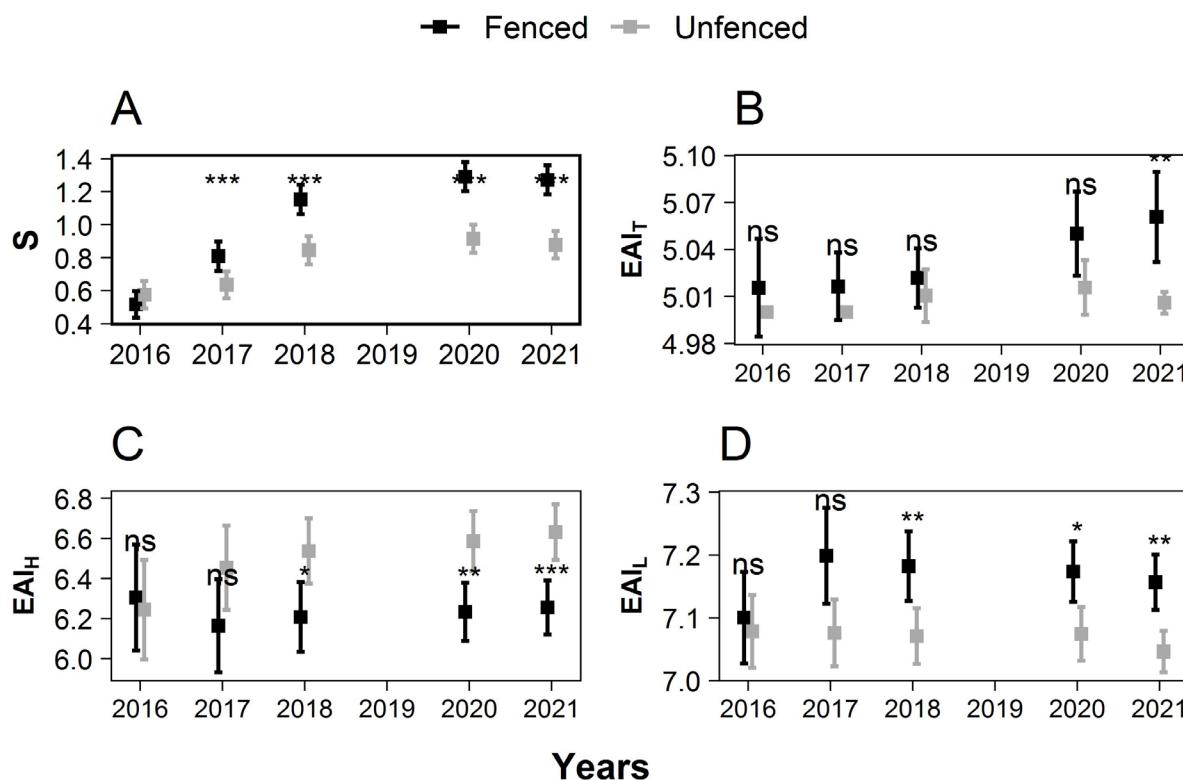


Figure 6. Change over time of species richness (A) and height-weighted ecological aptitudes indexes of the five tallest seedlings for temperature (B), atmospheric humidity (C), and light (D). High EAI values are obtained for species whose ecological niche is characterized by an elevated temperature, humidity, and light. The squares show the mean value. Error bars show the 95% confidence intervals. Significant treatment effects have stars depending on the level of significance (ns: $p > 0.05$; *: $0.01 < p \leq 0.05$; **: $0.001 < p \leq 0.01$; ***: $p < 0.0001$).

No significant differences were observed between treatments in 2016 for any EAI. The species richness of the seedlings (height > 50 cm) increased with time. This rising trend was more pronounced in the fenced than in the unfenced plots, resulting in a large difference between the two treatments in 2021, 1.27 ± 0.09 species.m $^{-2}$ in the fenced plots, versus only 0.88 ± 0.08 species.m $^{-2}$ in the unfenced plots in 2021 (significant difference, $p = 37.60 \times 10^{-15}$).

In 2021, the mean EAIT was higher in the fenced plots (5.061 ± 0.029) than in the unfenced plots (5.006 ± 0.007), and the mean EAIL was higher in the fenced plots (7.157 ± 0.044) than in the unfenced plots (7.046 ± 0.033). The mean EAIH was lower in the fenced plots (6.256 ± 0.135) than in the unfenced plots (6.631 ± 0.139) ($p < 0.05$).

Observations differed, however, across the three natural regions. The differences between fenced and unfenced plots showed the same patterns and significance for coniferous and broadleaves in Ardenne but were smaller and non-significant in Famenne, where the number of plots was also smaller (Figures S5 and S6).

4. Discussion

4.1. Study Scope and Limitations

Although our observations were limited to the first stage of natural regeneration development (Figure S3), we could confidently identify future tree recruitment bottlenecks. We measured mostly small seedlings that had not yet escaped ungulate browsing [24,42,60,61], but over the study period, we observed significant species-specific changes in seedling growth and, consequently, in the ranking of species in terms of height growth or competitiveness. As the tallest seedlings have the highest survival probability [23] and as species growth ranking generally remains stable [62], we can assume that the future species composition of tree recruitment can be deduced from seedling growth ranks. In particular, species with negligible growth can fail to recruit, which is well in line with the regeneration failures observed in the study area [50,63] (Figure S7).

Furthermore, our observations of ungulate impact on seedling growth are valid on a wide range of *Cervus elaphus* abundance and, unfortunately, an unknown abundance of *Capreolus capreolus*. Abundance indicators available are reliable for *Cervus elaphus* [43], contrarily to *Capreolus capreolus*, which can also have a severe impact on regeneration [64]. Indeed, *Capreolus capreolus* is a browser and income-breeder species whose population growth rate is sensitive to hunting pressure for lower browsing pressure levels [37,65,66] and is negatively affected by *Cervus elaphus* abundance since their diet partially overlaps. The diet of *Capreolus capreolus* is more restrictive than the diet of the *Cervus elaphus* [51,52,67–69]. Harvest statistics are thus susceptible to poorly representing the standing population of *Capreolus capreolus* because of the higher density dependence of population growth rate than red deer in the conditions of the study.

4.2. Interaction between Seedlings, Herbaceous Vegetation, and Browsing

Understory vegetation may substantially shape recruitment niches for tree seedlings, with both positive and negative effects on recruitment probability. A large cover of competitive understory vegetation may increase seedling mortality but also divert browsing from less palatable tree seedlings [61,70]. In parallel, browsing may facilitate seedling growth by preferentially consuming competitive species (e.g., *Rubus fructicosus* L.) or facilitate herbaceous species by preferentially consuming tree seedlings [70–72]. The results of this study show that ungulates reduced woody cover but did not affect non-woody cover (Figures 1 and 3). This is consistent with a recent meta-analysis [2]. This finding was nevertheless obtained for initial conditions with low cover of understory competing vegetation. Different results could have been expected if the initial conditions had been different [72], and particularly if the cover of competitive species such as *Rubus fructicosus* L. had been higher, as often occurs when canopy cover is lower.

4.3. How Browsing Alters Seedling Competition and Likely Recruitment

4.3.1. Seedling Height

Growth observations give information on the species' regeneration niches (the sets of conditions in which species naturally thrive). Walters (2020) [61] identified three distinct species groups (broad, high-light, and nowhere) according to their regeneration niches shaped by light, browsing pressure, and understory vegetation competition. Walters's study was carried out in eastern North America, but the species niches and their respective species groups are also relevant to our study.

The broad species are more shade-tolerant and less affected by browsing. Their juvenile growth in high-light conditions is lower than that of high-light species, but their seedlings can survive at lower light levels than the other groups. Their sit-and-wait strategy allows the establishment and maintenance of seedling populations (i.e., advance regeneration) that can then rapidly develop when the conditions become more favorable and thus dominate regeneration over wide ranges of stand density and ungulate pressure [62,72]. The high-light species are shade- and browsing-sensitive, but their growth is faster than other species under low canopy cover. In such conditions, they escape vegetation competition and

ungulate pressure. The nowhere species are browsing-sensitive and shade-intolerant. They are outcompeted by the other species, faster growing over the full range of light availability. As a consequence, they have no regeneration niche in forests.

Our results indicate that *Sorbus aucuparia* L. and *Betula pendula* Roth are high-light species, *Fagus sylvatica* L. and *Picea abies* broad species, and *Quercus* a nowhere species. The ranking of the species is consistent with the group definitions for browsing sensitivity [6,10,25,35,42,73–75], shade tolerance [23,76], and how their growth is affected by light conditions (Figure S8). When canopy cover is low, birch and *Sorbus aucuparia* L. grow faster than other species, and ungulate pressure reduction can strongly increase their recruitment, in contrast to *Quercus*, which grows slowly and whose development is strongly affected by other competing species.

Unlike the other species, *Carpinus betulus* L. can be classified into two regeneration groups as it combines both the competitive advantages of high-light and broad species and dominates these two regeneration niches. Like high-light species, *Carpinus betulus* L. has fast growth potential (Figure 3) and is highly palatable (e.g., [42]). However, because of its architectural traits and its high seedling density (Figure 4), *Carpinus betulus* L. is also highly browsing-resistant [77,78], and its growth remained sustained (Figure 3). We note that *Carpinus betulus* L. was not evenly distributed over the study area and was found mainly in the Famenne region.

4.3.2. Seedling Density and Species Occurrence

Our results suggest that ungulate impact on seedling presence and density is limited to particular species (Figures 1 and 4). After masts, the seedling density of *Quercus* and *Fagus sylvatica* L. significantly increased in the fenced but not in the unfenced plots (Figure 4). This is probably because acorns and beechnuts, contrary to the seeds or fruits of the other species, compose the greater part of the ungulate diet in autumn and winter [28,78,79]. Variation of seedling density is assumed, however, to have little effect on the growth and survival of already established seedlings and to barely affect the future diversity of tree recruitment.

Browsing did reduce the seedling occurrence of some species, but this reduction was observed only after approximately 4 years (Figure 2). Because of browsing, some species grow sparingly in height, become dominated by less browsing-sensitive species, and gradually disappear. This was observed for highlight species in our study (Figure 2) and supported our assumption that the browsing effect on seedling growth is a good indicator of future tree recruitment, according to [80].

4.4. Ungulate Impact on Forest Diversity, Resilience, and Succession

A recent literature review [8] gathers evidence that ungulates often counteract strategies to increase forest resilience against global changes in temperate and boreal forests. Such strategies are generally based on maintaining or increasing forest tree diversity [81], promoting the species best adapted to the expected future conditions [82]. In naturally regenerated forests, regeneration is a key component of this adaptation because the regenerated species may determine forest composition for decades. Forest disturbances, including anthropic disturbances, foster the development of heat-tolerant species and thus reduces the climate debt of understory plant communities [58,83].

Our results corroborate the trend highlighted by [8] in the *Quercus-Fagus* forest managed by continuous cover forestry (Figure 6B,C). Ungulates favored *Fagus sylvatica* L., and *Picea abies* over the less frequent and more heat- and drought-adapted species. *Fagus sylvatica* L. has been negatively affected by heat and drought extremes since the 1980s [84,85], and large diebacks may occur in large portions of the current species distribution range [20]. Similarly, *Picea abies* has suffered increasingly from bark beetle outbreaks, and its distribution is expected to shrink appreciably [86–88]. As several species are more heat- and drought-tolerant than *Fagus sylvatica* L. and *Picea abies*, increasing their share in the forest species composition would reduce climate risks [89–95]. Moreover, shade-intolerant species

in a mixture with *Fagus sylvatica* L. have been shown to reduce *Fagus sylvatica* L.'s sensitivity to extremes of drought [17,18,95–97].

Both our results and the literature show frequent directional effects of ungulates on the succession dynamics but with a direction varying with the relative browsing sensitivity of the early and late succession species. Ungulates accelerate succession dynamics in *Fagus sylvatica* L.-dominated forests [19,24,97] and *Picea abies*-dominated forests [98,99], where the late succession species are least palatable for browsing. In contrast, ungulates slowed the succession dynamics in mixed *Picea abies*-*Abies alba* forests [100] and in boreal forests of balsam fir [99], where late succession species are highly palatable.

Our results showed that both ungulate impacts on species richness and forest adaptation to future climate and on succession dynamics depend on the species assemblage, explained by the site conditions. We found that these impacts were significant in the *Quercus*-*Fagus* forests of the Ardenne region but not in the *Quercus*-*Carpinus* forests of Famenne. In Ardenne, ungulates reversed the dominance of the minority high-light species, whereas, in Famenne, *Carpinus betulus* L. dominated with and without ungulate exclusion. No significant differences in EAI and species richness were therefore found between treatments in Famenne, unlike Ardenne (Figures S5 and S6).

4.5. Management Perspectives: The Need to Consider Forest Succession

Our results evidenced that ungulate exclusion creates conditions compatible with high-light species regeneration in the silvicultural context of our study. Contrarily, ungulate exclusion seems not enough to guarantee *Quercus* establishment without additional appropriate interventions to limit competition with other seedlings and shrub species [21,101–106]. The *Quercus* regeneration niche corresponds mostly to transitional grassland-forest interfaces and a few specific forest sites where competition with other tree species is limited [107–109]. Nevertheless, excessive ungulate pressure potentially thwarts the installations of these two species groups and must be modulated adequately.

Population control is one of the most effective measures to mitigate the ungulate impact on forest regeneration [110]. However, as high-light species growth remained negligible, including in the parts of our study area without the presence of *Cervus elaphus* (Figures S9–S11), no credible abundance thresholds could be identified. Higher *Capreolus capreolus* and *Sus scrofa* populations could have compensated for the lower *Cervus elaphus* pressures in these areas [67]. Important *Sus scrofa* populations growth rates and increase of *Capreolus capreolus* populations growth rate below carrying capacity may raise feasibility and ethical issues to strategies only based on ungulate population control only [28,111]. Indeed hobby hunters are responsible for the majority of ungulates mortality, and their efficiency may be limited by their lack of motivation [112], falling number [31], and societal opposition [31,112–114], particularly without clear scientifically identified targets [31,35,113,114].

Cutting regimes could be instrumental in modulating ungulate pressure and recruitment of the most impacted species. Current cutting regimes, based on tree-level selective felling, create small resource hotspots for regeneration that are also resource hotspots for ungulates where their pressure on tree regeneration dramatically increases [42,60,70,115]. Such a foodscape is a typical 'herbivore pit' for the most preferred species [116]. This fine-level spatial behavior might explain why ungulate density estimated at a large scale often poorly accounts for local regeneration successes [24,70,117]. Moreover, these succession dynamics present positive feedback as tree species loss is exacerbated by high *Fagus sylvatica* L. proportion [24].

Reducing canopy cover in large areas is a promising way to counteract the species erosion caused by the natural succession process. Sharp increases in the preferred feeding resource abundance dilute ungulate impact [117] and create timely windows of opportunity for the regeneration of the most sensitive species. The benefits of such conditions as the establishment of early successional species may be decades long-lasting [118] and sustain underrepresented early successional dwelling species [119,120]. Higher stand-

and landscape-level diversity and higher ecosystem complexity could result from such a system than landscape-level homogeneous conditions not favorable to early succession installation [121–123]. Such strategies, combined with ungulate population control, have been identified as a key measure of *Quercus* regeneration success in North America [46]. Subordinating ungulate management to regeneration success and applying additional strategies such as alteration of ungulate frequentation from key regeneration areas [124] would potentially be more feasible and acceptable on such limited proportions of forest areas than long-lasting high regulation pressure generalized to the whole forest area.

5. Conclusions

Our study demonstrates the determinant impact of ungulates on the regeneration of *Quercus-Fagus* forests managed by continuous cover forestry. The analysis of 734 pairs of 6 m² fenced and unfenced plots pairs evidenced that ungulates strongly reduced the growth of the dominant seedlings, the seedling density, and the cover of herbaceous species, but no clear positive impact on seedling growth could be evidenced (i). Seedling growth reductions were species-specific (ii) and altered the ranks of the species' mean height growth in favor of *Fagus sylvatica* L. and *Picea abies* Karts ((iii) (a)). Ungulates reduced the species richness and favored a species composition less adapted to drought and heat conditions ((iii) (b–c)). Maintaining such conditions could increase risks of tree dieback if tipping points are reached for the species the less adapted to heat and drought extremes. Management strategies should be identified to increase the number of seedling species with significant height growth. Ungulate population reduction below the values sampled in this study could foster the regeneration success of *Betula pendula* Roth. and *Sorbus aucuparia* L., but is unlikely to significantly increase *Quercus* regeneration success if competition with other tree species is not controlled. Future studies should explore the benefit of a cutting regime aiming to produce a timely high abundance of palatable vegetation in the European *Quercus-Fagus* forests context. Such a management strategy could be more efficient than solely focusing on population control under the current cutting regime, as the local increase of resource utilization by ungulates thwarts the benefits of a local improvement of the growth conditions for shade-intolerant species seedlings.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14071330/s1>, Figure S1: Number of occurrences of studied tree species and of less abundant species; Figure S2: Drop of species occurrences; Figure S3: Distribution of the height of the highest seedling by plot regardless of the species and its evolution over time; Figure S4: Mean growth of the highest seedling by plot; Figure S5: Evolution over time of species richness (S) and height-weighted ecological aptitudes in Ardenne; Figure S6: Evolution over time of species richness (S) and height-weighted ecological aptitudes in Famenne; Figure S7: Mean of the basal area spread by tree girth classes. Data were provided by Regional Forest Inventory of Wallonia (SPW-ARNE). Only the plots that fitted the forest types of the article were included. The forest types included were the Oak, Oak-beech, and Beech (Alderweireld et al. (2015)) [50]. *Quercus robur* and *petraea* and *Fagus sylvatica* contribute at least to two thirds of the basal area in these plots (single or together). Inside these plots, the 6 species presented were those observed in the highest number of plots in the fenced-unfenced network. The plots selected for this figure had a basal area equal to, or greater than 10 m²/ha during the two inventory cycles as most the plots in the fenced-unfenced network. This figure shows that the tree species diversity is very weak in the oak-beech forests of Wallonia. Moreover, the frequency distribution of basal areas of the 2 most frequent species highlight an ongoing succession process. Beech is the only pervasive species whose tree recruitment sustain stable demographic structure. In contrary, oak abundance will strongly decline if its low recruitment rate is maintained in the long term. Other species are marginal for individuals with girth higher than 20 cm; Figure S8: Distribution of growth of the 6 studied tree species vs. basal area; Figure S9: Height growth frequency distribution vs. red deer shots at forest district level; Figure S10: Height growth frequency distribution vs. spatially smoothed red deer harvests; Figure S11: Height growth frequency distribution vs. red deer abundance estimates.

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Appendix A

Table A1. Main climatic, soil, and vegetation conditions in the three main natural regions of the study area. Climate data are from Van der Perre et al. 2015. Climax vegetation was evaluated by Hendrickx and Van der Kaa, 2015 and is described following the 2020 EUNIS habitat classification [125].

	Ardenne	Famenne	Lorraine
Sampled area (km ²)	2271	320	239
Mean altitude (m a.s.l.)	425	227	322
Soil	silty	silty	sandy
Gravel fraction	sandstone/shist	shale/chalk	
Climax vegetation	Western Hercynian collinar woodrush <i>Fagus</i> forests (T1-8111), Western Hercynian woodrush-hawksbeard <i>Quercus</i> forests (T1B711), and Sphagnum-rich <i>Betula pubescens</i> wood (T1-612)	Famenian <i>Quercus-Carpinus betulus</i> forests (T1-E15)	Medio-European wood barley <i>Fagus sylvatica</i> forests (T1-7111) and Sub-Atlantic sessile <i>Quercus</i> forests (T1-B21)
Mean temperature (°C)	7.7 to 8.7	9.5	8.9 to 9.3
Mean annual precipitations (mm)	1170 to 1219	976	1170 to 1179
Duration of vegetation period (days)	151 to 163	174	163 to 168

Appendix B



Figure A1. Fenced plot (backward in wooden lattice) and unfenced plot (forward, center at wooden pole).

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