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Ungulates and succession dynamics reduce tree species richness in temperate unevenaged forests

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Wallonie service public SPW

Belgian Science Policy Office belspo

Maintaining biodiversity is required to maintain resilient forest

Applying CCF relying on natural regeneration

Future tree diversity depends on :

- Interspecific competition
- Environmental conditions
- Ungulate pressure

Ungulate populations have increased throughout Europe and North America.

Now listed as one of the main forest disturbances in Europe.

Need to better quantify ungulate impacts and understand how they affect forest functioning (e.g., to define achievable regeneration goals and set shooting plans).

ForestEurope. 2020 State of Europe's Forests
Apollonio et al. 2010 Cambridge University Press

Monitoring ungulate impacts

Bio-indicators have been developed (e.g., browsing rate). They brought valuable information but are generally poorly correlated to ungulate abundance .

Large fenced plots (up to 20 ha) have been established, but generally in small numbers providing results that are difficult to generalize.

Establishing and monitoring many small plots over a large area seems to be a promising alternative.

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Study objectives

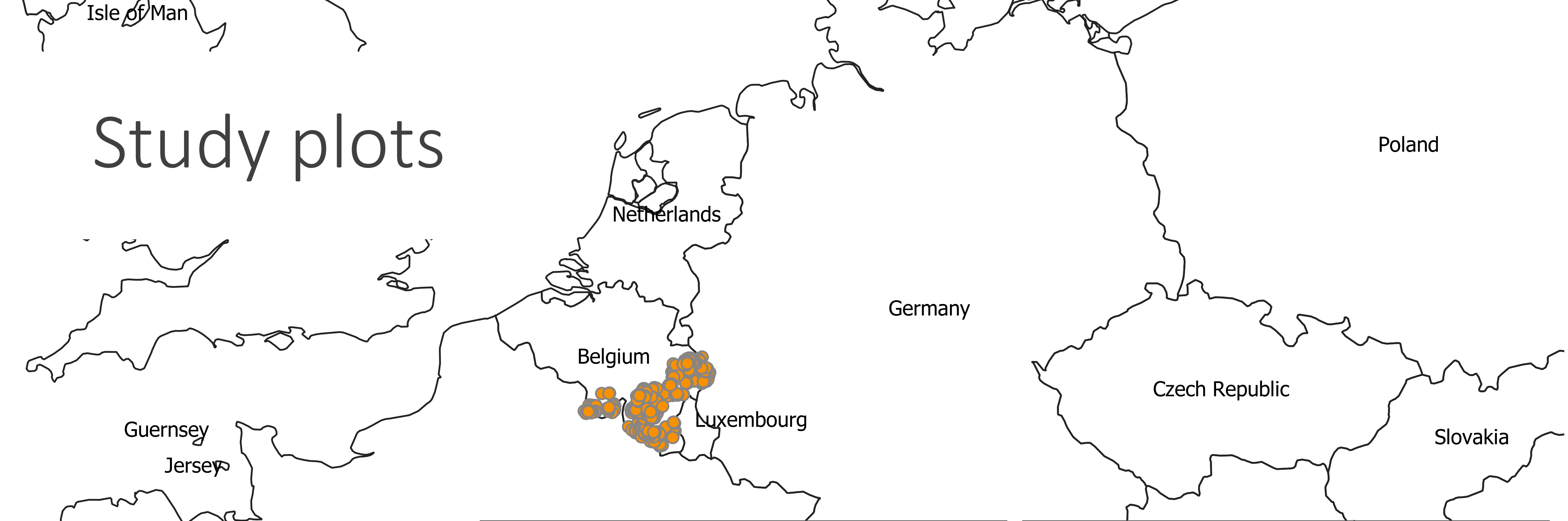
- How much ungulates reduce herbaceous and seedling height and cover over a large area ?
- Is seedling height reduction correlated with ungulate density?
- Can ungulates reduce future stand diversity (and resilience) under CCF?

Study area

7.5 – 9.0 °C

800-1300 mm/year

Study plots



73% in broadleaved stands dominated by beech and oak

27% in coniferous stands dominated by Norway spruce and Douglas-fir

Study area

Wild boar - *Sus scrofa*

1.4 – 21.6 culled animals/year/km²

Roe deer - *Capreolus capreolus*

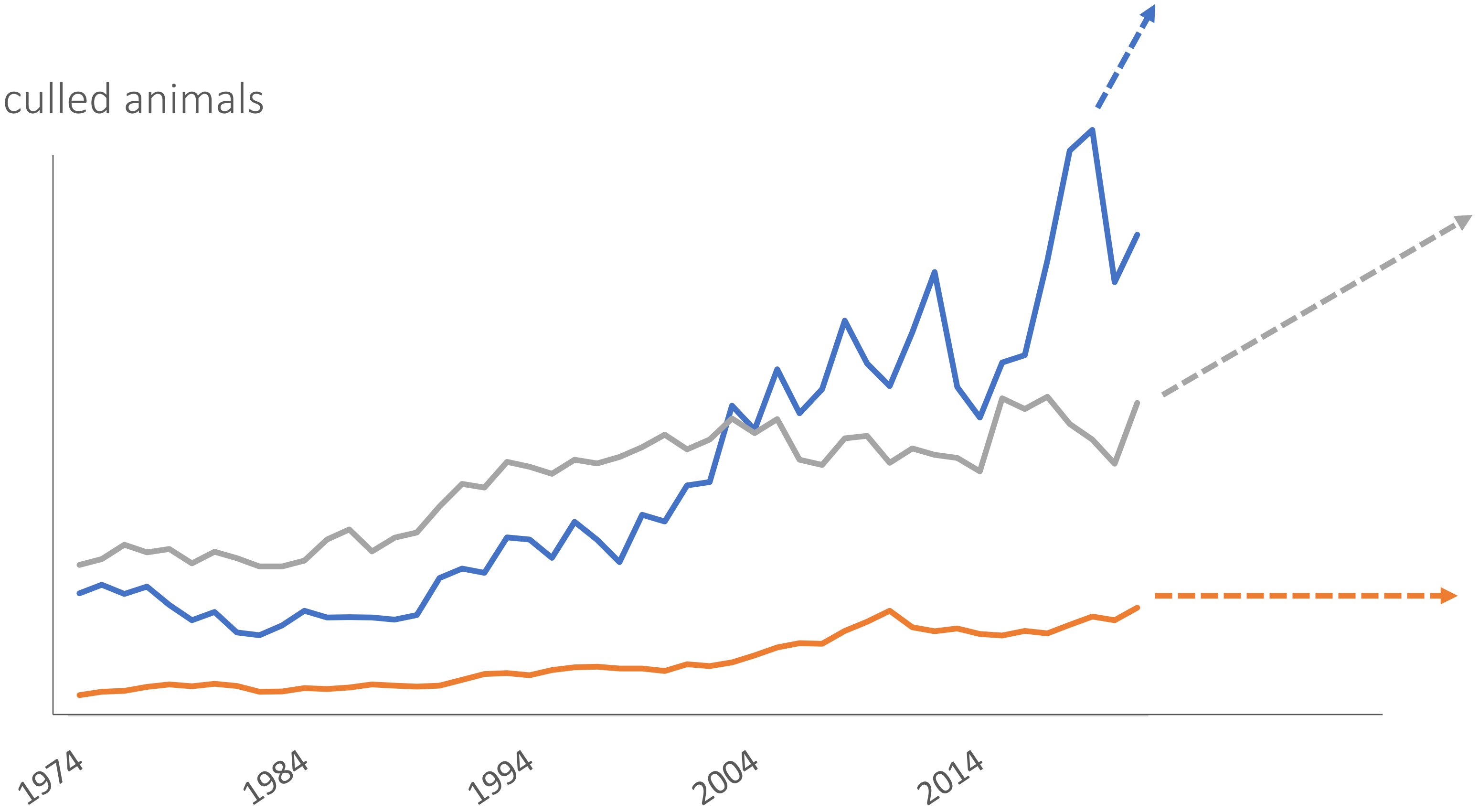
0.8 – 6.3 culled animals/year/km²

Red deer - *Cervus elaphus*

0 – 16.5 deer/km²

0 – 6.7 culled animals/year/km²

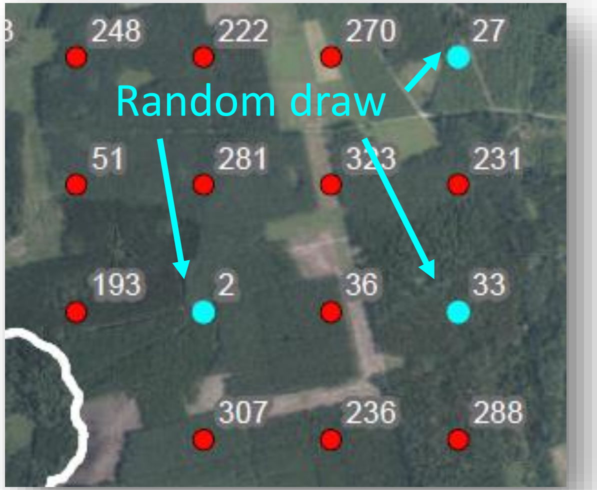
Total culled animals



Sampling scheme

1

Sampling grid (400 x 400 m)



2

Check that regeneration was expected to thrive, i.e., understory was:

- With adequate light availability
- Without abundant herbaceous vegetation
- With seed trees nearby
- Without advanced regeneration (H < 50 cm)

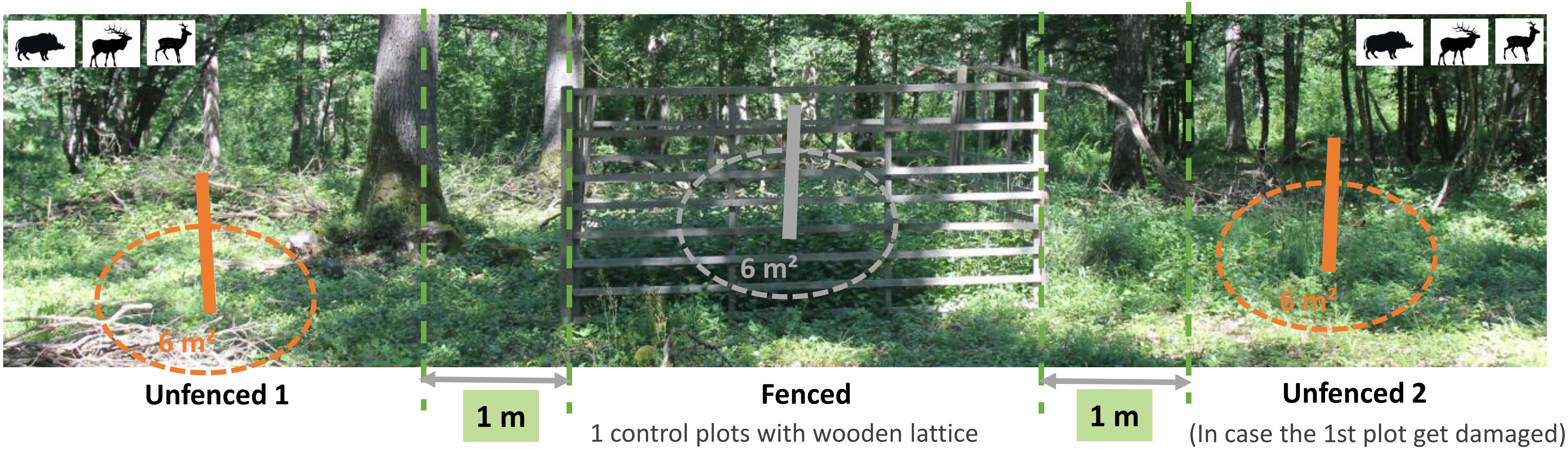
N = 930 sites (in 2016)
N = 726 sites (in 2021)

Sampling plots

Pairs of unfenced and fenced plots (control) in each selected sites and in approx. the same conditions (light, herbaceous cover)

No ungulates in the fenced plots

Two unfenced plots in case the first one became damaged (timber exploitation)



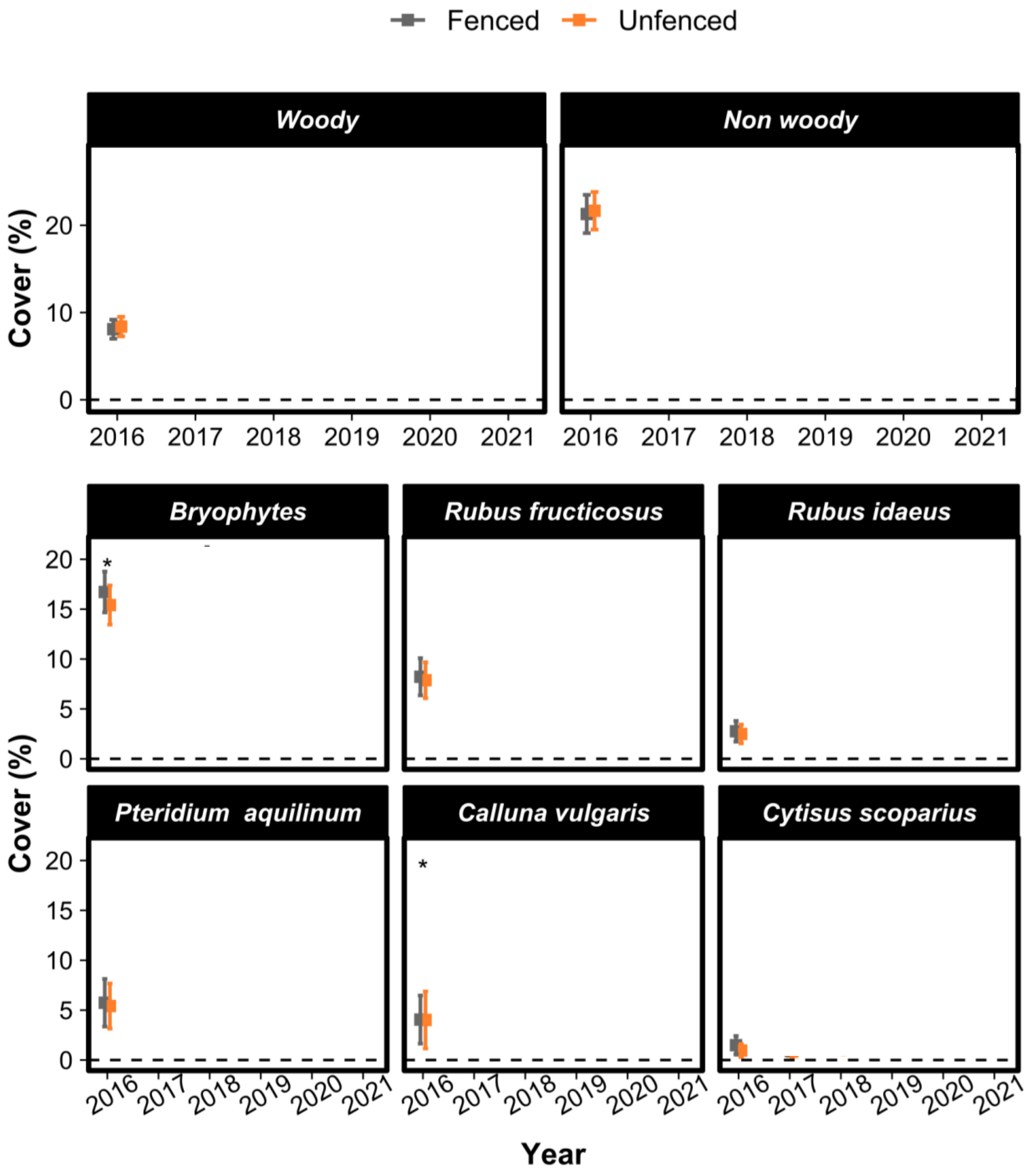
Data collection

- Annual monitoring (2016-2021)
- Seedling density
- Species identity and height of the 5 tallest seedlings
- Cover of woody/non-woody species
- Cover of the main competitive herbaceous species (*Rubus fructicosus*, *Rubus idaeus*, *Pteridium aquilinum*, *Calluna vulgaris*, *Cytisus scoparius*) and bryophytes.

Results

Similar initial conditions with seedlings < 50 cm.

The cover of saplings and some herbaceous species increased faster in the fenced plots



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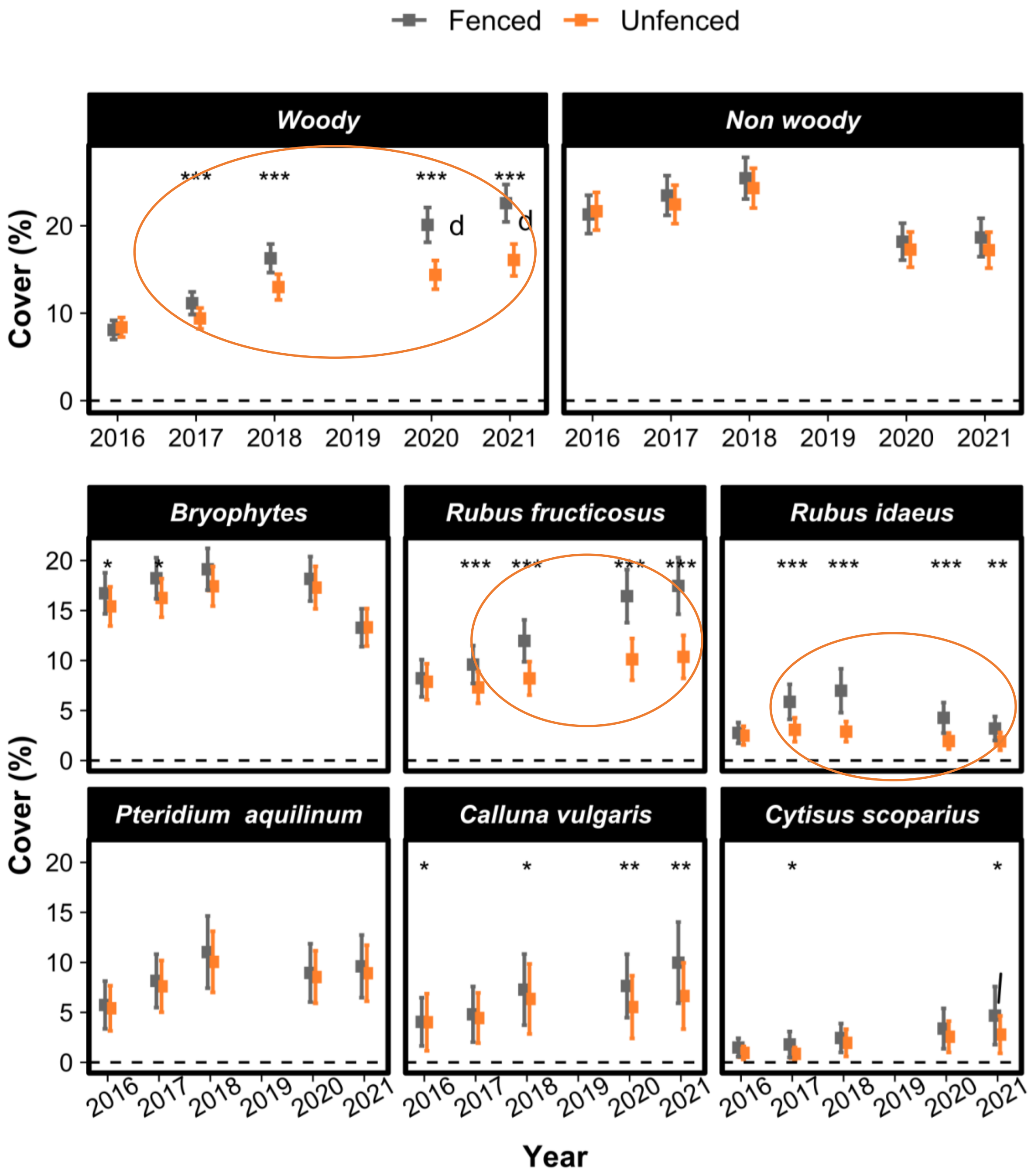
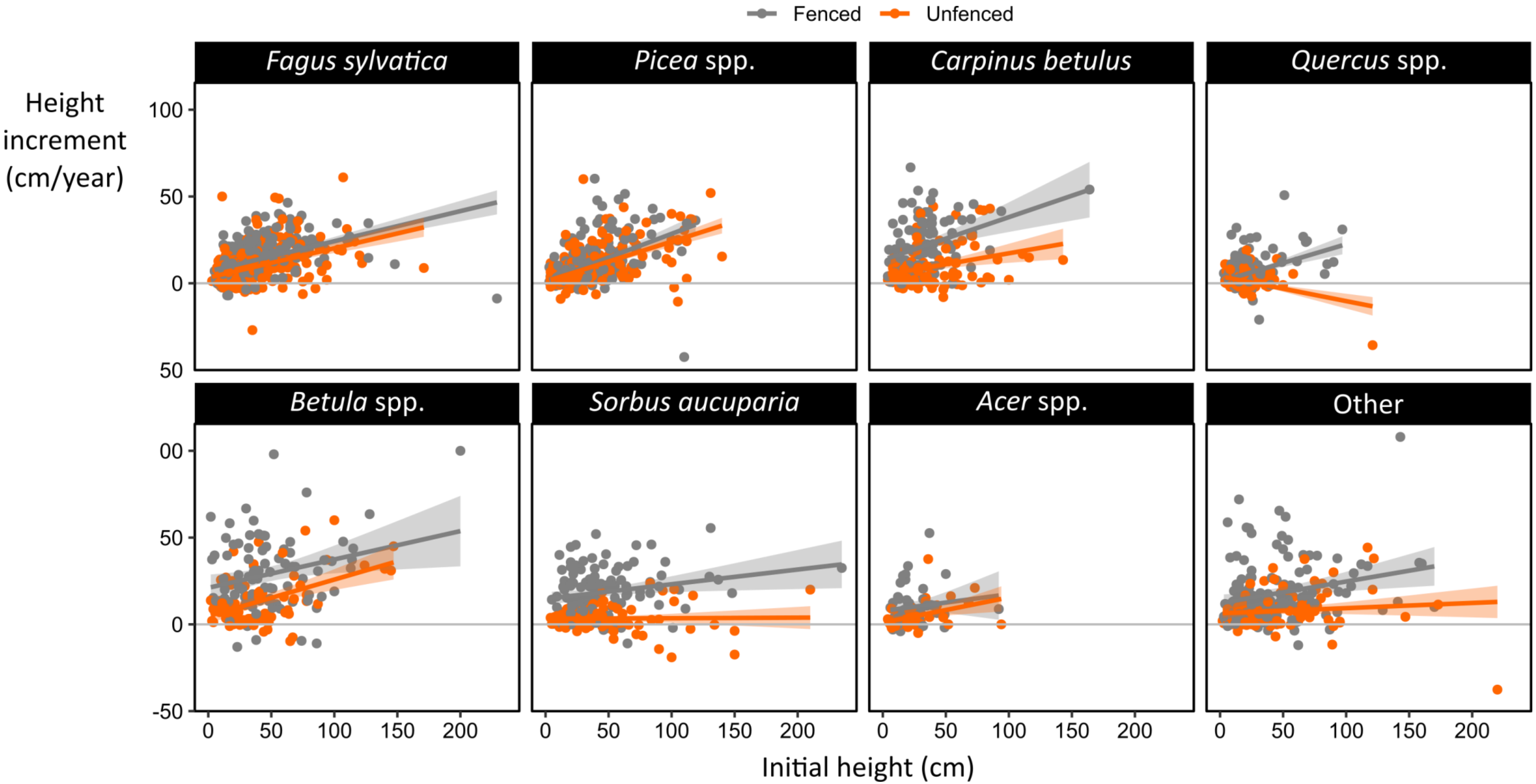


Considering only the tallest saplings, the height increment of all species but beech and spruce was significantly reduced by browsing.



Browsing affected interspecific competition

In fenced plots	
Species	**iH (cm/yr)**
Birch (Betula sp.)	25
Rowan (Sorbus aucuparia)	18
Hornbeam (Carpinus betulus)	17
Beech (Fagus sylvatica)	13
Maple (Acer pseudoplatanus)	11
Norway spruce (Picea abies)	10
Oak (Quercus sp.)	7

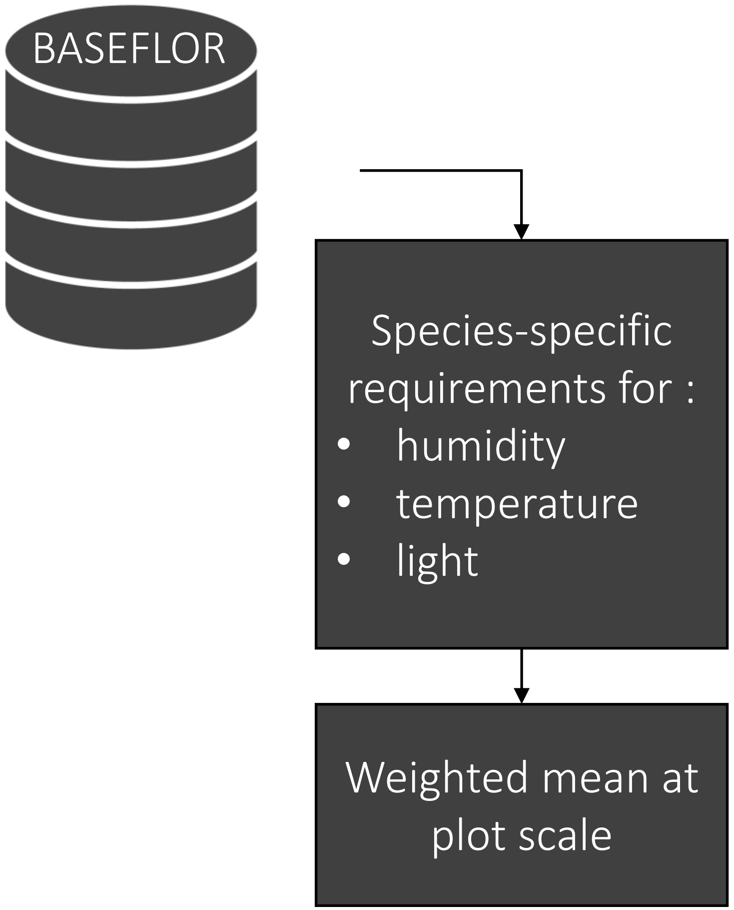
Unfenced plots			
Species	**iH (cm/yr)**	**Δ (cm/yr)**	**Δ (%)**
Birch	10	15	60
Spruce	10	n.s.	n.s.
Beech	9	4	30
Hornbeam	6	11	65
Maple	5	6	54
Rowan	3	15	83
Oak	3	4	57

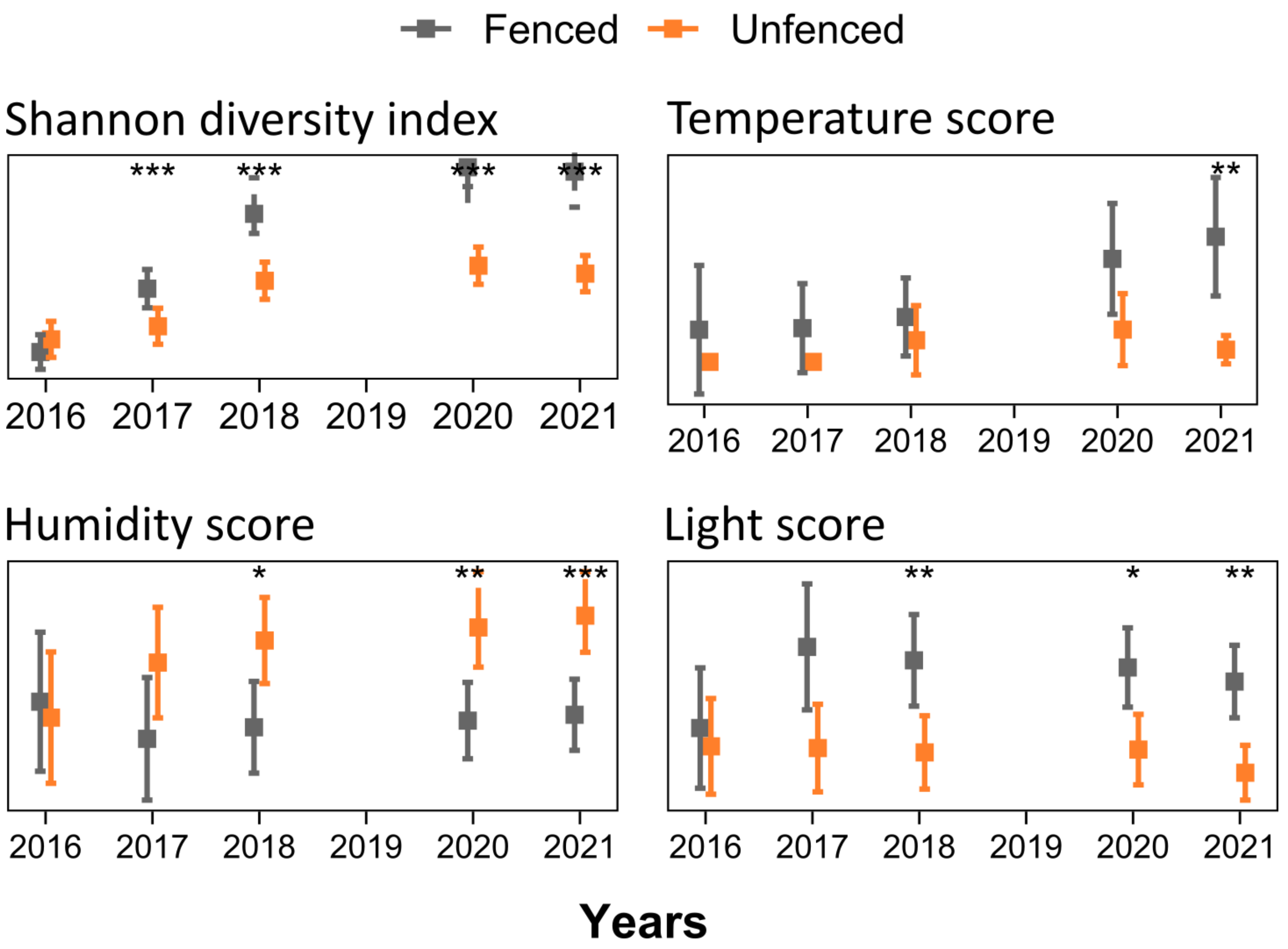
strongly suppressed species

⚠ Theses results does not take into account that the composition of the 5 tallest saplings could change through time

e.g. A given species could be represented among the five tallest individuals in 2016, but not later, particularly for the heavily browsed species.

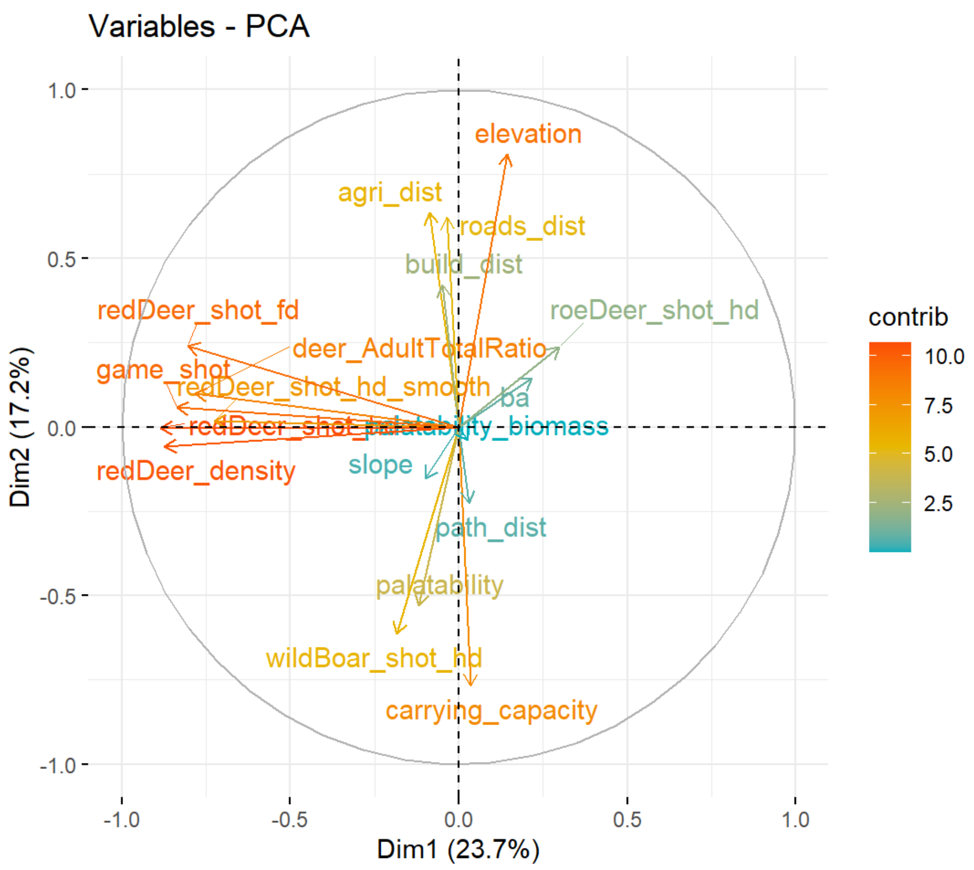
Browsing affected regeneration diversity, increased the share of shade tolerant species and species less-tolerant to warmer and drier conditions





Is there a correlation between browsing effect and ungulate density?

- 9 indicators of ungulate abundance (number of shot animals, carrying capacity index, red deer density estimate)
- 9 ecological variables (distance to roads, urban areas, agricultural areas, paths, buildings, elevation, mean species palatability, slope…)
- PCA (PC1 and PC2 explained 41%)



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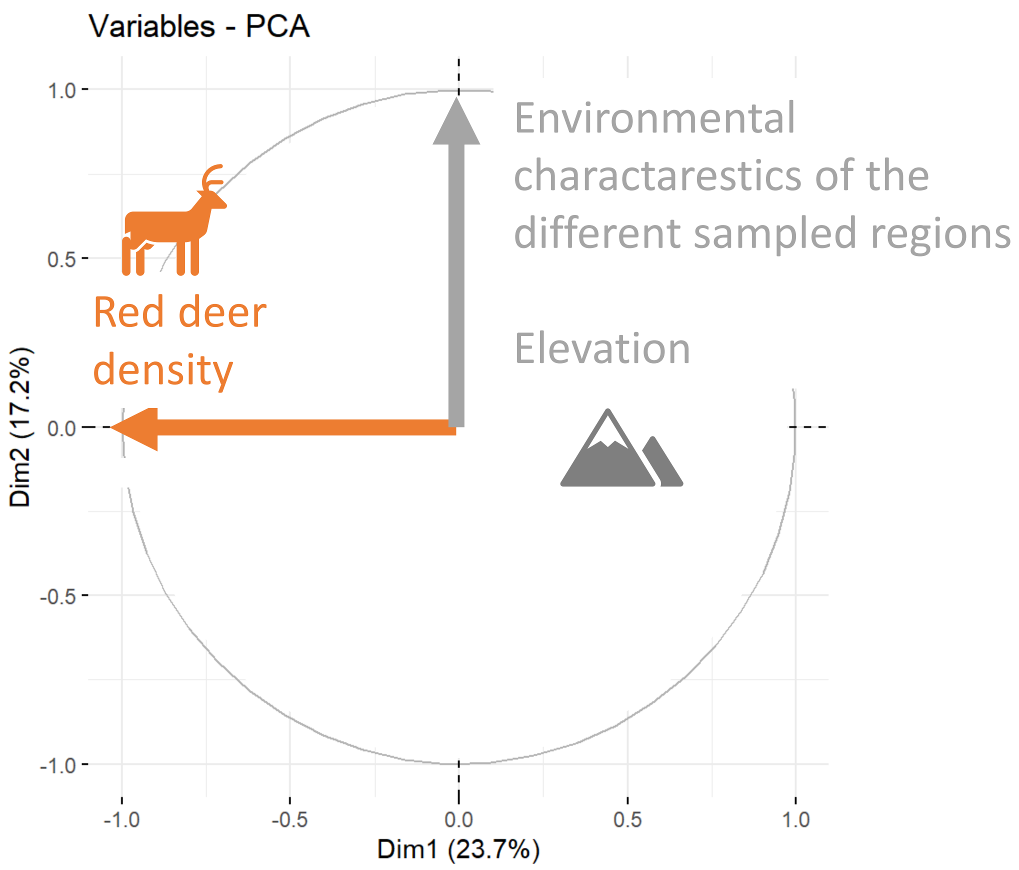

Fitting a linear model to evidence a relationship between ungulate abundance and height growth reduction

$$iH_{j,t,r} = a + b_t + c \cdot PC1_j + d \cdot PC2_j + e_t \cdot PC1_j + f_t \cdot PC2_j + \alpha_j + \epsilon_{j,t,r}$$

Correlation with height increment in **fenced** plots

Correlation with the treatment effect on height increment

	c	d	e_t	f_t
***Carpinus* sp.**	1.26 ***	n.s.	-1.08 ***	- 2.50 *
***Sorbus* sp.**	1.46 *	1.48 *	-1.98 *	n.s.
***Quercus* sp.**	n.s.	n.s.	n.s.	n.s.
***Fagus* sp.**	n.s.	- 0.76 *	n.s.	n.s.
***Acer* sp.**	1.73 *	n.s.	n.s.	n.s.
***Picea* sp.**	1.09 *	1.09 *	n.s.	-1.22 *
***Betula* sp.**	2.88 *	2.02 *	n.s.	-2.63 *

The height growth reduction was significantly correlated to ungulate density for two species

$$iH_{j,t,r} = a + b_t + c \cdot PC1_j + d \cdot PC2_j + e_t \cdot PC1_j + f_t \cdot PC2_j + \alpha_j + \epsilon_{j,t,r}$$

Correlation with height increment in **fenced** plots ($c \cdot PC1_j + d \cdot PC2_j$)

Correlation with the treatment effect on height increment ($e_t \cdot PC1_j + f_t \cdot PC2_j$)

	c	d	e_t	f_t
***Carpinus* sp.**	1.26 ***	n.s.	-1.08 ***	- 2.50 *
***Sorbus* sp.**	1.46 *	1.48 *	-1.98 *	n.s.
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The treatment effect was stronger in areas with abundant red deer.

Species-specific and ambiguous relationships

$$iH_{j,t,r} = a + b_t + c \cdot PC1_j + d \cdot PC2_j + e_t \cdot PC1_j + f_t \cdot PC2_j + \alpha_j + \epsilon_{j,t,r}$$

Correlation with height increment in **fenced** plots

Correlation with the treatment effect on height increment

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***Acer* sp.**	1.73 *	n.s.	n.s.	n.s.
***Picea* sp.**	1.09 *	1.09 *	n.s.	-1.22 *
***Betula* sp.**	2.88 *	2.02 *	n.s.	-2.63 *

BUT, height increment also increased with red deer density in **fenced** plots.

Species-specific and ambiguous relationships

	c	d	e_t	f_t
***Carpinus* sp.**	1.26 ***	n.s.	-1.08 ***	- 2.50 *
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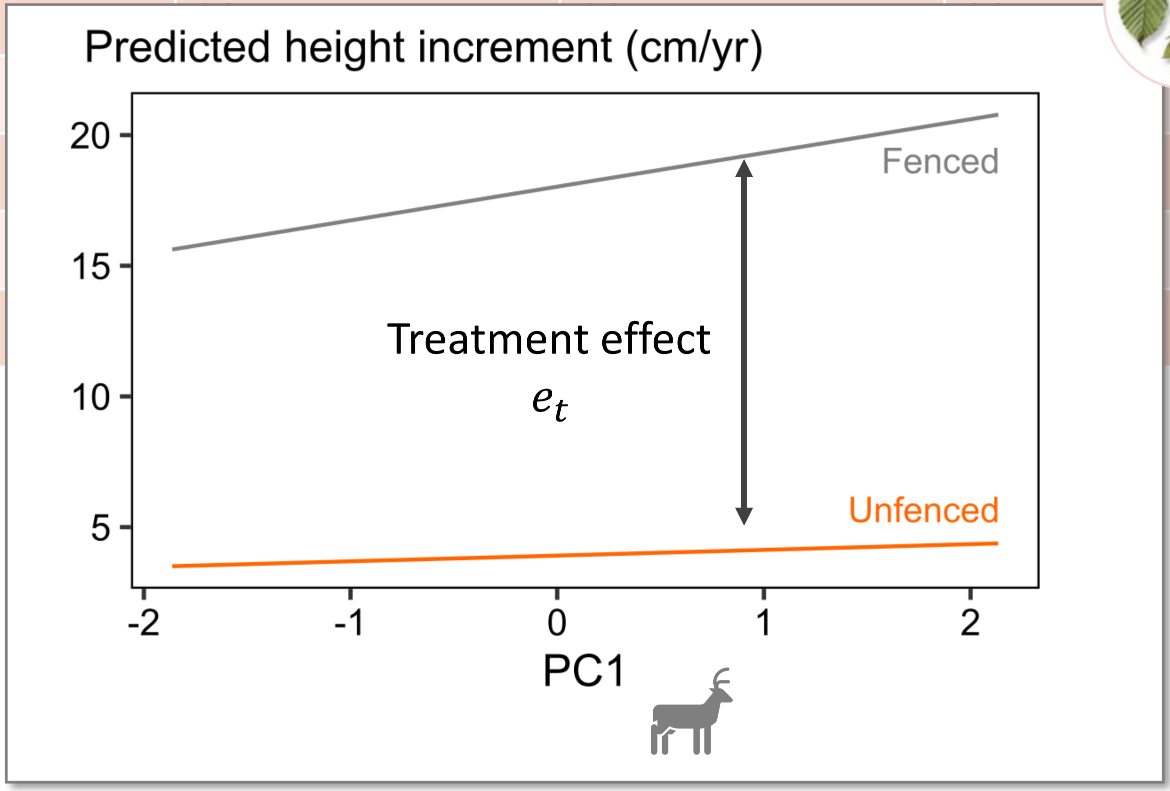

Species-specific and ambiguous relationships

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Correlation with height increment **in fenced plots**

Correlation with the treatment effect on height increment

	c	d	e_t	f_t
***Carpinus* sp.**	1.26 ***	n.s.	-1.08 ***	- 2.50 *
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The treatment effect could not be dissociated from environmental characteristics

Discussion

Broad	High light	Nowhere
• Shade tolerance : ++ • Browsing resistant : ++ • Growth rate : + Grow well in the understory, sit-and-wait strategy	• Shade tolerance : - • Browsing resistant : -- • Growth rate : ++ Grow well in large gaps and/or if ungulate pressure is low.	• Shade tolerance : - • Browsing resistant : - • Growth rate : -- Do not regenerate easily, could regenerate better outside forests.

Walter et al. 2020 FORECO

Take-home messages

Over a large region covered mostly by oak-beech temperate forest managed with CCF

- Ungulates favor late-successional species that are less tolerant to dry and warm conditions
- Ungulate pressure is one factor that could hamper future forest resistance and resilience
- Ungulate exclusion would benefit to “high-light” species but that would not be enough for “nowhere” species (oak).
- Optimal ungulate density could not be defined due to multiple uncontrolled interactions.

forests
MDPI

Article

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

Romain Candaele [1,*], Gauthier Ligot [1], Alain Licoppe [2], Julien Lievens [2], Violaine Fichefet [2], Mathieu Jonard [3], Frédéric André [3] and Philippe Lejeune [1]

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2 Department of Natural and Agricultural Environment Studies, Public Service of Wallonia, 5030 Gembloux, Belgium
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* Correspondence: romain.candaele@gmail.com

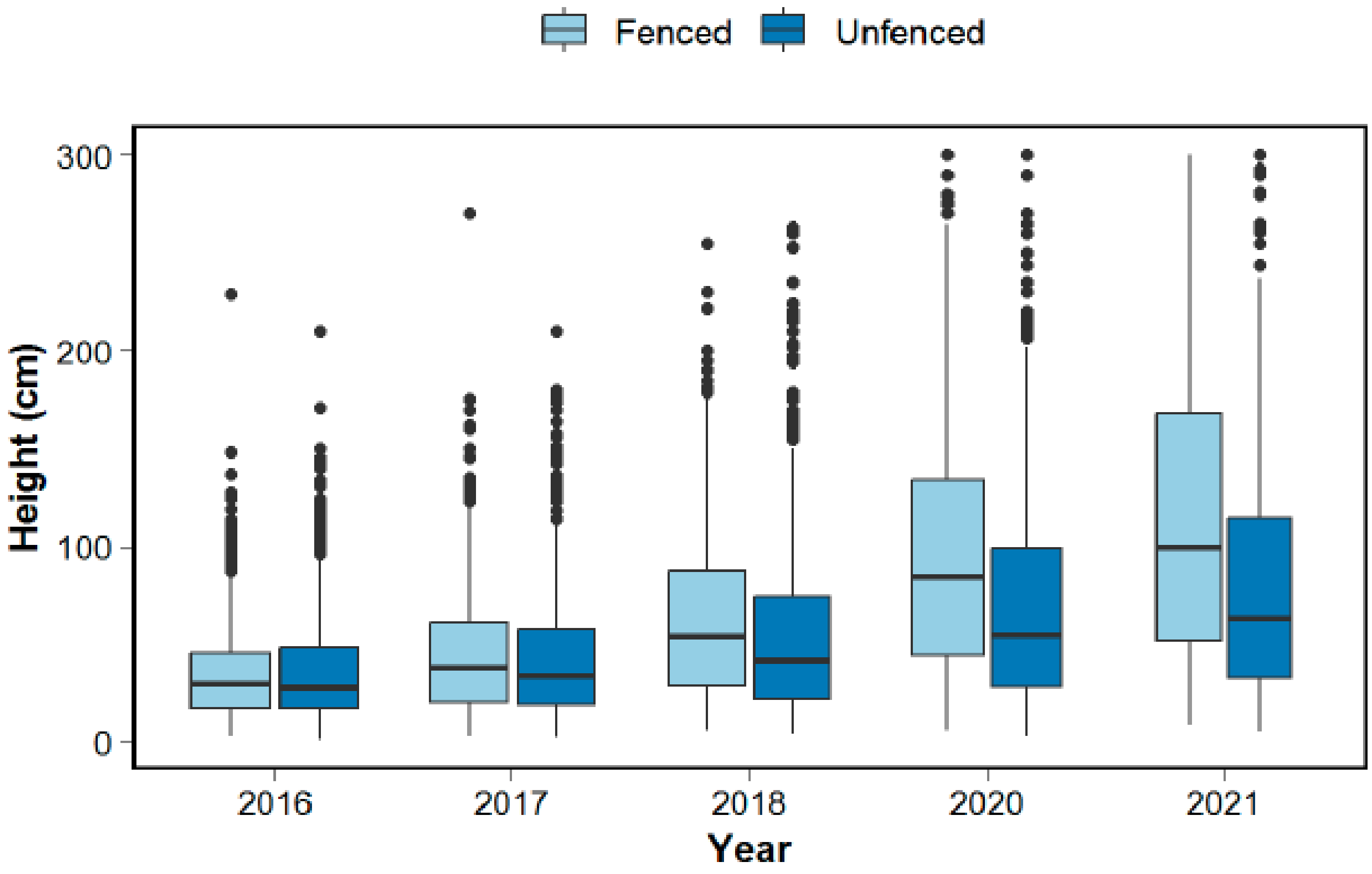
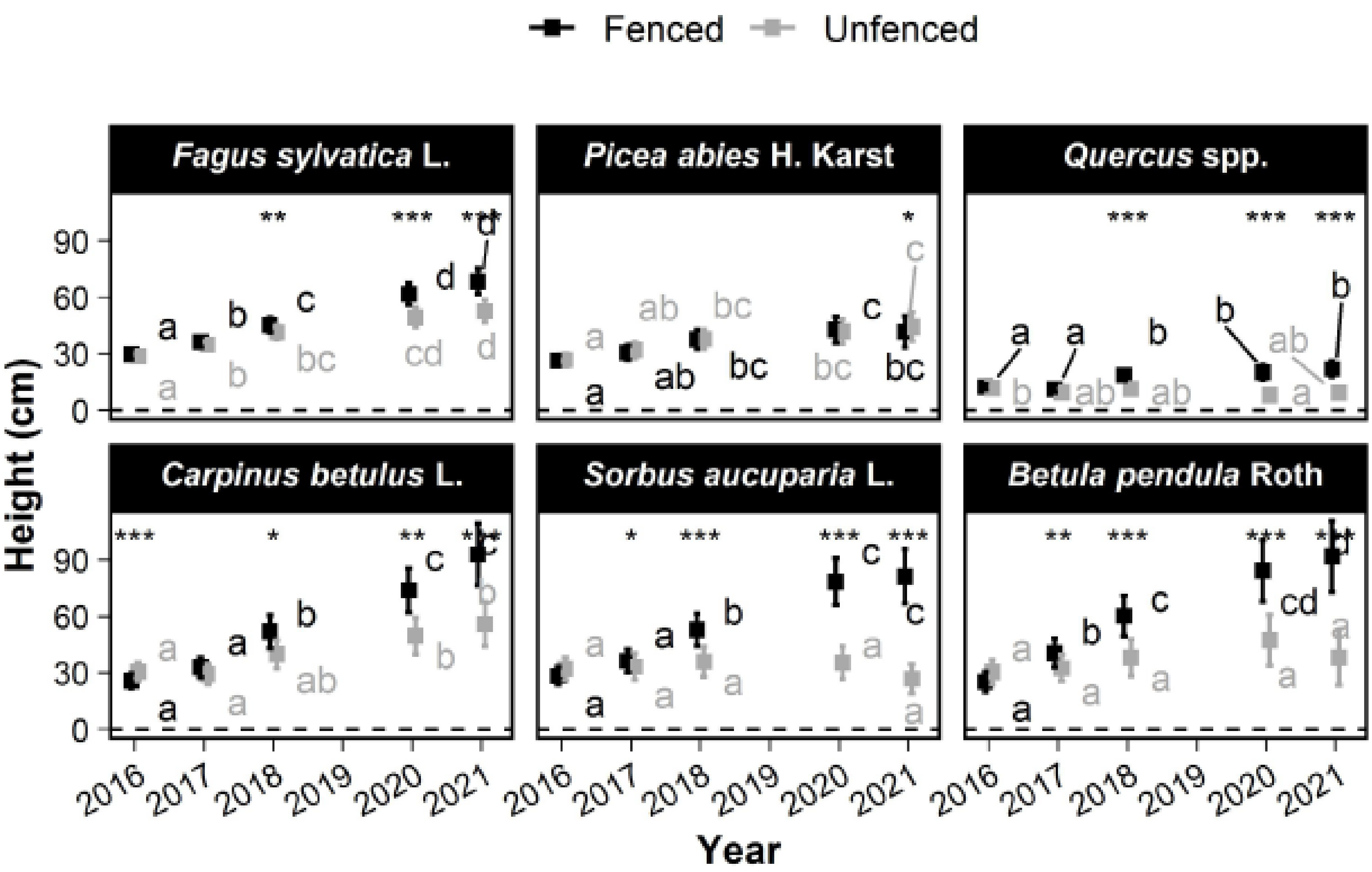
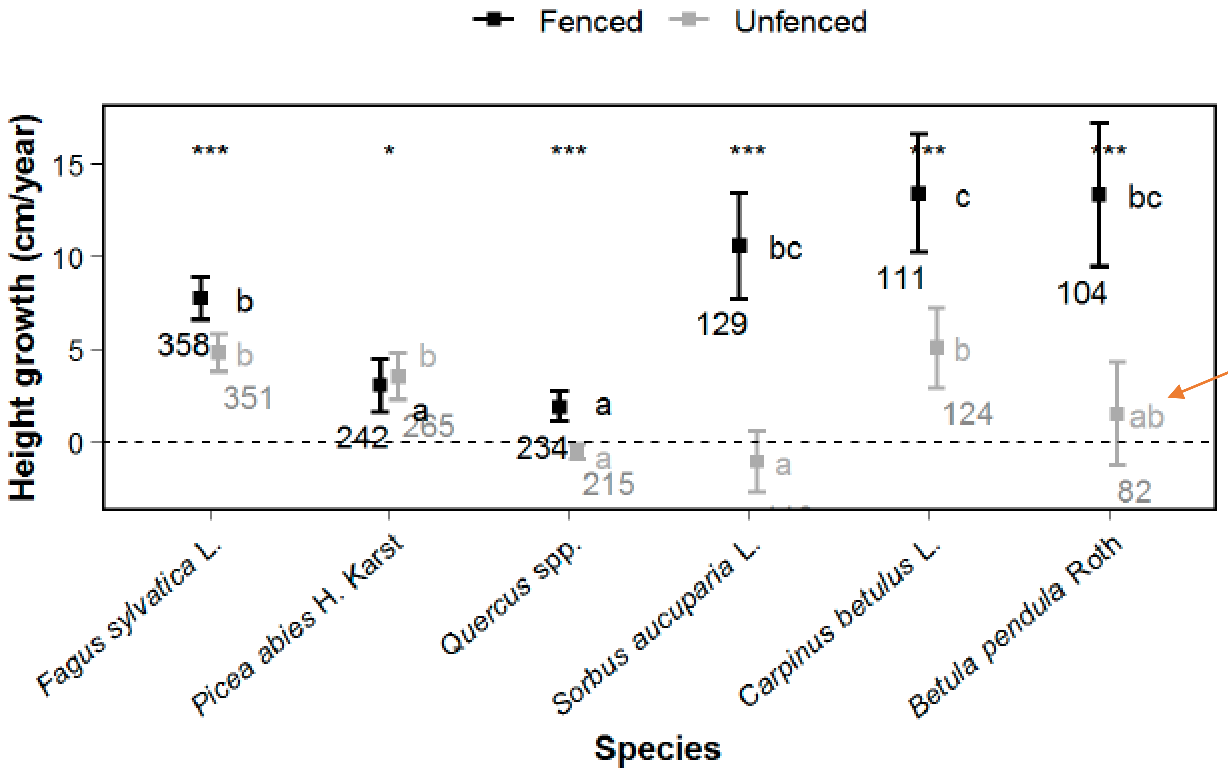


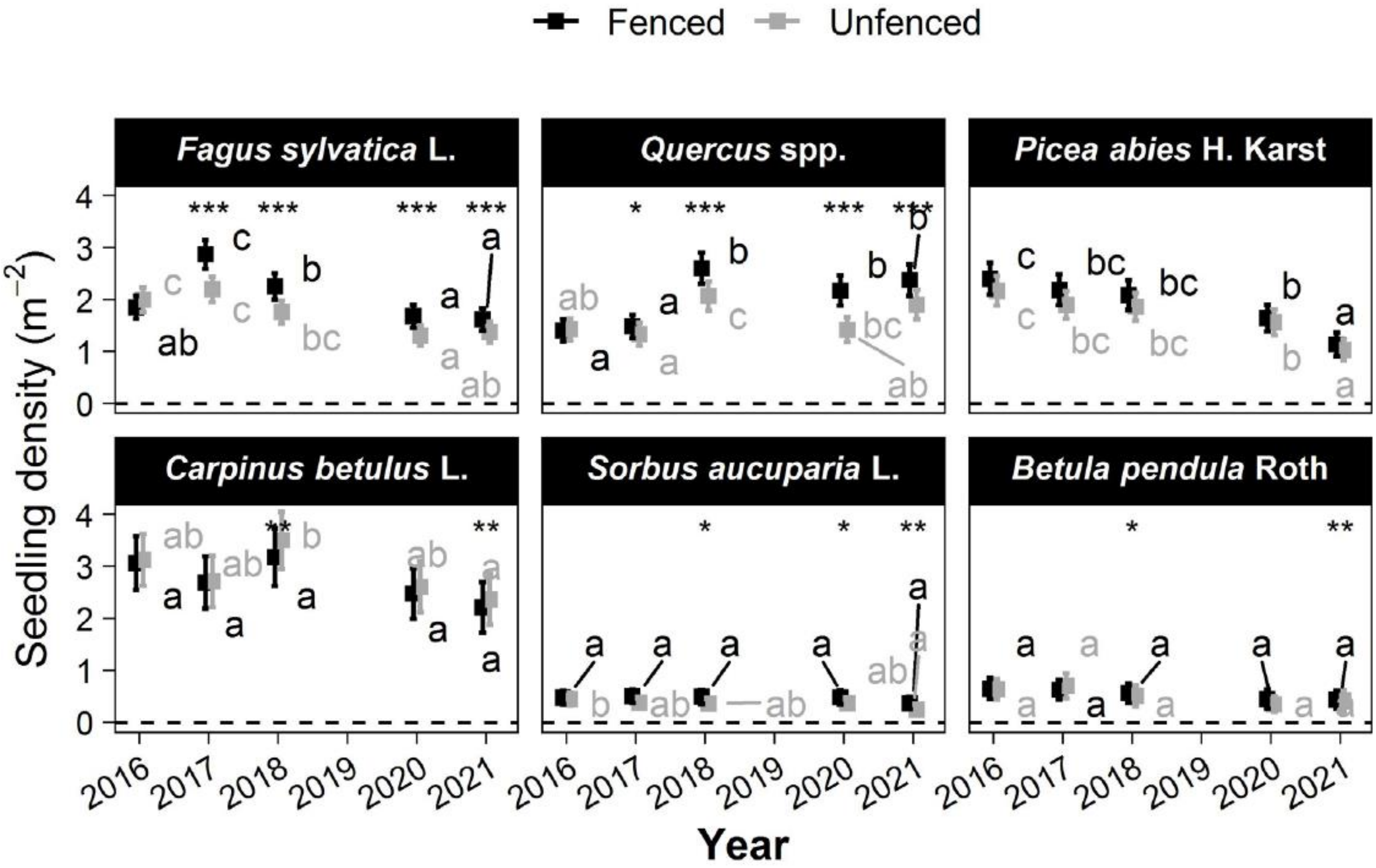
Figure S3: Distribution of the height of the highest seedling by plot regardless of the species and its evolution over time. As no seedlings overreached 1.80 meters in most of the plots, they remained sensitive to browsing at the end of the study period.


Fenced
Unfenced
Fagus sylvatica L.
Picea abies H. Karst
Quercus spp.
Carpinus betulus L.
Sorbus aucuparia L.
Betula pendula Roth
Height (cm)
Year



Slightly different results, because here the increment was set to zero if birch disapeared from the five tallest saplings…

Figure S4: Mean growth of the highest seedling by plot. Only seedlings among the 5 highest seedlings in their plots are considered. The mean growth are computed without accounting for the zero counts, except for plots where the species was observed only at the beginning or only at the end of the study period. Within one treatment, growth are compared based on max-t test. The groups that did not share common letters were statistically different. Between treatments, growth of each species were compared based on student t.tests when application conditions were met. The comparison was based on Wilcoxon rank sum test otherwise. For this comparison, the zero counts were included when the species was observed in the plot a the same pair (other treatment).



Fenced
Unfenced
Fagus sylvatica L.
Quercus spp.
Picea abies H. Karst
Carpinus betulus L.
Sorbus aucuparia L.
Betula pendula Roth
Seedling density (m^{-2})
Year
2016
2017
2018
2019
2020
2021

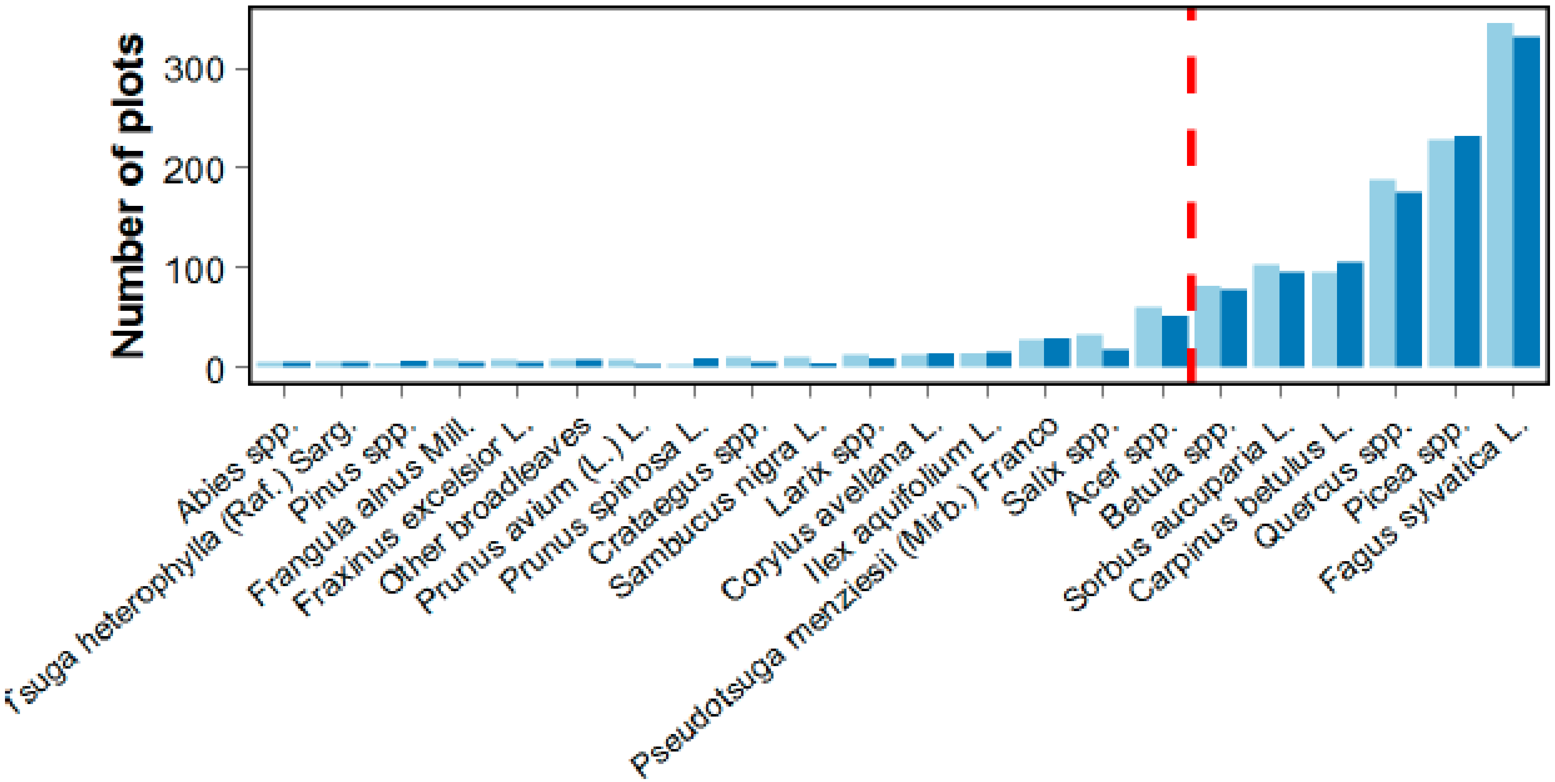


Figure S1: Number of occurences of studied tree species and of less abundant species. An occurence is accounted for a species when one or more seedling of that species was present in a plot during the study period (2016 - 2021). Species on the right side from the red dotted line were included in the study.