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Climate and ungulate browsing impair regeneration dynamics in spruce-fir-beech forests in the French Alps

Mithila Unkule[1*], Christian Piedallu[2], Philippe Balandier[3] and Benoit Courbaud[1]

Abstract

Key message: Different components of water balance and temperature reduce density and height growth of saplings of *Picea abies (L.) H. Karst* (Norway spruce), *Abies alba Mill.* (silver fir) and *Fagus sylvatica L.* (European beech) in mixed uneven-aged forests in the French Alps and Jura mountains. Ungulate browsing is an additional pressure on fir and beech that could jeopardise the renewal of these species in the future.

Context: The uncertainty in tree recruitment rates raises questions about the factors affecting regeneration processes in forests. Factors such as climate, light, competition and ungulate browsing pressure may play an important role in determining regeneration, forest structures and thus future forest composition.

Aims: The objective of this study was to quantify sapling densities and height increments of spruce, fir and beech and to identify dominant environmental variables influencing them in mixed uneven-aged forests in the French Alps and Jura mountains.

Methods: Sapling height increment and density were recorded in 152 plots, and non-linear mixed models were obtained to establish relations between them and environmental factors known to affect regeneration, namely altitude, slope, aspect, canopy openness, soil characteristics, temperature, precipitation and ungulate browsing.

Results: Regeneration density, varying from 0 to 7 saplings per m^2, decreased with sapling height and was also negatively affected for spruce by PET, but positively for fir by precipitation and for beech by mean annual soil water content. Height increment reached up to 50 cm annually, increasing with sapling height and canopy openness and decreasing under high maximum summer temperatures for spruce and beech. The statistical effect of different environmental variables varied slightly among species but trends were quite similar. Additionally, ungulate browsing was high, with fir being the most intensely browsed, followed closely by beech, while spruce was rarely browsed.

Conclusions: All these results suggest that more temperature warming and a decrease in water availability could negatively impact sapling growth and density in the three species, with possible reduction of forest renewal fluxes. The observed increase of ungulate populations leading to increased browsing could be particularly detrimental to fir saplings.

Keywords: Regeneration, Mixed forest, Canopy openness, Water availability, Summer Temperature, Ungulate browsing, *Picea abies*, *Abies alba*, *Fagus sylvatica*

1   Introduction

Mixed uneven-aged forests of Norway spruce (hereafter spruce), silver fir (hereafter fir) and European beech (hereafter beech) occupy extensive areas in Europe (Brus et al. 2011), specially in the French Alps (Toïgo et al. 2015). Their presence throughout Europe, in such wide environmental conditions, makes them a target of rapidly changing climatic extremes such as increasing frequencies and intensities of droughts (Cailleret et al. 2013; Diaci et al. 2020) and ever increasing summer temperatures (Schurman et al. 2019; Lombaerde et al. 2020). The last few decades have also witnessed increasing number of wild ungulates in the Alps, which also puts plants in these forests at a higher risk of being browsed (Heuze et al. 2005; Nagel et al. 2015; Bernard et al. 2017). Different studies have highlighted changes in plant demography (Gray and Brady 2016), inconsistent demographic responses to climate at species range edges (Kunstler et al. 2020), limitation of regeneration and tree recruitment (Silva et al. 2012; Dey et al. 2018; Löf et al. 2019), stressing a potential risk of reduced forest regeneration. For a species to maintain its range, regeneration must compensate mortality and harvesting in a climate warming context. Several articles document and predict increasing frequency of mortality events because of changing climate (Bodin and Wiman 2007; Allen et al. 2010; Manso et al. 2015). Natural regeneration in many forests is especially variable and already low (Dey et al. 2018). If regeneration reduces while mortality increases with climate change, even if harvesting events remain constant, this could jeopardise forest renewal. A diminution of regeneration because of global changes could therefore have a major impact on species distributions and their persistence.

In mountain forests, regeneration processes are especially slow and scarce. Regeneration has often been stressed as a limiting process in mountain forest dynamics (Kräuchi et al. 2000). To better understand and anticipate degraded regeneration dynamics and potential species resilience or adaptability, it is necessary to identify key drivers of regeneration demographic processes. These include processes such as seed production, germination, and seedling growth, mortality and survival, up to the stage of tree recruitment. Our objective in this study was to quantify sapling densities and height growths of spruce, fir and beech in mountain forests and to identify key environmental factors influencing them. Studies such as Balandier et al. (2006); Diaci et al. (2020) have shown the role of many different factors in these processes. Stands of spruce, fir and beech are known to largely depend on light availability for their regeneration growths (Dyderski et al. 2018; Diaci et al. 2020; Lombaerde et al. 2020; Gaudio et al. 2017). The role of soil nutrients and water availability in facilitating regeneration is also well studied (Madsen and Larsen 1997; Dyderski et al. 2018).

Besides, regeneration depends on a large scale on inter- and intra-specific competitors. However, the species identity and cover determine if plants can act as facilitators or competition to certain species (Balandier et al. 2006; Collet and Chenost 2006; Laurent et al. 2017; Thrippleton et al. 2017). Disturbances such as fires (Dey et al. 2018), frost (Defossez et al. 2015) and insect infestations (Dobrovolny 2016) also affect regeneration processes. In spite of this knowledge, accurate estimation of regeneration demographic rates and precise identification of the effects of climate and other environmental factors on regeneration in mountain forests is difficult. This could be because saplings are scattered in space with high variability among sites, environmental factors could be highly inter-correlated, and saplings are difficult to monitor over successive years because of their small size and low survival rates. We tried to overpass some of these difficulties by analysing sapling densities and height increments by sampling a large environmental gradient in the French Alps and Jura mountains.

In this study, we address the following questions related to the regeneration of spruce, fir and beech in mixed uneven-aged forests:

1. Studies have observed and predicted high variability as well as decreasing regeneration densities and height increments. What are the magnitudes of sapling height increments and densities in the French Alps and Jura mountains?
2. Many factors such as light, temperature, soil conditions, water availability and presence of ungulates are known to affect regeneration. What are the key drivers of sapling height increments and densities of spruce, fir and beech?

We also discuss if there is a risk to the current species distribution and forest structures because of regeneration shortage and unreliability.

2   Materials and methods
2.1   Field sampling
2.1.1   *Study sites and plot sampling strategies*
The study was carried out in the French Alps (44.17° N, 5.23° E to 46.39° N, 6.90° E) in mixed uneven-aged mountain forest stands, with at least one out of spruce (*Picea abies (L.) H. Karst*), fir (*Abies alba Mill.*) and beech (*Fagus sylvatica L.*) as dominant species. Sampled plots were distributed over 11 mountain ranges, to cover a wide range of climates, elevations and site conditions (Fig. 1, Table 1). The sampling locations were determined based on existing networks of permanent plots established by the Office National des Forêts (ONF), France and INRAE, with information of the species tree basal area on the plots. The plots in these networks were first categorised into 24

Fig. 1 Locations of sampled plots and mountain ranges in the French Alps and Jura mountains, with each point representing a sampled plot, and colours of points representing altitude gradients
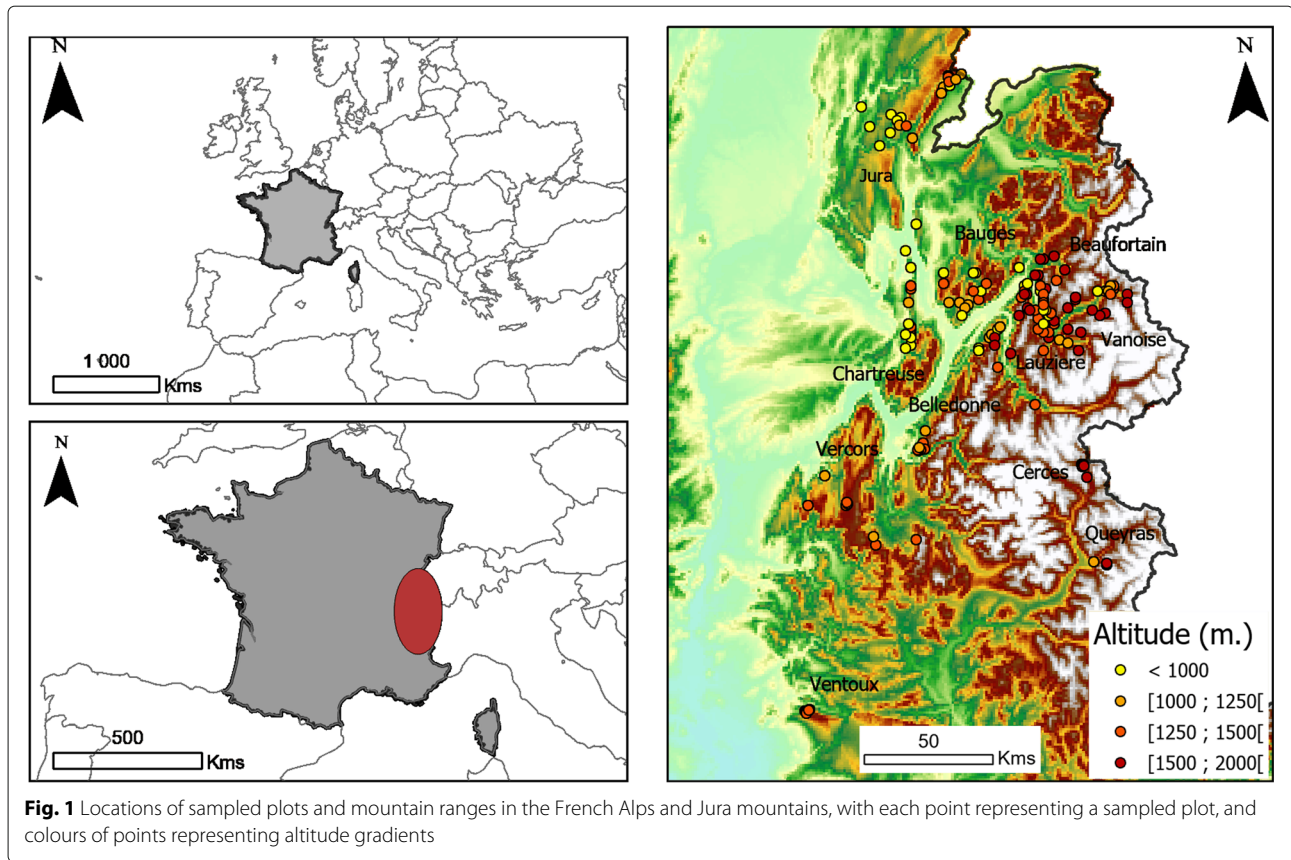
classes, and then subsets taken to cover various stand structures and environmental conditions in the sampling. The categorisation was based on the following variables:

1. Total basal area (BA) of adult trees on the plot (2 classes: higher and lower than the mean of all plots)
2. Mean annual air temperature (T°C) of the plot (2 classes: higher and lower than the mean of all plots)

3. Annual mean of monthly precipitation (mm) on the plot (2 classes: higher and lower than the mean of all plots)
4. Identity of the dominant species on the plot (spruce, fir or beech)

Thus, we covered a wide range of stand structures, tree densities and compositions (BA of the different species

Table 1 Site-wise distribution of sampled plots, with distributions of altitude, temperature and plot basal area covered

Mountain range	Altitude (masl)				Summer temp (°C)				Tot. BA (per ha)				No. of plots
	Min.	*Mean*	*Max.*	*SD*	*Min.*	*Mean*	*Max.*	*SD*	*Min.*	*Mean*	*Max.*	*SD*	
Bauges	806	1137	1439	203	9.7	11.8	14.1	1.3	14.8	34.8	50.7	10.2	13
Beaufortain	741	1390	1769	296	8.4	11.0	15.1	1.9	14.1	33.8	64.5	13.3	25
Belledonne	936	1271	1619	208	8.8	11.3	13.1	1.3	19.9	37.9	97.1	16.9	19
Cerces	1303	1666	1765	150	10.1	10.9	11.7	0.5	23.1	36.7	59.3	11.4	8
Chartreuse	515	937	1380	313	9.8	12.7	15.7	2.1	13.4	23.6	36.4	7.7	14
Jura	544	1035	1444	249	9.4	12.0	15.2	1.6	17.8	54.4	133.3	33.5	18
Lauziere	660	1341	1679	298	8.6	11.0	15.4	2.0	12.1	39.6	78.2	19.2	18
Queyras	1029	1512	1774	419	11.3	13.1	16.4	2.8	20.4	23.7	29.7	5.2	3
Vanoise	1001	1448	1796	271	8.9	11.6	14.9	1.8	10.7	33.6	57.8	13.1	16
Ventoux	1010	1219	1357	116	11.3	12.2	13.6	0.7	28.6	36.1	46.3	5.6	9
Vercors	1136	1357	1495	140	10.1	11.1	13.0	1.0	20.4	35.4	73.9	15.7	9

as a proxy) for the different climates encountered in the area, including the distribution edges of the species (temperature and precipitation as a proxy). Thus, 24 categories were formed, and up to five plots were chosen by random selection from each category. A total of 152 plots were sampled across all mountain ranges. The observations described in the following sections were carried out by the authors. All data is available here: Unkule et al. (2021).

2.1.2 Assessing stand structure

In order to characterise stand structure and composition, two concentric circular plots of radii 10 m and 15 m were marked from the centre, to measure the tree basal area (BA) for each species. Diameter at breast height (DBH) of all adult trees above 7.5 cm and 17.5 diameter were measured in the 10-m and 15-m radius circle, respectively, using a tape or a caliper, and the species identity noted. This information was used to calculate tree BA per hectare and per species for the plot.

2.1.3 Assessing sapling growth, density and browsing rates

The Point Center Quadrat Method (PCQM) was used to estimate sapling density, with a maximum radius of 10 m (Mitchell 2015). This method was selected after a survey of different regeneration sapling methods (Carnet et al. 2018). A big advantage of this method is that it makes it possible to adjust the prospected area to sampling density and avoids empty plots due to small plot sizes.

The 10-m radius circular plot was divided into four quadrants, with boundaries in the north, east, south and west directions. Saplings were divided into 4 height classes: 10–50 cm (H1), 51–150 cm (H2), 151–300 cm (H3) and above 300 cm, but below DBH of 7.5 cm (H4). This division was made in order to evaluate, if any, an effect of the sapling height. Across 152 plots, we sampled 2370 individual saplings (plants between height 10 cm, and DBH <7.5cm), 720 spruce, 891 fir and 759 beech.

In each quadrant (i), the sapling nearest to the plot centre, of each species, and in each height class, was selected, and the following measures noted to the smallest count of 0.5 cm: sapling length when held straight (H); mean of annual shoot length increments for the past 3 consecutive years (ΔH), at least when it was possible; and distance (D_i) (in m) of sapling from the centre of the plot (Fig. 2). The annual shoot increments were determined by measuring the length between marks of two bud scars, which are known to be indicators of one growing season. Using this information, the density of saplings of each species and height class was computed as: $(1/((\sum D_i)/(N_0/N_Q))^2) \times CF$ where N_0 is the total number of quadrants (here 4) and N_Q is the number of vacant quadrants. CF is a correction factor obtained from a table developed by Warde and Petranka (1981) to take into account the presence of vacant quadrants. As the role
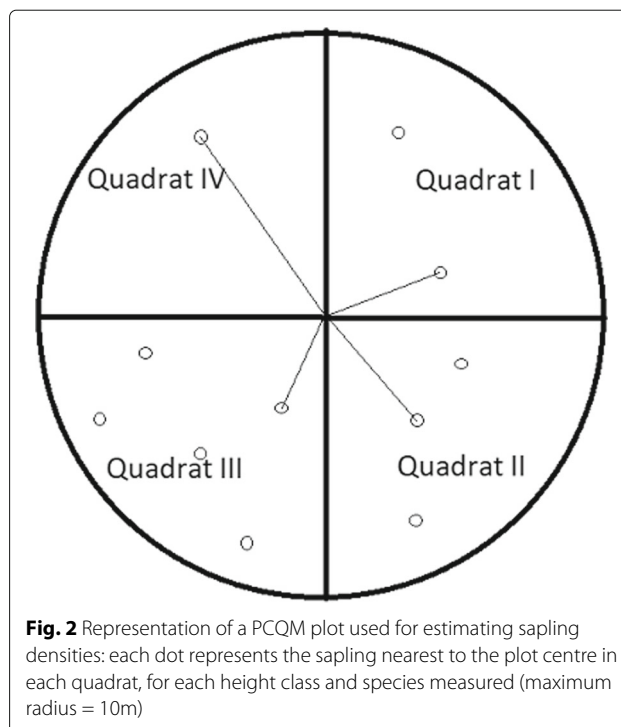

Fig. 2 Representation of a PCQM plot used for estimating sapling densities: each dot represents the sapling nearest to the plot centre in each quadrant, for each height class and species measured (maximum radius = 10m)

of wild ungulates on sapling growth and survival is often highlighted, any physical damage to the terminal bud of a sapling was noted as an incident of browsing by an ungulate, in order to quantify the browsing rate for each plant species. The height increment of browsed saplings was considered zero.

2.1.4 Calculation of competition and browsing pressure indices

A competition index was calculated to quantify competition of spruce, fir or beech with other understory vegetation (all plants less than 150 cm height, either herbaceous or woody species). First, dominant understory plant species were identified. Their cover was estimated by a visual assessment of ground cover occupied by the vertical projection of their foliage onto the soil (GC). The different species were assigned scores (SC) according to their potentially negative competition effect on regenerated saplings. Very strong interfering species such as gramminoids and dense ferns were ranked 3, less competitive species such as *Rubus* sp. 2, tall shrubs and midstorey trees 1 and other small forbs 0 (SC) (Balandier et al. 2006). A competition index was computed for each quadrant as: $\sum GC * SC$, which was then averaged for the plot. Additionally, an approximate percentage of browsed plants on the plot was noted (BP), and the browsing pressure index was computed as: $(\sum GC * BP) / \sum GC$. These indices were calculated using approximate visual covers of the vegetation.

2.1.5 Evaluating canopy openness

Canopy openness (O) of a site influences stand microclimate and light. In each quadrant, canopy openness was measured in the four cardinal directions at a distance of 4 m from the centre, using a convex densiometer (Baudry et al. 2013).

2.1.6 Laboratory analyses of soil samples

Within a 1-m radius around the plot centre, a soil sample was collected, up to 20-cm depth (excluding litter and humus) using a soil auger. This sample was later used in the laboratory to estimate the C:N ratio and pH of the soil.

Soil samples were first air dried in the lab and were then placed in aluminum trays in a ventilated oven at 40°C. After complete drying, they were manually sieved through a 2-mm mesh (Retsch steel analytical sieve, ISO 3310-1 standard). Next step was to fine grind them with a 0.25-mm mesh for carbon and nitrogen determination (using an ultracentrifugal mill ZM200 Retsch, stainless steel rotor 8 teeth). Carbon and nitrogen were detected on the 0.25-mm sample by a total combustion process, using an elemental analyser by the company Vario Micro Cube, Elementar, whereas the pH determination was done on the 2-mm-sieved samples using a SevenExcellence pH meter from Metler-Toledo, InLab Solids Pro-ISM electrode.

2.1.7 Soil and climate data extracted from digital maps

To complement data from field surveys, soil and climate information was extracted, described during the period from 1985 to 2010 for each plot, using digital maps belonging to the Digitalis database by Laboratory SILVA, Université de Lorraine-AgroParisTech-INRA (https://silvae.agroparistech.fr/home/). Monthly solar radiation calculated using the Helios model (Piedallu and Gégout 2007), minimum and maximum temperatures modelled and mapped using Meteo France weather stations and potential evapotranspiration (PET) calculated with Turc formula (Turc 1961; Piedallu et al. 2016) were used to represent available energy.

Precipitation (Prec) and climatic water balance (CWB, Prec minus PET) were used to estimate available water for plants from climatic data. Soil water balance distribution was also estimated, combining monthly climatic variables with soil water holding capacity maps (SWHC) using the Thornthwaite formula (Thornthwaite 1955) with a Geographical Information System. This calculation provided the spatial distribution of mean annual values of actual evapotranspiration (AET), soil water content (SWC) and soil water deficit (SWD) (Piedallu et al. 2013).

The resolutions of all the digital maps was 50 m, except precipitation and SWHC, which had 1-km resolution. All climatic data were provided as monthly average of the 1985–2010 period, which were later also aggregated into seasonal and annual means.

2.2 Data analyses

All data analyses and models were calibrated separately for the three species, spruce, fir and beech, using R software version 3.6.0 and version 4.0.2 (R Core Team 2017), and figures were produced using the package ggplot2 (Wickham 2009). Two different datasets were used for the analyses of densities and growth of saplings. For the density analyses, plot-level data were used, with sapling densities for each species and height class pooled at the plot scale ($n = 152$). For the analyses of growth of saplings, each data point consisted of information of a single individual sapling ($n = 2370$). The final models determining annual height increment was formulated using the subset of unbrowsed saplings ($n = 2128$), as the height increment of browsed saplings was assumed to be zero.

2.2.1 Analysis strategy

The variables potentially affecting sapling density and growths were grouped into categories described in Section 2.1: sapling height, climate, soil, topography, competition and stand structure (Table 2). A systematic approach was used to formulate multivariate non-linear mixed models, testing the progressive addition of variables from a new category. Preliminary exploration indicated that the variable influencing sapling densities and height increments the most was sapling height. We tested then the addition of stand structure variables such as canopy openness, total and conspecific tree basal area. In the next step, we added climate and soil category variables to the earlier model, such as maximum summer temperature, minimum winter temperature, mean monthly precipitation, annual mean of monthly soil water content, soil water deficit, soil water holding capacity, its CN and pH. The last step was to test the addition of competition (competition index, browsing index), followed by topographical factors (slope, altitude, aspect). The order of these steps was chosen based on the importance of these variables derived from literature, and considering increasing pressure of climate change. When a variable from one category was selected, other variables from the same category were systematically avoided to prevent correlated variables being present in the same model (except topographical factors). The function "nlme" from the R package "nlme" (Pinheiro et al. 2021) was used to run these models. Evaluation of the models was done by comparing graphical predictions made by different models and their ecological significance, and by comparing the observed vs. predicted values, along with the Akaike Information Criteria (AICs), mean square deviations (MSD) and the distribution of residuals. A *p*-value of 0.05 was deemed significant. Based on the principle of parsimony, the simplest model with the most accurate predictions was selected. Even though a number of variables were tested, the selected models were relatively simple, with 2

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Table 2 Distribution of important variable values sampled and evaluated in the models

Category	Variable	Min	Mean	Max	SD
Climate	Mean monthly prec (mm) - Prec	65.67	118.26	190.79	24.07
Climate	Max monthly temp (°C)	8.41	11.56	16.39	1.71
Climate	Mean monthly PET (mm) - PET	31.35	47.27	69.90	6.78
Climate	Max summer temp (°C)	13.76	16.78	20.89	1.70
Climate	Min winter temp (°C)	−7.71	−4.74	−0.96	1.37
Competition	Browsing Index	0.00	12.99	100.00	22.01
Competition	Competition index	0.00	49.54	212.50	53.16
Competition	Spruce browsing rate (0–1)	0.00	0.03	0.21	0.06
Competition	Fir browsing rate (0–1)	0.00	0.15	0.70	0.16
Competition	Beech browsing rate (0–1)	0.00	0.11	0.63	0.16
Soil	Soil water content (mm) - SWC	7.04	107.86	254.15	62.17
Soil	Soil water deficit (mm) - SWD	0.00	12.62	164.97	23.29
Soil	Soil water holding capacity (mm) - SWHC	13.08	46.89	85.83	16.46
Soil	Soil pH	3.95	5.89	8.48	1.30
Soil	Soil C:N	7.64	16.87	42.38	5.42
Stand structure	Canopy openness (%) - O	0.59	13.21	56.29	10.67
Stand structure	Total basal area (m²/ha)	10.72	36.65	133.30	18.46
Stand structure	Spruce basal area (m²/ha)	0.00	13.40	66.89	13.32
Stand structure	Fir basal area (m²/ha)	0.00	12.72	107.07	16.09
Stand structure	Beech basal area (m²/ha)	0.00	6.49	64.28	9.62
Topography	Altitude (masl)	515.42	1275.03	1795.79	307.11
Topography	Slope (°)	0.00	26.40	56.00	10.84

predictive variables for sapling densities and 3 for height increments.

2.2.2 Sapling densities

The model that explained sapling densities (N_{ijk}) for height class i of species j on plot k, as a function of sapling height (H_{ijk}) and a climate variable (V_{jk}), when significant, different for each species was:

$$N_{ijk} = a_j \times e^{(b_{jk} H_{ijk})} \times e^{(c_j V_{jk})} + \epsilon_{ijk}$$
$$b_{jk} \sim N(0, \tau_j)$$
$$\epsilon_{ijk} \sim N(0, \alpha_j)$$

(1)

a_j and c_j were species-dependent parameters and b_{jk} were parameters depending both on species and plot.

2.2.3 Unbrowsed sapling height increments

The other equation was inspired by the formulation of height increment of conifers by Ligot et al. (2020). A similar approach as earlier was followed for obtaining models explaining annual height increments. The chosen model for sapling height increments (ΔH_{ijk}) for an individual i of species j on plot k, as a function of sapling height (H_{ijk}), canopy openness (O_k) and a climate variable (V_{jk}), different for each species, was:

$$\Delta H_{ijk} = a_j \times H_{ijk}^{(b_{jk} + c_j V_{jk})} \times O_k^{d_j} + \epsilon_{ijk}$$
$$b_{jk} \sim N(0, \tau_j)$$
$$\epsilon_{ijk} \sim N(0, \alpha_j)$$

(2)

Both equations had a random plot effect, which was tested on different parameters.

2.2.4 Browsing

Due to the absence of height increment on a browsed sapling, it was not possible to include it as a factor in the earlier models. Hence, a preliminary exploration was carried out to identify the extent of browsing pressure and its possible damage. Browsing proportions of each species, and saplings of different heights were compared using 2 proportion z-tests, in order to estimate similarities and differences between different proportions. A proportion test (R function "prop.test" (Newcombe 1998)) was used to make comparisons, by specifying the alternative hypothesis to find out if the browsed proportions of each category are significantly different from one another.

3 Results

3.1 Main factors affecting sapling densities

Out of 152 sampled plots, 116 plots (76%) displayed some spruce regeneration, 128 fir regeneration (84%) and 104 beech regeneration (68%). However, the most obvious observation was the overall low regeneration densities (Table 3). Globally, even though only 3 plots (1.9%) displayed no regeneration, 40 plots (26%) had total sapling densities below 0.1 sapling per m^2, and only 22 plots (14.4%) displayed total sapling densities above 1 sapling per m^2. Only 2 plots had total sapling density of more than 3 saplings per m^2, indicating the low levels of regeneration.

Even though survival rates were not recorded, it was observed that smaller saplings of all three species (<50 cm height) were much more abundant than taller saplings (Fig. 3). Density of saplings of height above 50 cm quickly tended towards zero, which suggested the possibility of survival of very few saplings to older ages.

The equations and parameters representing models that best explained sapling densities are shown in Table 4. The graphic representations shown in Fig. 3 represent predictions and confidence intervals (95%) from these models. All the models that were tested are described in Table 5.

The selected models showed that densities of saplings in all three species decreased exponentially with increasing height. Additionally, spruce densities decreased exponentially with increasing mean monthly PET (Fig. 3a); fir densities increased exponentially with increasing mean monthly precipitation over the year (Fig. 3b); and beech densities increased exponentially with increasing annual mean of monthly soil water content (SWC) (Fig. 3c). Apart from that, a random effect was observed for sapling densities, which could be a result of many other potential plot-specific factors that could not be separated and/or quantified. This effect was stronger for spruce, followed by beech, and least for fir (Fig. 3).

Among all climate and soil variables (V) tested in Eq. 1, even though the most significant ones were selected for each species, there were some other models that were significant as well, but did not make sense ecologically. For example, the density model for beech with height and PET had the lowest AIC value, but the model produced negative sapling densities, and had to be discarded. Additionally, some significant models had higher AIC values (Table 5). For example, spruce sapling densities were more affected by temperature and precipitation variables, but not so much by soil water conditions. Fir and beech however showed more sensitivity to soil nutrients and soil water conditions. Unfortunately, addition of biotic factors like the competition index and browsing index to the model was not found to be significant. The level of significance of these models also differed, as described in Table 5.
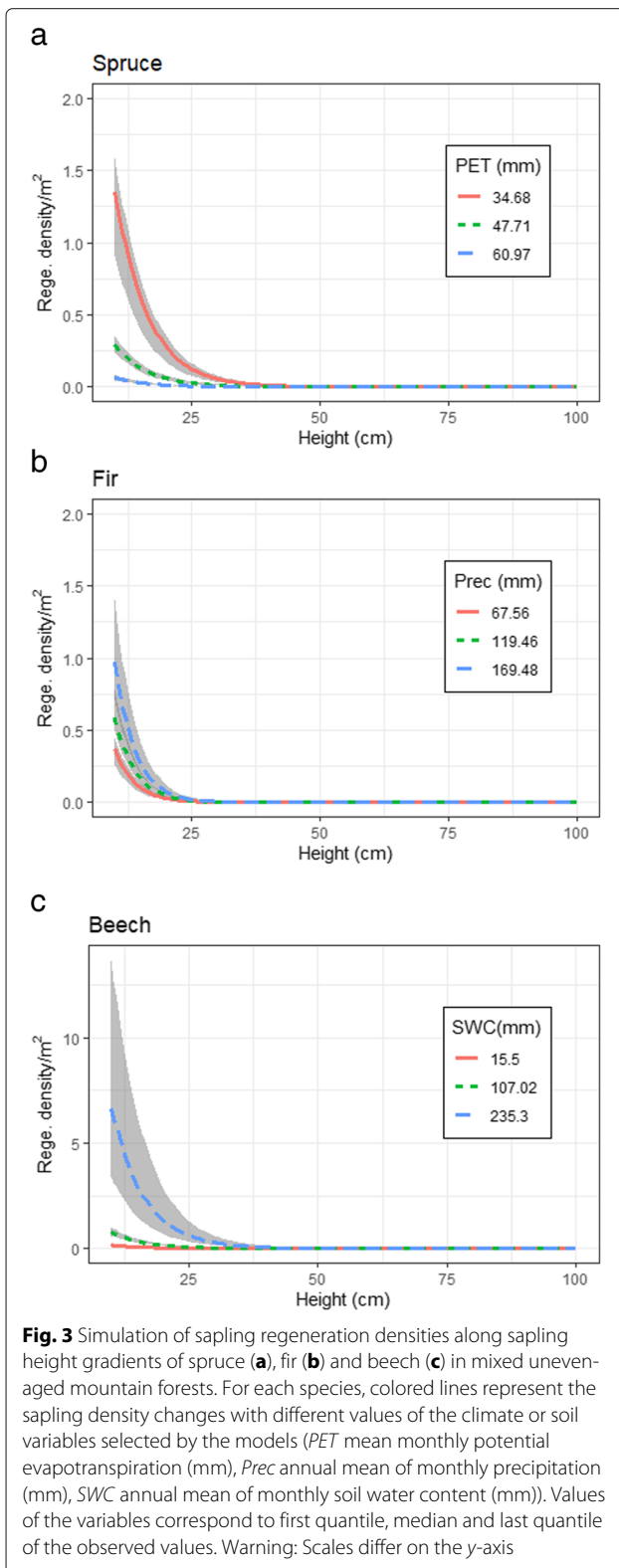
3.2 Main factors affecting unbrowsed sapling height increment

The measured annual height increment of saplings varied from 0 to 50 cm. The increment of unbrowsed saplings was highest for beech, followed by spruce, and fir displayed the lowest annual height increment, specially for saplings taller than 300 cm. The same approach and environmental variables were tested for models explaining height increments, as for sapling densities.

The most significant model showed that the annual height increment of an unbrowsed sapling depended on species, height, canopy openness and the maximum summer temperature observed on the plot (for spruce and beech). The equations and parameters representing models that best explained sapling height increments are

Table 3 Distribution of regeneration density and annual height increment values across species and height classes (H1 = 10–50cm, H2: 51–150cm, H3: 151–300cm, H4: 301cm–DBH 7.5cm)

Species	Ht. class	No. of inds.	Rege densities (per m^2)			Annual increment (cm)		
			Mean	**Max**	*SD*	**Mean**	**Max**	*SD*
Spruce	1	243	0.052	2.195	0.201	1.802	6.670	1.167
	2	228	0.017	0.304	0.037	3.048	16.500	2.441
	3	147	0.007	0.177	0.019	5.656	21.500	4.612
	4	102	0.006	0.154	0.017	10.310	50.000	9.203
Fir	1	326	0.138	2.778	0.383	1.336	5.120	1.026
	2	248	0.022	0.309	0.044	3.242	10.330	2.343
	3	166	0.009	0.130	0.019	6.498	23.000	4.969
	4	151	0.008	0.141	0.017	11.308	36.670	7.641
Beech	1	232	0.130	7.506	0.642	2.570	11.170	2.332
	2	204	0.058	2.041	0.214	4.568	11.890	3.521
	3	166	0.016	0.790	0.067	9.349	37.830	7.203
	4	157	0.011	0.346	0.035	11.181	38.330	9.572

Fig. 3 Simulation of sapling regeneration densities along sapling height gradients of spruce (**a**), fir (**b**) and beech (**c**) in mixed uneven-aged mountain forests. For each species, colored lines represent the sapling density changes with different values of the climate or soil variables selected by the models (*PET* mean monthly potential evapotranspiration (mm), *Prec* annual mean of monthly precipitation (mm), *SWC* annual mean of monthly soil water content (mm)). Values of the variables correspond to first quantile, median and last quantile of the observed values. Warning: Scales differ on the *y*-axis

shown in Table 6, whereas the results shown in Fig. 4 represent predictions and confidence intervals (95%) from these models.

Among our sampled species and individuals, the annual height increment of an unbrowsed sapling was most importantly limited by the height of the sapling. Smaller saplings typically grew slower, with differences among species. Canopy openness (hereafter, O) also determined the growth levels of saplings. The results of the selected model (explained in Section 2.2) revealed that the growth of all saplings was very low at canopy openness below 10%, growing rapidly as it increased, following a power function and reaching almost a horizontal curve at canopy openness levels above 40%. Taller saplings reached this horizontal asymptote at higher canopy openness than smaller saplings.

Saplings belonging to different species also displayed different maximum growths. Beech saplings grew most rapidly followed by spruce, while the least height increment was recorded by fir.

Beech and spruce growth was negatively affected by maximum summer temperature (Fig. 4a, c). Silver fir growth did not directly depend on any other environmental factors that we took into account in our dataset (Fig. 4b). Apart from that, plot-specific differences were observed in sapling height increments as well, indicating a considerable random effect. This effect was stronger for beech, followed by spruce, and least for fir.

The significance of other tested climate and soil variables was less obvious for height increment of saplings of all species than for densities, based on high *p*-values for other variables (Table 7). The closest models strengthened the dependence of beech and spruce on temperature, as they included different temperature variables like minimum winter temperatures and maximum monthly temperatures.

3.3 Browsing rates

Out of a total of 2370 saplings that we documented, 242 saplings were browsed or damaged by ungulates at the terminal shoot. This number varied greatly among saplings of different heights and species. Among the different height classes, the most browsed were saplings below 150 cm, which were easily accessible to most browsers. However, within the three species, there was a clear difference in the preference of wild ungulates. As seen in Fig. 5, and confirmed by the two-proportion *z*-tests, fir was the most browsed species among the three (14%), followed by beech (11%). However, the *z*-test showed no significant difference between the total browsing proportions of the two species ($p = 0.127$). Spruce was the least browsed with 2% of all the saplings browsed, much less than beech ($p = 3.447e{-}16$) and fir ($p = 1.128e{-}11$).

Table 4 Parameter values for density models of each species. For each of the fixed parameters (a, b, c) are shown the estimates, the SD and the *p*-value, along with the random effect SD and residuals
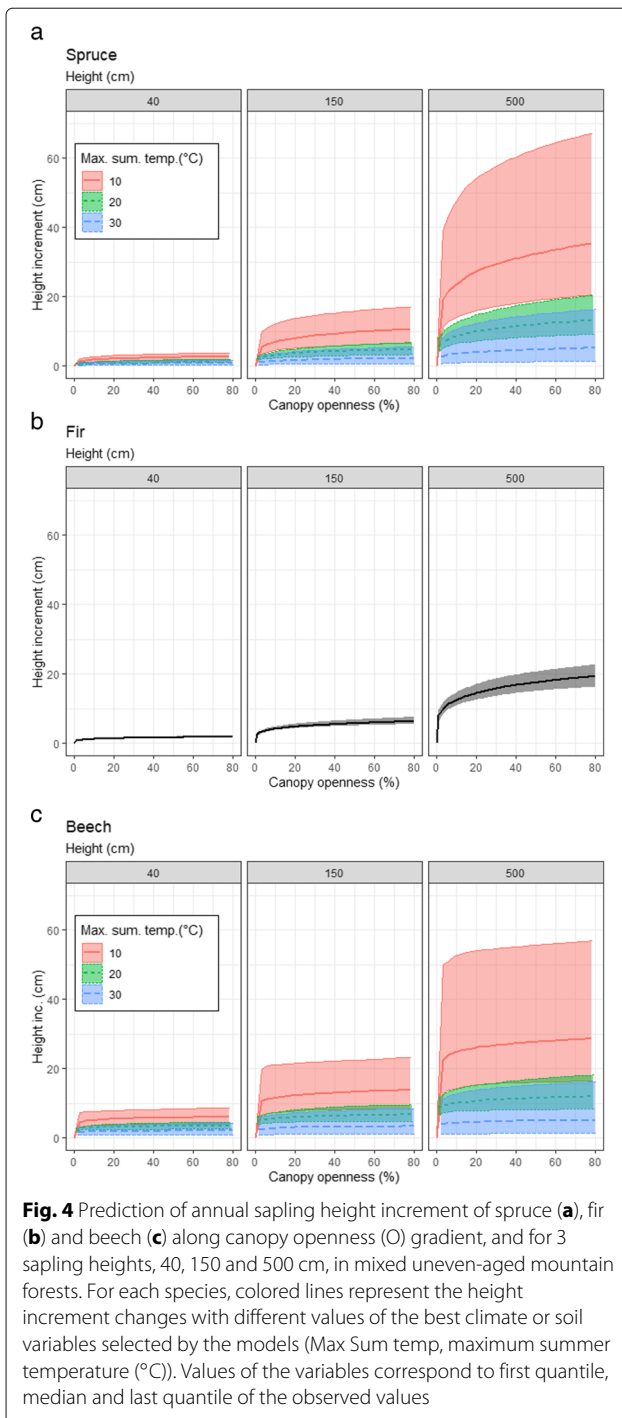
Species (j)	a_j	σ_a	*p*-value	b_j	σ_b	*p*-value	c_j	σ_c	*p*-value	σ (RE)	Residuals
Spruce	381.07	139.271	0.007	−0.159	0.006	0	−0.115	0.01	0	0.046	0.022
Fir	2.489	0.56	0	−0.256	0.01	0	0.01	0.003	0	0.074	0.031
Beech	0.611	0.055	0	−0.16	0.01	0	0.017	0.001	0	0.071	0.096

Table 5 AIC, MSD and *p*-values of NLME models tested for estimating sapling densities of spruce, fir and beech, V* = V_{jk} from the equation $N_{ijk} = a_j \times e^{(b_{jk}H_{ijk})} \times e^{(c_jV_{jk})} + \epsilon_{ijk}$, where N_{ijk} = sapling densities for height class *i* of species *j* on plot *k*, as a function of sapling height (H_{ijk}) and a climate variable (V_{jk})

Category	V* (density)	Spruce			Fir			Beech		
		AIC	MSD	*p*-value	AIC	MSD	*p*-value	AIC	MSD	*p*-value
Climate	Max montly temp (°C)	−2708.05	0.00	0.01	−2176.43	0.00	0.57	−836.59	0.01	0.81
Climate	Max summer temp (°C)	−2709.64	0.00	0.01	−2176.42	0.00	0.46	−836.59	0.01	0.81
Climate	Mean monthly prec (mm)	−2721.86	0.00	0.00	−2192.21	0.00	0.00	−434.47	0.03	1.00
Climate	Min winter temp (°C)	−2734.95	0.00	0.00	−2176.01	0.00	0.83	−819.25	0.01	0.02
Climate	PET	−2735.27	0.00	0.00	−2175.99	0.00	0.70	−976.68	0.01	0.00
Soil	Soil C:N	−2706.40	0.00	0.01	−2224.78	0.00	0.00	−887.11	0.01	0.00
Soil	Soil pH	−2699.82	0.00	0.10	−2182.65	0.00	0.01	−926.09	0.01	0.00
Soil	Soil water content	−2697.33	0.00	0.23	−2188.04	0.00	0.00	−948.82	0.01	0.00
Soil	Soil water deficit	−2696.23	0.00	0.45	−2178.15	0.00	0.03	−857.57	0.01	0.00
Soil	Soil water holding capacity	−2695.30	0.00	0.84	−2195.53	0.00	0.00	−892.56	0.01	0.00

Table 6 Parameter values for growth models of each species. For each of the fixed parameters (a, b, c, d) are shown the estimates, the SD, and the *p*-value, along with the random effect SD and residuals

Species (j)	a_j	σ_a	*p*-value	b_j	σ_b	*p*-value	c_j	σ_c	*p*-value	d_j	σ_d	*p*-value	σ (RE)	Residuals
Spruce	0.030	0.006	0.000	1.170	0.130	0.000	−0.016	0.007	0.030	0.190	0.030	0.000	0.102	2.727
Fir	0.029	0.006	0.000	0.904	0.037	0.000	0.201	0.030	0.000	–	–	–	0.104	2.733
Beech	0.431	0.072	0.000	0.774	0.133	0.000	−0.015	0.008	0.056	0.077	0.041	0.059	0.094	1.478

Fig. 4 Prediction of annual sapling height increment of spruce (**a**), fir (**b**) and beech (**c**) along canopy openness (O) gradient, and for 3 sapling heights, 40, 150 and 500 cm, in mixed uneven-aged mountain forests. For each species, colored lines represent the height increment changes with different values of the best climate or soil variables selected by the models (Max Sum temp, maximum summer temperature (°C)). Values of the variables correspond to first quantile, median and last quantile of the observed values

4   Discussion

4.1   Understanding regeneration densities

As observed by forest managers and scientific studies such as Kräuchi et al. (2000); Lines et al. (2019), our study sites had low overall regeneration density of spruce, fir and beech. On an average, all three species had a large number of saplings lower than 50 cm height (Table 3), with a steep decrease in the number of taller saplings.

This suggested that the reason for low total sapling densities was not the limitation of seed rain or germination, but low survival rates (Simon et al. 2019). As annual survival rates were not recorded, we relied on diminution of densities across height classes to evaluate survival. Fir densities decreased most rapidly with sapling height, indicating high early mortality, possibly due to high browsing rates of fir. This has also been observed by Nagel et al. (2015) and Bernard et al. (2017). There was no direct effect of browsing observed on sapling densities. However, through its strong effect on growth, browsing maintained saplings at lower heights, and higher mortalities, reducing the density of taller saplings indirectly. Comparison of sapling densities with enclosed experimental plots is necessary to clarify this effect of browsing on density (Bernard et al. 2017). We, however, identified other key factors affecting sapling densities and height increments.

As stand conditions are often the result of multiple historic events (climate extremes, management, browsing pressure etc.), it was impossible to disentangle the different effects, or put in evidence general rules of what is a compromising factor in a given environment (Benavides et al. 2016). Models were tested to evaluate the effect of light (Ligot et al. 2014; Orman et al. 2021; Lochhead and Comeau 2012), basal area (Stancioiu and O'Hara 2006), water availability (soil and atmospheric) (Löf and Welander 2000; Moser et al. 2016), temperature (Schurman et al. 2019; Lombaerde et al. 2020), competition with other species (Thrippleton et al. 2017), browsing (Bernard et al. 2017) and many other variables that are known to affect regeneration densities (Table 2). We succeeded in identifying the most dominant variables affecting spruce, fir and beech densities, among the ones that we tested. However, the extent and intensity of these effects was species specific (Caron et al. 2021). Spruce regeneration densities improved in lower PET (potential evapotranspiration) levels, and significantly declined in higher PET levels, which is supported by Cienciala et al. (1992), who demonstrated high sensitivity of spruce trees to evapotranspiration. Among all the models tested, there were sometimes more than one significant models. In the case of spruce, all significant models (that were not selected) indicated temperature sensitivity of spruce. None of the models with soil conditions as an explanatory variable (except C:N) showed any significance. This is in contradiction to Dyderski et al. (2018), who showed the importance of soil pH and water logging for spruce regeneration. Beech densities increased with higher SWC. Many studies support this result as soil water availability is known to have an effect on both beech saplings and adults (Gessler et al. 2006; Pröll et al. 2015; Diaci et al. 2020). Fir densities relied least on climate factors, though it showed some sensitivity to annual precipitation, requiring higher water

Table 7 AIC, MSD and *p*-values of NLME models tested for estimating sapling annual height increments of spruce, fir and beech, V* = V_{jk} from the equation $\Delta H_{ijk} = a_j \times H_{ijk}^{(b_{jk}+c_jV_{jk})} \times O_k^{d_j} + \epsilon_{ijk}$, where ΔH_{ijk} = sapling annual height increment for an individual *i* of species *j* on plot *k*, as a function of sapling height (H_{ijk}), canopy openness (O_k) and a climate variable (V_{jk})

Category	V (Δ H)	Beech			Spruce			Fir		
		AIC	MSD	*p*-value	AIC	MSD	*p*-value	AIC	MSD	*p*-value
Climate	Max summer temp (°C)	3492.59	16.45	0.06	3386.98	6.66	0.03	3982.75	9.50	0.69
Climate	Max montly temp (°C)	3492.89	16.44	0.10	3387.15	6.67	0.04	3982.82	9.50	0.75
Climate	Min winter temp (°C)	3658.48	15.35	0.09	3387.15	6.67	0.04	3982.90	9.51	0.89
Climate	Mean monthly prec (mm)	3660.58	15.39	0.40	3389.27	6.69	0.07	3982.72	9.51	0.61
Soil	Soil pH	3488.73	16.50	0.15	3389.23	6.70	0.09	3982.29	9.50	0.47
Soil	Soil water holding capacity (mm)	3489.98	16.48	0.16	3389.22	6.66	0.10	3389.22	6.66	0.10
Climate	PET (mm)	3492.80	16.47	0.83	3388.85	6.71	0.10	3982.68	9.50	0.62
Soil	Soil water deficit (mm)	3493.23	16.52	0.24	3390.11	6.72	0.15	3390.11	6.72	0.15
Soil	Soil C:N	3492.53	16.48	0.47	3391.11	6.68	0.23	3391.11	6.68	0.23
Soil	Soil water content (mm)	3492.26	16.47	0.73	3391.00	6.65	0.28	3391.00	6.65	0.28

input to survive better. Though there are studies that indicate that fir can survive soil water deficits (Tinner et al. 2013), some also predict that the species will most likely suffer in severe drought conditions (Bottero et al. 2021). However, it is interesting to note the detrimental effect of water constraints on the three species, with either limitations in water input, uptake or evaporation. A look at Fig. 3 also suggests that the effects are stronger for spruce

and beech and that they are more climate sensitive than fir. There are multiple studies discussing tree and sapling drought tolerance of the three species which conclude that all three species show signs of drought sensitivity (Cailleret et al. 2013; Löf et al. 2005; Silva et al. 2012), though there is a debate about their comparative sensitivities (Diaci et al. 2020; Schall et al. 2012; Zang et al. 2014; Vitali et al. 2017).
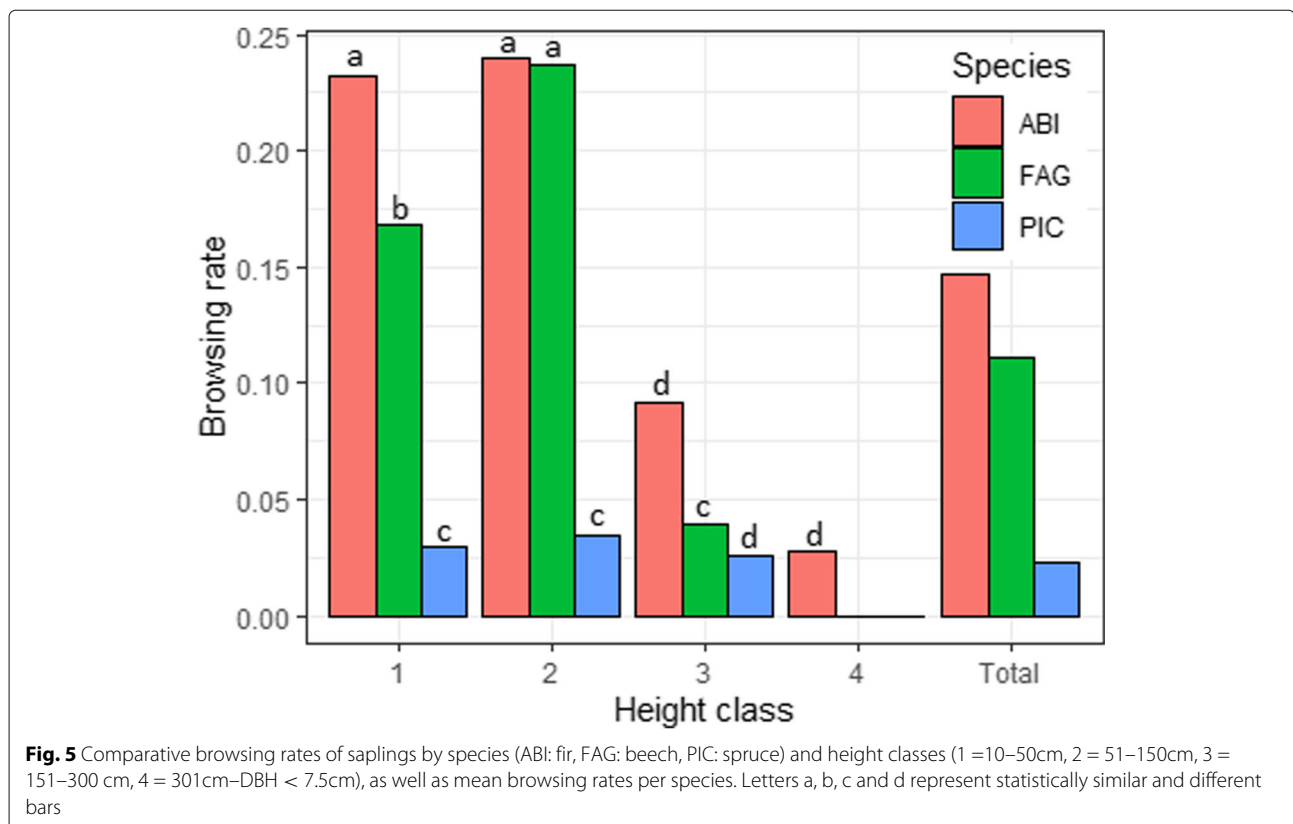

Fig. 5 Comparative browsing rates of saplings by species (ABI: fir, FAG: beech, PIC: spruce) and height classes (1 =10–50cm, 2 = 51–150cm, 3 = 151–300 cm, 4 = 301cm–DBH < 7.5cm), as well as mean browsing rates per species. Letters a, b, c and d represent statistically similar and different bars

We assumed fecundity (or seed rain) of a species to be directly proportional to its conspecific basal area on the stand (similar to Paluch et al. (2019)), and we expected sapling densities be directly proportional to the conspecific BA as well. However, higher BA also reduces light availability, which can hinder regeneration. There was no clear relation between regeneration and BA, perhaps because the two effects could compensate each other, or maybe our plot size was too small for BA to be a good predictor of the local seed rain, or BA was not a good predictor of light at this local scale (the canopy is too heterogeneous). Similar observations have been made by Comeau et al. (2006).

There was high variability in the regeneration data collected both within and between plots. The variability within a plot was probably due to the strong heterogeneity of the environmental factors experienced by individual saplings (Schurman et al. 2019; Diaci et al. 2020): gaps could make a strong difference below the heterogeneous canopies of these forests, soil was extremely heterogeneous with large rocks, modifying soil depth drastically within distances of a few centimetres. The variability between plots was often difficult to interpret and was translated into high plot effects in our model. These could be due to many factors difficult to record: past management history, soil conditions and complex climate effects poorly represented in the interpolated climate data to name a few.

4.2   Sapling height increments
The maximum annual height increment reached by a sapling was primarily determined by its height, canopy openness of the plot and maximum summer temperature (for spruce and beech).

The height increment of a sapling was limited by its height, with taller saplings showing higher increments. In comparison with studies like Ligot et al. (2013) carried out in forests in the Belgian Ardennes (40 cm/year increment for 250-cm-high beech sapling), sapling height increments in our study were relatively modest (15 to 25 cm/year for a 700-cm-high beech sapling), but comparable to other studies such as Dobrovolny (2016) (16 cm for a 200-cm-high beech sapling) carried out in mountain forests.

When plotted against canopy openness (O), the shape of height increment curves for saplings of different heights were similar for the three species (Fig. 4). In particular at low O (<10%), the three species presented very low growth, with beech growth slightly above fir and spruce. This finding was in contradiction with those of Stancioiu and O'Hara (2006) who reported out-competition of spruce by beech and fir growths, but in agreement with Ligot et al. (2020), who observed comparable height growths for spruce and fir. Fir is known to be more shade

tolerant than spruce (Diaci et al. 2020; Klopcic et al. 2012) and is expected to have a low growth rate in shade with a low mortality (Kobe et al. 1995). However, more recent work showed that sapling size (ontogeny) must also be considered in that tolerance to shade (e.g. Niinemets (2006)). Messier et al. (1999) defined a critical size for a given light level above which the sapling do not survive. This critical size is higher for shade-tolerant species. It could also explain why small saplings can easily be found under low canopy openness and that higher saplings are only found under higher canopy openness (Dreyer et al. 2005).

However, height and canopy openness were not the only factors affecting height increment. Being sensitive to summer temperatures (Schurman et al. 2019), spruce grew slower in sites with higher maximum summer temperatures. The growth of beech was also inversely proportional to maximum summer temperatures, as also shown in adult trees by Seynave et al. (2008), which is probably due to its sensitivity to higher temperatures and droughts (Gessler et al. 2006; Maes et al. 2018). We could not see any direct climate effect on fir, possibly due to multiple interacting effects that could not be caught in our models. There is also a possibility that high browsing rates, and hence a high proportion of saplings with zero increments (which were not included in the model), led to an inconclusive effect of any environmental variable on fir sapling increments. Even though spruce and beech have different niches, and occur more frequently in different altitudes, it is crucial to note that summer temperatures affect the growth of regeneration of both species. This trend seems rather general and could potentially affect fir as well (Vitasse et al. 2019).

4.3   Browsing
A significant number of saplings (18.6%) were browsed by wild ungulates such as deer, roe deer and chamois, either at the terminal shoot or at peripheral branches, though the actual impact of these animals on sapling density and growth is difficult to evaluate. However, it does reduce or stunt the growth of a significant number of saplings by chewing off the terminal buds that are sometimes even fatal for small saplings (picture of a representative sapling shown in Fig. 6). Very often, the saplings are also browsed very frequently while they are very young, dying or disappearing even before they are counted for studies like ours. This alters the regeneration composition altogether and could result in loss of data needed to understand the process. This remains a challenge in regeneration studies attempting to understand the effect of browsing.

Establishing a direct relation of ungulate browsing with sapling densities or height increments was hence a difficult task, and we did not succeed to include it in the above models. However, the extent of damage by browsing on

Fig. 6 An old fir sapling, completely browsed every year by animals, thus losing any chance to grow

the field prompted us to explore browsing rates, which turned out to be concerning. Among the three species that we observed, there was a clear and strong preference of browsers towards fir, followed by beech (comparable to fir), and spruce was seldom touched. The affinity of various ungulates to fir is well studied and documented (Bernard et al. 2017; Heuze et al. 2005; Häsler and Senn 2012; Nagel et al. 2015), with an alarming reduction in fir regeneration in areas of high ungulate population. Beech, however, is not commonly known as one of the popular choices of these animals. This indicates that the browsing pressure was quite high in our field sites, and ungulates were forced to eat beech as there was no fir available anymore. It also highlights once again, the high vulnerability of fir, and possibly beech in the future, to browsing by ungulates.

4.4   Regeneration dynamics and management implications

Saplings of all the three species can grow faster as they grow higher, but their mortality also increases, leading to very few of them reaching a tree recruitment stage. It is not difficult to conclude that these processes could lead to low tree recruitment, and that is exactly what we observed. Only 34 plots out of 152 sampled had trees

between the DBH of 7.5–8 cm (assumption is that they have been recruited in the last 5 years), with 5 spruce trees, 45 fir trees and 34 beech trees. Many of them looked evidently old, or unhealthy, thus unlikely that the reported number will survive or grow and contribute to overstory canopy or seed rain. This confirms the concerns of the foresters about limited tree recruits.

It has been well established that the challenge of climate change is already affecting growth and survival of regeneration in forests. The most studied effect is probably that of temperature, as shown in studies all over the world (Schurman et al. 2019). Higher temperatures affect survival of plants and trees, causing species moving to higher elevations to find optimal temperatures (Munier et al. 2010; Tingstad et al. 2015; Benavides et al. 2016). However, the direct effect of temperature is often not so obvious, because temperatures are also involved in potential evapotranspiration. We observed a strong plant response to temperature, as well as variables that change water availability to the plant. Increasing temperature and decreasing precipitation is leading to increased frequency and intensity of droughts, and spring and summer droughts, in the growing season of plants could seriously jeopardise regeneration. Additionally, decreasing snow cover could affect water balance. This could be an indicator that mountains are transitioning from temperature to moisture limitation as discussed by Schurman et al. (2019), making predictions even more challenging as this will increase the weight of forest dynamics on local drivers.

All three species are seen to grow better in canopy openness of more than 10% in the plot, which could be an important management implication, to create big enough gaps to allow saplings to grow fast. At present in our sampling, half sites had canopy openness lower than 9.4% (median). This has also been studied and reported by others such as Diaci et al. (2020). Reducing BA will also reduce water losses by tree transpiration and could lead to a better water balance, favourable to regeneration (e.g. Bréda et al. (1995); Aussenac (2000)).

Our model predictions point out that among spruce, fir and beech, fir saplings have the highest mortality and lowest annual height increments. Added to that, the ungulate browsing is the highest in fir. This could create an advantage for spruce and beech regeneration, thus possibly starting a change in species composition of the stands (Dobrowolska and Bolibok 2019; Häsler and Senn 2012; Bernard et al. 2017; Heuze et al. 2005; Diaci 2002; Senn and Suter 2003; Thrippleton et al. 2017; Weisberg et al. 2005; Cretaz and Kelty 2002). However, spruce and beech are also more sensitive to climatic changes, specially limited by high temperatures and water availability. This could also reduce their chances of better survival. In spite of all this information, in our dataset, and in spite of being highly browsed, the highest observed tree recruits in the

last few years (7.5cm < tree DBH <8cm) belong to fir. Tinner et al. (2013) has also specified a much larger range of fir in the past. This could indicate a lower browsing pressure, and more favourable climatic conditions for fir in the past. However, when comparing it with the other two species, it could also be either that fir is more resilient than spruce to the factors that hinder its growth and spread, or is simply a lag in response by fir, or a lag in detection of this change by us.

4.5   Limitations and the way forward

One of the limitations in this study was the uncertainty about the reliability of measured and obtained data. In particular, due to the presence of large rocks, or heterogeneous soil conditions within a plot, soil variables could have been misled. The proxy of canopy openness did not always correspond well to the light available for saplings (Comeau et al. 2006), often due to the presence of intermediate layers of canopy formed by tall understory vegetation, or sometimes because of a wider-than-expected spread of the overstory canopy. Thus, we see in our data, a possibility of low basal areas, and low light levels occurring in the same plot.

The explored variables related to climate were all modelled, as it was unrealistic to directly measure them on-site for such a large area. Instead, we used the platform digitalis to simulate long-term climate on a 50-m spatial grid. This can lead to imprecisions in the climate really prevailing in the different considered sites, in particular in mountainous areas with strong topological effects (Piedallu et. al. 2021 (submitted)). But most importantly the simulated variables give the general climate above tree canopy and not the one experienced by the saplings in the understory, that is to say the micro-climate. Indeed, micro-climate at the soil level can be very different from the climate depending on stand density and structure (Aussenac 2000). Of course, the first affected variable is radiation we approximated by canopy openness, with some concerns we already debated above. Linked to attenuated radiation, air temperatures are buffered by the tree canopy, with lower maximum and higher minimum (Gaudio et al. 2017). Tree canopy also intercepts precipitation resulting in less water available in the understory than predicted by incident climate variables and affecting the stand water balance (Barbier et al. 2009). Therefore, the micro-climate experienced by the sapling has opposite components, in one hand a buffered air temperature limiting extreme events such as frost and heat, and also lowering vapour pressure deficit and PET, and so sapling evapotranspiration and in the other hand a periodic soil water deficit in the upper soil horizons linked to rainfall interception by trees. At the difference of adult trees, as sapling roots cannot reach the deeper soil horizons where water can be still present in drought periods, they are sub-

jected to periodic water constrains not monitored in the simulated general climate variables. All these considerations could explain why we had difficulties to have strong effects of other climate variables on sapling growth and density. Such a lag between the general increase in temperature linked to climate change and the effective shift in understory plant composition (including tree saplings) has already be reported (e.g. Dietz et al. (2020)). We also highlight the necessity to better monitor and understand the actual water regime experienced by the saplings as suggested by the high number of water-related variables having a significant effect in our models.

The variability in field studies such as this is so high that it questions the reliability of the "space for time" assumption if we want to use our results to predict changes in time. Monitoring of sites would be necessary to have more accurate results, but the very low fluxes of regeneration densities as well as tree recruitment require to do the monitoring on large scales or long durations.

5   Conclusions

To our knowledge, this is one of the first studies monitoring the regeneration state of spruce-fir-beech on such a large scale. It gives insights of the likely evolution of forest dynamics and composition in the considered area, with a slightly pessimistic prediction for some areas and species. The three species may be at risk because they respond negatively to factors such as low light conditions, browsing, high temperatures and drought. Spruce and beech suggest a possibility of higher vulnerability in instances of frequent and intense summer heat and drought situations. The strong preference of ungulates for fir puts it in a high risk in case of a rapid increase in ungulate browsing. We could therefore expect a diminution of adult tree recruitment and adult stand density of either species depending on local water and browsing conditions. This real diminution of adult density could lead to an increase of light under canopy beneficial to saplings, which could slow the changes. We could have a kind of resilience mechanism here that could prevent species exclusion. Smaller density would also mean smaller competition between adult trees and the total production could remain moreover the same for a while. However, we do not know how far such a mechanism could compensate the effect of recruitment diminution, with a potential risk of changing forest structures, with migration of species at one point.

Authors' contributions
BC, MU and PB conceptualised and designed the study. MU carried out the data collection with help from BC and PB. BC wrote the primary R codes for analyses, and the analyses were carried forward by MU. All the climate and soil

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satellite data was obtained by CP. MU wrote the manuscript with inputs from BC, PB and CP. All authors read and approved the final manuscript.

Availability of data and materials
The datasets generated during and/or analysed during the current study are available on the INRAE data portal www.data.inrae.fr with the following reference: https://doi.org/10.15454/J0NVlK.

Code availability
The code for all analyses was written in R software version 3.6.0 and version 4.0.2 (R Core Team (2017)). The function "nlme" from the R package "nlme" (Pinheiro et al. (2021)) was used to run models. All figures were produced using the package ggplot2 (Wickham (2009)). The custom code will be made available by the authors on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
The authors of this manuscript give their consent for publication of the manuscript on an open access basis. We understand that it will be freely available on the Internet and be seen by the public.

Competing interests
The authors declare that they have no competing interests.

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