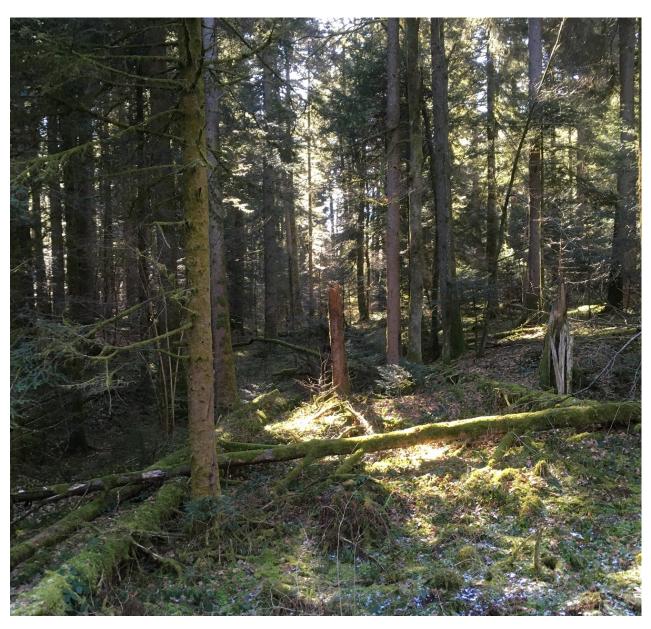


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Sample plot inventory in the Parc naturel du Jorat 2021



Swiss Federal Research Institute WSL, Birmensdorf December 2023

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Supplementary information is available on envidat https://www.envidat.ch/metadata/sample-plot-inventory-parc-naturel-du-jorat

Cover image:

A forest stand in the Parc naturel du Jorat (G. Projer)

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Abbrevations

CE Common era

CWD Coarse Woody Debris

D₇ Diameter at 7 m height

DBH Diameter at breast height (Diameter at 1.3 m)

FRM Forest Reserves Monitoring

NFI National Forest Inventory

PNJ Parc Naturel du Jorat

PNV Potential natural vegetation

SE Standard error

SP Sample plot

SPI Sample plot inventory

TreM Tree related Microhabitat

VLT Very large tree

WSL Swiss Federal Institute for Forest, Snow and Landscape Research WSL

Abstract

The Jorat is one of the largest continously forested areas in the Swiss Plateau. On a forested area of 778 ha, the Parc Naturel du Jorat (PNJ), a periurban parc, has been established in 2022. To document the initial state of the forest within the perimeter of the PNJ, a sample plot inventory (SPI) was carried out on 132 sample plots (SP) in winter 2021/22. The aim was to describe the condition and development of the forest structure and to compare it with the results of previous sample inventories in the same area carried out in 1994 and 2004. This report presents the results and interprets them in the context of research results from natural and virgin forests. The analysis is based on the two zones (core and buffer) of the PNJ.

Between the inventories 1994, 2004 and 2021, only slight changes in basal area can be observed whilst there was a pronounced decrease of the number of stems between 1994 and 2004. Since, the number of stems has increased again.

Within the forests of the PNJ, we found a high diversity of 25 tree- and shrub-species, including some non-native species such as Douglas fir ($Pseudotsuga\ menziesii$) and northern red oak ($Quercus\ rubra$). The long management history of the forest has not only introduced non-native species but as well altered the species composition. Whilst in absence of anthropogenic influence, beech ($Fagus\ sylvatica$) would dominate these forests, Norway spruce ($Picea\ abies$) and silver fir ($Abies\ alba$) dominate in the tree layer and make up about 60% of the number of stems and the basal area. In the regeneration layer, the dominance of these coniferous species is less pronounced, especially with trees $\geq 1.3\ m$ height and $< 7.0\ cm$ diameter at breast height (DBH) where beech is the most important species.

The only recently ceased management as well has an effect on the number of dead standing trees and on the volume of lying deadwood. The volume of both, dead standing trees (5.2 \pm 0.9 $\text{m}^3/\text{ha})$ and lying deadwood (8.0 \pm 2.8 $\text{m}^3/\text{ha})$ is lower than the values found in other beech dominated reserves and in primeval beech forests.

The results of the SPI 2021 show that former management still influences the forests in PNJ. In the coming decades, the forest will develop towards a more natural state. Basal area and volume will increase and the trees will grow bigger, resulting in more large trees, which provide habitat for a variety of organisms.

Effects of global change will increase the dynamics and consequently accelerate the development of the forests in the PNJ towards more natural species composition through an increase in mortality rates which will affect spruce in particular. This will result in increased light availability allowing an increase in recruitment and growth of other, most likely broadleaved pioneer species. Increased mortality will result in higher levels of standing and lying deadwood as well. In general, these developments will be favourable for the PNJ: The impression of the forest will become "wilder" as traces of previous management slowly disappear and the amount of dead wood increases.

1 Introduction

1.1 Site and management history

The Jorat is a forest area located north of the city of Lausanne in the Swiss Plateau and extending as far as Moudon. It is one of the largest forest areas in the Swiss Plateau, with about 40 km² of continuous forest. In a part of the Jorat, the Parc Naturel du Jorat (PNJ), a nature discovery park, was created in 2021 as part of the Swiss network of parks. The park covers an area of 9.4 km² and lies entirely within the boundaries of the city of Lausanne. It is only the second nature discovery park in Switzerland after the Sihlwald nature discovery park near Zurich. Since 2020, the core zone of the park has been designated as a natural forest reserve, where no management takes place, while the buffer zone will also be managed in the future. Management in the buffer zone will follow principles of "close to nature silviculture" based on natural regeneration and aim at increasing the volume and quality of deadwood. The PNJ is situated to the north of the city of Lausanne (46.58° N, 6.67° E) at an elevation between 750 m as a L(Ancien Abbay de Montheron) and 881 m as L (Plat Dessus). The terrain

between 750 m a.s.l (Ancien Abbay de Montheron) and 881 m a.s.l (Plat Dessus). The terrain is undulating and streams and rivers have cut shallow valleys into the plateau. The main river within the perimeter is the Talent, which has it's source near Chalet-à-Gobet in the south of the perimeter. Five clearings of varying sizes used for agriculture lie within the perimeter (Figure 2).

Geologically, the region is mainly characterised by moraines. Beneath the moraine material there is molasse consisting of sandstone banks with almost no marl layers. This layer is partially exposed in the valleys (Bersier 1953). Depending on the thickness of the moraine-layer, it's clay content and the topographic position, the soils are more or less permeable.

The forested area, which covers 778 ha of the perimeter, is mainly characterised by sites that would be dominated by beech in the absence of human intervention. In the valleys, there are also site types dominated by Ash and Elm, but these cover only a small proportion of the total area (Table 1).

The long history of management in the region has altered the forest both in terms of structure and species composition. The first forest planning for the forests of the city of Lausanne dates back to 1842 with the aim of managing the forests as high forests with an annual felling of about 5.8 m³/ha (Buchet 1925). Although the management history of the forest within the perimeter of the PNJ is documented, it was beyond the scope of this report to gather more information on the management history. However, aerial images spanning the period between ca. 1950 and 2021 show the effects of management and natural disturbances on the forest and the species composition (see Figure 1).

1.2 Research in the PNJ

1.2.1 Forest monitoring and dynamics

Besides the Sample plot inventory (SPI), the program Long-term Forest Ecosystem Research (LWF) of the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (WSL) maintains a permanent plot of 2 ha within the perimeter of the PNJ. This plot was established in September 1994 (Sutter and Waldner 2019). On the north-eastern edge of the

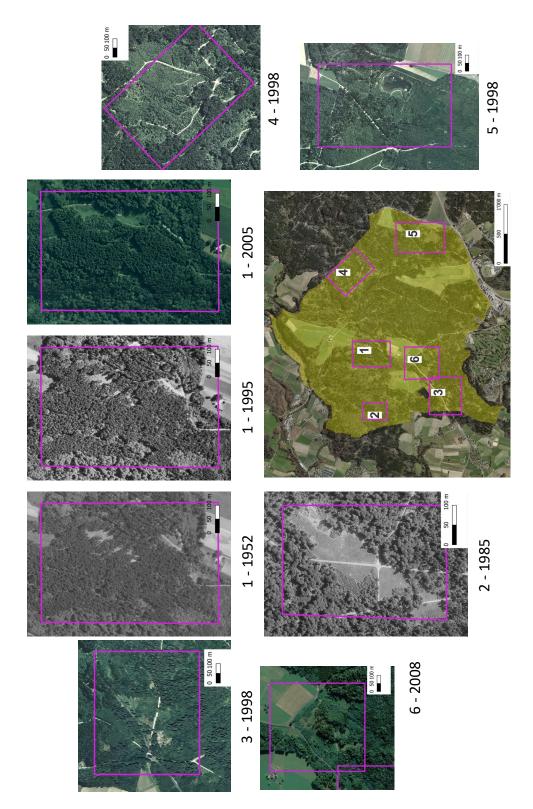


Figure 1: Indicators for management and tree planting within the perimeter of the PNJ. 1: Coniferous trees planted in the 1950. Images show the same extent in 1952, 1995 and 2005 respectively. 2: Clear cut patch with planted trees. Image aquisition in 1985. 3: Tree plantings of coniferous trees. Image aquisition in 1998. 4: Tree plantings (probably coniferous trees). Image acquisition in 1998. 4: Tree plantings (probably coniferous trees). Image acquisition in 1998. 6: Tree plantings. Image acquisition in 2008. All images by Federal Office of Topography swisstopo.

PNJ a site to study different planting-schemas to initiate the reforestation of windthrow-areas (Brang et al. 2015) was established in 2001 after the storm Lothar. The cantonal inventory (Direction générale de l'environment 2013), using non-permanent sample plots on a grid of 100 x 100 m, was carried out on the perimeter of the PNJ in 1994, 2004 and 2016.

1.2.2 Faunistic monitoring

In late 2020 and early 2021 a faunistic monitoring using 20 camera traps on an area of 1 km² was carried out to document the fauna at the time of the creation of the PNJ (Moreno and Christe). One important finding of the monitoring was that roe deer (*Capreolus capreolus*) is the most common species. More information can be found in the document itself

1.3 Aim of the sample plot inventory

The SPI in the PNJ was carried out to document the initial condition of the forest within the perimeter of the PNJ at the time of the designation of the parc. This will allow to track and quantify the development of structures important for biodiversity such as lying deadwood, changes in forest structure and in species composition. The sample plot inventory was carried out in winter 2021/2022 and allows to describe the state of the forest after the growing period 2021.

2 Inventory methods

2.1 Perimeter of the inventory and stratification

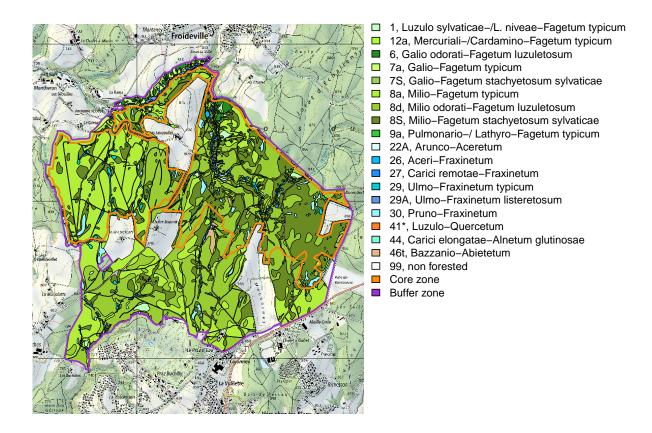
The perimeter for the sample plot inventory includes the forested area within the buffer and core zone of the PNJ and covers a total of 793 ha, of which the core zone covers 444 ha and the buffer zone 349 ha (Tables 1 and 2).

The stratification is based on the phytosociological map and the two zones (transition and core zone). For the phytosociological associations, we have combined all associations belonging to the *Milio-Fagetalia* in one stratum, while all other associations form the *Other associations* stratum. Due to the dominance of the *Milio-Fagetalia* within the perimeter, the *Other associations* stratum might not be analysable on its own, as the number of plots (N=19) is too small and the associations combined in this strata are too heterogeneous to be analysed. That is why we focus on the three strata *Core Zone*, *Buffer Zone* and *Milio Fagetalia* (Figure 2) and the total perimeter. Based on these strata we present estimates for the relevant forest characteristics and compare them over time based on the inventory of the Canton of Vaud.

2.2 Sample plot grid

To obtain approximately 60 plots in the strata *core zone* and *buffer zone*, we chose a grid of 200×300 m for the FRM inventory in 2021, resulting in a total of 132 sample plots (Table 2, Figure 3). Within the perimeter of the sample plot inventory there are a total of 778 non-permanent sample plots of the cantonal forest inventory, placed on a 100×100 m grid. Since these are not permanently marked, the development of individual trees can not be analysed but the data can be compared to the results of the strata and the perimeter.

Figure 2: Phytosociological associations within the perimeter of the sample plot inventory. One gridline on the background map represents 1km. Background map from Federal Office of Topography swisstopo.



2.3 Sample plot design

2.3.1 Inventory FRM

Sample plot inventories in the Forest Reserves Monitoring (FRM) project are based on the methods used in the Swiss NFI (Düggelin et al. 2020). On two concentric sample plots of 200 and 500 m², all living and dead standing and lying trees with a diameter at breast height (diameter at 1.3 m) (DBH) \geq 7 and 36 cm respectively are assessed. On these trees, DBH is measured and rounded down to cm. All trees are identified to species if possible and additional features, which are considered important for the indirect measurement of biodiversity such as Tree related Microhabitats (TreMs), are assessed. On a subset of all living and dead trees, tree height is measured. On three concentric subplots of 5, 10 and 20 m² trees below the calliper threshold of 7 cm are assessed in 3 height classes. On 3 transects of 15 m each, all coarse woody debris (CWD) intersecting with the transect with a diameter \geq 7 cm at the intersection is measured and the wood type (conifer / broadleaved) and the degree of deadwood decay assessed. Figure A2 gives an overview on the sample plot design.

Table 1: Strata formation and area of the respective strata in Parc naturel du Jorat

Stratum	Code Nais	Name Nais	Area
	8a	Milio-Fagetum typicum	228.3
Milio Eggetum	8d	Milio odorati-Fagetum luzuletosum	261.8
Milio-Fagetum	8S	Milio-Fagetum stachyetosum sylvaticae	206.7
	Total		696.8
	1	Luzulo sylvaticae-/L. niveae-Fagetum typicum	7.3
	6	Galio odorati-Fagetum luzuletosum	6.5
	7a	Galio-Fagetum typicum	5.8
	7S	Galio-Fagetum stachyetosum sylvaticae	4.6
	9a	Pulmonario-/ Lathyro-Fagetum typicum	0.1
	12a	Mercuriali-/Cardamino-Fagetum typicum	7.2
	22A	Arunco-Aceretum	0.9
Others	26	Aceri-Fraxinetum	0.4
Others	27	Carici remotae-Fraxinetum	15.8
	29	Ulmo-Fraxinetum typicum	5.8
	29A	Ulmo-Fraxinetum listeretosum	3.3
	30	Pruno-Fraxinetum	19.6
	41*	Luzulo-Quercetum	0
	44	Carici elongatae-Alnetum glutinosae	0.1
	46t	Bazzanio-Abietetum	3.6
	Total		81.1
Unstocked	Total		0.6
Jorat	Total		778.5

2.3.2 Cantonal inventory

The cantonal inventory of the Canton of Vaud does not permanently mark the centre of the sample plot nor the trees that are part of the sample plot. Depending on the stand type/number of stands and the dominant diameter on the respective plot, the area of each sample plot can be adapted (Direction générale de l'environment 2013). For plots with a dominant diameter < 30 cm, the radius is 9 m (area = 254.5 m² at 0° slope). On plots with a dominant diameter between 30 and 50 cm the radius is 10 m (area = 314.2 m² at 0° slope) and it is 11 m on plots with a dominant diameter \geq 50 cm (area = 380.1 m² at 0° slope). If the slope is \geq 30°, 1 m is added to the radii described above. If the dominant diameter is mixed, the "mean" of the two diameters is chosen (e.g., 10 m if the plot is covered by two stands with a dominant diameter > 50 cm and < 30 cm). For plots on slopes \geq 30°, the radius is adjusted by adding one meter to the radius just as for plots with only one dominating diameter. The tree population comprises all living trees with a DBH \geq 9.5 cm.

Table 2: Number of plots per stratum in the *Parc naturel du Jorat*. Columns *Plots FRM* and *Plots VD* identify the number of plots of the respective inventory per stratum. The 15 sample plots of the cantonal inventory (column *Plots VD*) that could not be assigned to a stratum might lie on parts of the perimeter that were not included in the phytosociologial mapping (e.g., roads).

Stratum	Plots FRM	Plots VD	Area [ha]
Core zone	73	429	444
Buffer zone	59	349	349
Total	132	778	793
Milio Fagetum	113	680	697
Others	19	83	81
Not assigned	0	15	-
Total Phyto	132	778	778

3 Data management and analysis

3.1 Datamanagement

The data gathered during the SPI 2021 has been checked for consistency and stored as raw data in the database "TreeDB" at WSL. The data gathered during the inventories 1994 and 2004 was provided by the canton of Vaud. The data of the 2016 inventory was not included in this report, as this inventory represents a state very close to the latest inventory. Derived data is available as supplementary material on envidat.ch (Stillhard et al. 2023).

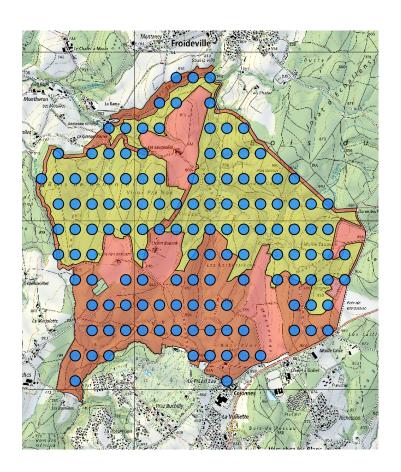
3.2 Data analysis

All data was analysed using the statistical software R, version 4.2.1 (R Core Team 2022). The scripts are based on the analysis presented in Brändli et al. (2020) and in Stillhard et al. (2021). These scripts rely on the package "forestinventory" (Hill et al. 2017).

3.2.1 Statistical framework

The analysis is based on a one-stage systematic random sampling approach (see Mandallaz 2008 for more information). In a first step, we calculated local densities (Y) of the target variable x (e.g., basal area), standardised to one hectare depending on the size of the sample plot located within the forest. Based on these values, the estimate for target variable (\hat{Y}) can be calculated as shown in equation 1 where s_2 is a set of n_2 uniformly drawn points that are independent of each other. The variance of $\hat{\mathbb{V}}$ of \hat{Y} is calculated following equation 2.

Figure 3: Strata and sample plots. One gridline on the background map represents 1km. Background map from Federal Office of Topography swisstopo.



Core zoneBuffer zoneSample plots

$$\hat{Y} = \frac{1}{n_2} \sum_{x \in s2} Y(x) \tag{1}$$

$$\hat{\mathbb{V}}(\hat{Y}) = \frac{1}{n_2} \frac{1}{n_2 - 1} \sum_{x \in s2} \left(Y(x) - \hat{Y} \right)^2 \tag{2}$$

3.2.2 Volume estimation

The volume estimation is based on the species specific volume functions applied in the National Forest Inventory (NFI) for Norway spruce, silver fir, European larch (*Larix decidua*), Douglas fir, beech and oak species (*Quercus* sp.) (Kaufmann 2001). For the remaining species, we applied the generalized functions for coniferous and broaleaved species respectively.

These functions require the following attributes: DBH, Diameter at 7 m height (D₇) and tree height. Whilst we assessed DBH on all trees, tree height was only measured on a subset of

about 25% of the population and D_7 was not measured. Tree height was predicted using a linear model based on the measured tree heights whilst D_7 was predicted using a linear model based on data from other forest reserves and managed plots in the Central Plateau.

3.2.3 Lying deadwood

Data for lying deadwood is based on Line intersect sampling on the three transects (see Figure A2). The volume of the lying deadwood per plot was calculated using equation 3 which follows Böhl and Brändli (2007).

$$V_j = \frac{\pi^2}{8 * L_j} * \sum_{i=1}^N \left(\frac{(d1_i + d2_i)}{2} \right)^2 * \frac{1}{\cos(\alpha_i)}$$
 (3)

where:

V_i: Volume of lying deadwood on Sample plot (SP) [m³]

L_i: Total length of the transects on the SP [m]

 d_1 , d_2 : Crosswise measuremed diameter of the i-th deadwood piece at the intersection with the transect [cm]

 α_i : Deviation of the *i*-th deadwood piece from the horizontal [degrees]

3.3 Inclusion of cantonal inventory

Data from the cantonal inventory includes only living standing trees with a DBH \geq 9.5 cm. To make this data comparable to the data collected during the sample plot inventory and the NFI-data, we removed all trees with a DBH < 12 cm. We only included sample plots that were assessed in both, the 1994 and 2004 inventory. As the sampling-grids in these two inventories were not fully congruent, we only retained 669 of the 778 non-permanent sample plots for the analysis.

4 Results

4.1 Development since 1994

Throughout all inventories, the species composition is dominated by the coniferous species Norway spruce and silver fir. Coniferous species had a share of about 60 % throughout all inventories, both regarding basal area and number of stems. There are slight changes between the inventories regarding the number of stems between the inventories. Between the 1994 and the 2004 inventory, we observe a decrease of about 25% of the number of trees (Table 3) but only a minor decrease of the basal area. The latter remained relatively stable throughout all inventories (Table 4).

Table 3: Number of trees of living standing trees with a DBH \geq 12 cm. Dataset: 669 SPs in 1994 and 2004, 132 accessible SPs 2021.

Species		994 /ha]		004 /ha]	2021 [N/ha]		
		± SE	x	\pm SE	Ā	\pm SE	
Picea abies	145	8	98	6	101	13	
Abies alba	106	5	95	4	112	10	
Pinus	-	-	0	0	-	-	
Larix decidua	2	1	2	1	2	1	
Pseudotsuga menziesii	9	2	7	2	12	5	
Other conifers	1	0	0	0	-	-	
Total conifers	262	9	204	7	227	15	
Fagus sylvatica	76	4	61	3	51	7	
Quercus	4	1	3	1	5	2	
Fraxinus excelsior	-	-	18	2	17	5	
Acer	38	4	12	1	14	3	
Populus	-	-	1	0	2	1	
Prunus	-	-	1	0	2	1	
Other broadleaves	15	2	19	2	24	6	
Total broadleaves	134	6	115	4	116	11	
Total	397	9	319	7	344	17	

4.2 State 2021

During the inventory 2021, a total of 1709 trees were assessed on 129 SPs.1645 were considered to be living, 64 to be dead. In total, 25 species were found for living trees and 12 for dead trees. The most frequent species was silver fir, the most frequent broadleaved species was beech, (Table 5). The maximum DBH measured was 152 cm on a silver fir (Figure 5) whilst the highest tree measured was a Norway spruce with a total height of 53.7 m (Figure A1).

4.2.1 Living trees

Number of stems On the total perimeter, we found 535 (\pm 27) living stems per ha with a DBH \geq 7.0 cm. With 341 (\pm 24) stems per ha, conifers are considerably more important than broadleaved species with 194 (\pm 19) stems per ha. The most common tree species was silver fir (183 \pm 19 N/ha), followed by spruce (144 \pm 19 N/ha) and beech (80 \pm 11 N/ha, Table 5). The number of stems in the core zone was slightly lower than in the buffer zone (548 \pm 45 N/ha, Table A2) with 525 (\pm 32) N/ha (Table A1). Conifer species were more frequent in the buffer zone (371 \pm 38 N/ha) than in the core zone (317 \pm 30 N/ha) while broadleaved species were more frequent in the core zone (208 \pm 24 N/ha) than in the buffer zone (176 \pm 30 N/ha, Tables A1 and A2).

Table 4: Basal area of living standing trees with a DBH \geq 12 cm. Dataset: 669 SPs in 1994 and 2004, 132 accessible SPs 2021.

Species		994 ² /ha])04 ²/ha]	2021 [m²/ha]		
	Ā	\pm SE		\pm SE	Ā	\pm SE	
Picea abies	14.1	0.7	11.4	0.6	10.2	1.2	
Abies alba	6.7	0.4	7.5	0.4	10.5	0.9	
Pinus	-	-	0.0	0.0	-	-	
Larix decidua	0.1	0.1	0.2	0.1	0.3	0.2	
Pseudotsuga menziesii	0.4	0.1	0.6	0.1	1.1	0.4	
Other conifers	0.0	0.0	0.0	0.0	-	-	
Total conifers	21.4	0.8	19.7	0.7	22.1	1.4	
Fagus sylvatica	5.9	0.3	6.1	0.4	5.0	0.6	
Quercus	0.3	0.1	0.2	0.0	0.3	0.1	
Fraxinus excelsior	-	-	1.0	0.1	1.2	0.3	
Acer	1.5	0.2	0.5	0.1	0.9	0.2	
Populus	-	-	0.0	0.0	0.5	0.3	
Prunus	-	-	0.1	0.0	0.1	0.0	
Other broadleaves	0.8	0.1	0.8	0.1	0.7	0.2	
Total broadleaves	8.4	0.4	8.8	0.4	8.7	0.8	
Total	29.8	0.7	28.5	0.7	30.8	1.4	

The DBH-distribution (Figure 5) shows that the number of trees decreases exponentially with increasing DBH. This is true for the total perimeter as well as for both, the buffer and the core zone.

Basal area The basal area on the total perimeter was 32 (\pm 5.7) m²/ha. More than 70 % of the basal area were covered by conifers (22.8 \pm 1.4 m²/ha). As with the number of trees, silver fir was also the most common tree species in terms of basal area (10.9 \pm 0.9). However, Norway spruce was more important than in the number of trees, with a total basal area of 10.5 (\pm 1.2) m²/ha. Beech, with 5.1 (\pm 0.6) m²/ha, covered only about half the basal area of the two dominant conifer species.

The basal area in the core zone (32.4 \pm 2.0 m²/ha) and in the buffer zone (31.4 \pm 1.7 m²/ha) did not differ considerably. However, when looking at the species, there was a higher basal area of Norway spruce in the core zone (11.3 \pm 1.8 m²/ha) compared to the buffer zone (9.5 \pm 1.7 m²/ha) and the basal area covered by beech was considerably lower in the buffer zone (3.7 \pm 0.8 mr/ha) than in the core zone (6.3 \pm 0.9 m²/ha).

Volume The volume on the total perimeter was 424.2 (\pm 20.6) m³/ha. As with basal area and number of stems, conifer species also contribute a considerably higher share to the total volume (305.6 \pm 19.9 m³/ha) than broadleaved species (118.6 \pm 11.3 m³/ha). As for basal area, this proportion exceeded 70% of the total volume.

Table 5: Absolute number of living and dead trees assessed during the SPI 2021 in PNJ. Dataset: 129 accessible SPs 2021.

species	Living	Dead
Picea abies	468	7
Abies alba	561	13
Larix Mill	12	
Pseudotsuga menziesii	47	
Other conifers		4
Fagus sylvatica	248	3
Quercus robur	8	
Quercus petraea	6	
Quercus rubra	6	
Fraxinus excelsior	72	17
Acer pseudoplatanus	58	
Populus nigra	3	
Populus tremula	9	
Betula pendula	13	2
Alnus glutinosa	40	1
Tilia cordata	10	
Prunus avium	8	1
Prunus padus	1	
Prunus mahaleb	6	
Salix caprea	24	11
Sorbus aucuparia	21	1
Sorbus torminalis	2	1
Carpinus betulus	4	
Other broadleaves		2
Corylus avellana	13	
Sambucus nigra	2	1
Hedera helix	3	
Total	1645	64

In contrast to basal area, the most important tree species in terms of volume share was Norway spruce, with a total volume of 149.8 (\pm 18.6) m³/ha. Silver fir was the second most important species with a volume of 138.0 (\pm 11.7) m³/ha, followed by beech with a volume of 70.8 (\pm 10.1) m³/ha.

4.2.2 Dead trees

In total we found 48 $(\pm$ 6) dead standing trees per ha. The total volume of these trees was 5.2 $(\pm$ 0.9) m³/ha. As with living trees, both the number and volume of dead standing trees were dominated by conifers (6). We observed a higher total number of dead standing trees in the buffer zone (59 \pm 12 N/ha) compared to the core zone (40 \pm 6 N/ha, Tables A1 and A2). However, the volume of dead standing trees did not differ between the core (5.4 \pm 1.3 m³/ha) and buffer (5.0 \pm 1.1 m³/ha) zone.

4.2.3 Tree related microhabitats

We found a total of 39.1 (\pm 4.6) habitat trees per ha on the total perimeter. Of these, 4.5 (\pm 1.2) per ha were giants (living trees with DBH \geq 80 cm, Table 7). The most frequent TreM on the total perimeter was dead wood in crown (14.0 \pm 3.9 N/ha). In total, we found 47.6 (\pm 6.5) TreMs per ha on living and dead trees (Table A4).

4.2.4 Lying deadwood

The total volume of lying deadwood amounted to 8.0 (\pm 2.8) m³/ha. About 50% of the total lying deadwood was considered to be solid (4.5 \pm 2.1 m³/ha), with rotten (1.7 \pm 1.3 m³/ha) and mould (1.2 \pm 1.1 m³/ha) deadwood being the second and third most common degrees of decay. Conifers were more common in the lying deadwood than broadleaves (Table 8).

We found a higher total amount of lying deadwood in the core zone (9.9 \pm 3.1 m³/ha) than in the buffer zone (5.6 \pm 2.4 m³/ha). This difference is mainly due to higher shares of rotten (2.3 \pm 1.5 m³/ha) and mould: (2.0 \pm 1.4 m³/ha) deadwood in the core compared to the buffer zone (rotten: 0.9 \pm 0.9, mould: 0.2 \pm 0.4 m³/ha). We observed a higher volume of broadleaved deadwood in the core zone (4.8 \pm 2.2 m³/ha) in comparison to the buffer zone (1.4 \pm 1.2 m³/ha).

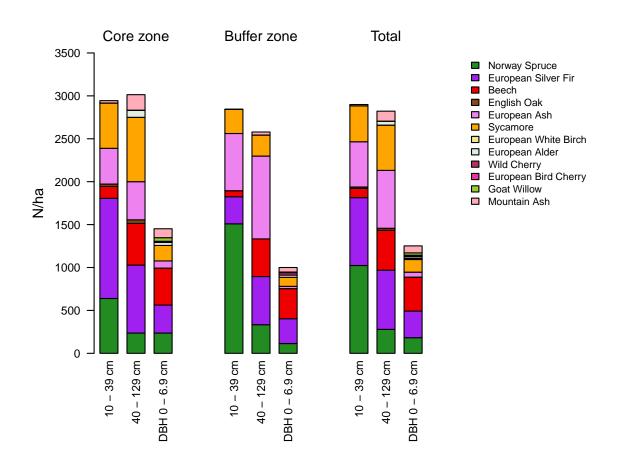
The Standard errors (SEs) for both, the degrees of decay and the total volume, are relatively high. The SE for the total volume of the lying deadwood - where we expect the SE to be lowest - spans about 70% of the estimate. This is an indicator for a high variability of deadwood availability between plots.

4.2.5 Regeneration

In the regeneration layer between a height \geq 10 cm and a DBH \leq 6.9 cm we found 12 tree species with a total number of 6973 (\pm 1133) stems per ha. The most common species in this layer was silver fir, followed by spruce and ash (Figure 7). The three most important species regarding the number of stems in the tree layer (silver fir, Norway spruce, beech) were found in the regeneration layer as well. However, European ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) accounted for more than 30% of the total number of stems in the regeneration layer whilst they only accounted for about 8 % of the number of stems in the tree layer.

We observed no decrease between the classes 10-39.9 cm height (2899 \pm 685 N/ha) and the class 40-129.9 cm height (2822 \pm 533 N/ha, Table A3). When looking at the two zones, only slight differences can be found. Three species found in the core zone did not appear in the buffer zone - English oak (*Quercus robur*), European alder (*Alnus glutinosa*) and wild cherry (*Prunus avium*) whilst conversely with European bird cherry (*Prunus padus*) and European white birch (*Betula pendula*) two species appearing in the core zone did not appear in the buffer zone.

Figure 7: Regeneration density [N/ha] in the regeneration layer by perimeter and species. Database: Core Zone 72 SP, Buffer Zone 57 SP, Total 129 SP. The three classes are assessed on three concentric subplots (see Figure A2). While trees in classes 10-39 cm and 40-129 cm are included on the basis of their height, trees in class DBH 0-6.9 cm are included on the basis of their DBH.



5 Discussion

5.1 Development 1994-2021

The species composition of the living trees reflects the long history of management within the perimeter of the PNJ. In the absence of anthropogenic influence, most forest types within the perimeter of the PNJ would be dominated by beech, with the only admixed coniferous species being silver fir. However, we observed a high proportion of the coniferous species Norway spruce and silver fir, accounting for more than 60 % of the total basal area in all inventories since 1994. In the 2004 inventory, we observed a slight decrease of both, the total basal area (1994: 29.8 m²/ha, 2004: 28.5 m²/ha) and the basal area of the conifers (1994: 21.4 m²/ha,

2004: 19.7 m^2/ha) which can be attributed to the windthrow caused by the storm "Lothar" in 1999. The total basal area of all broadleaved spieces remained relatively stable throughout all inventories (1994: 8.4 m^2/ha , 2004: 8.8 m^2/ha , 2021: 8.7 m^2/ha).

Compared to the latest results of the NFI, the total estimates for basal area for all inventories are in the range of the estimate presented for the economic region "Western Plateau" (31.9 \pm 1.9 m²/ha, Abegg et al. 2023*e*). However, the NFI reports a basal area of 15.0 (\pm 1.7) m²/ha for coniferous species and of 16.9 (\pm 1.5) for broadleaved species (Abegg et al. 2023*d*). Compared to the results of the NFI, the estimate for the basal area of conifers is higher and, conversely, the estimate for basal area of broadleaves is about 50% lower on the perimeter of the PNJ.

Looking at the number of trees per hectare, we found a similar pattern to that of basal area: A high proportion of about 60 % are conifers, with spruce being the most important species in the 1994 and 2004 inventories, whereas in the 2021 inventory, silver fir was the most important species. Beech, the most important broadleaved species, accounts for less than 20% of the number of trees in all inventories. This proportion, as well as the absolute estimate for number of trees, even decreased between the 2004 and 2021 inventories.

The forest covering the PNJ has changed only slightly since 1994. The dominance of coniferous species, mainly spruce and silver fir, can be seen as a legacy of past management that favoured these species. At present, there is no indication that the dominance of coniferous species will decrease in the near future.

5.2 State 2021

5.2.1 Living trees

Species composition The species composition of the living trees reflects the long management history within the perimeter of the PNJ. The high proportion of the coniferous species Norway spruce and silver fir does not correspond to the predominant phytosociological associations, namely the different types of Milio-Fagetalia. Without human intervention, these forests would be dominated by beech, with an admixture of silver fir and Norway maple. Another indicator of the past management is the presence of the non-native species douglas fir and red oak. Broadleaved species such as beech are less common than expected in these phytosociological associations, accounting for only about 40% of the number of trees.

The dominance of coniferous species is slightly less pronounced in the core zone than in the buffer zone. In the latter, even for trees with a DBH < 12 cm coniferous species make up more than 60 % whilst in the core zone, this value, about 55%, is slightly lower. The species compositition is still relatively far from what we would expect in a natural ecosystem.

Number of stems The number of stems does only slightly differ between the core (525 \pm 32 N/ha) and the buffer zone (548 \pm 45 N/ha). The number of stems on the perimeter of the PNJ (535 \pm 27 N/ha) is higher than in the Milio-Fagetalia stratum of the nature discovery park Sihlwald (435 \pm 37 N/ha, Brändli et al. 2020) but lower than the one found in the beech forests of the forest reserve Bettlachstock (756 \pm 56, Commarmot et al. 2017). The relatively sharp decrease in the number of stems between the lowest diameter class (7-11 cm DBH)

and the next lowest class (12-15 cm DBH) might be an indicator for former management and regeneration through tree planting.

Basal area As with number of stems, there are only slight differences in basal area between the core ($32.4 \pm 2.0 \text{ m}^2/\text{ha}$) and the buffer zone ($31.4 \pm 1.7 \text{ m}^2/\text{ha}$). Compared to other beech dominated reserves in Switzerland, the basal area of $32.0 (\pm 1.3) \text{ m}^2/\text{ha}$ is relatively low. Commarmot et al. (2017) found $35.5 (\pm 1.6)^2/\text{ha}$ in the beech forests of the forest reserve Bettlachstock, Brändli et al. (2020) found $36.1 (\pm 1.6) \text{ m}^2/\text{ha}$ in the Milio-Fagetalia of the nature discovery park Sihlwald and the basal area reported for a primeval beech forest in Western Ukraine is 36.3 ± 1.6 (Stillhard et al. 2022). Heiri et al. (2012) found mean values of about 39 m²/ha for 16 beech dominated forest reserves in Switzerland which have not been managed for at least 20 years. However, when compared to the latest results of the Swiss NFI, the basal area is comparable to that of the economic region "Plateau-West", reported with $31.9 \text{ m}^2/\text{ha}$ (Abegg et al. 2023e).

This relatively low value for basal area is, as the points mentioned above, a result of the former management wich just recently ceased. After the cessation of management, forests tend to accumulate biomass which is a function of basal area, until they reach the maximal basal area that can be sustained by the respective site and will then enter into a "steady state" where the respective values fluctuate around or just below the carrying capacity (Bormann and Likens 1979). Swiss forest reserves within the FRM network seem not to have reached this steady state even several decades after the cessation of management (Idoate-Lacasia et al. under Review).

Volume As with basal area and number of stems, there are only minor differences in volume between the core (436.8 \pm 31.5 m³/ha) and the buffer zone (408 \pm 23.5 m³/ha). The volume found on the total perimeter of the PNJ (424 \pm 20.4 m³/ha) is, as for basal area, lower than the volume found in Sihlwald (556 \pm 26.6) but higher than the 395.2 (\pm 29.0) m³/ha in the beech forests of Bettlachstock. Compared to the results of the NFI, the volume is higher than the volume of 373.5 (\pm 20.6) m³/ha found in the economic region "Western Plateau" (Abegg et al. 2023*a*).

There are forest reserves where, altough the basal area is higher, the volume estimates are lower (e.g., Bettlachstock, basal area: 35.5 m² ha⁻¹, volume: 395.2 m³ ha⁻¹). This can be attributed to differences regarding site productivity. Lower site productivity will result in trees that grow less high. Height however is an important variable in volume estimation, and changes in tree height will directly influence volume estimation. Just as for basal area, volume will increase in the coming decades in the absence of management.

5.2.2 Dead trees

There are non-significant differences in the numbers of dead standing trees between the core $(40 \pm 6 \, / \text{ha})$ and the buffer zone $(59 \pm 12 \, / \text{ha})$. These differences are partly caused by a high number of 26 (± 6) stems per ha of "Other conifers" in the buffer zone. The fact that these trees were not identified to genus or species level is an indicator of an advanced degree of decay that prevents identification. Although the number of stems is higher in the buffer zone

the total volume of the dead standing trees does only slightly differ between the two strata (Tables A1 and A2). The number of dead trees is within the range of the 52.5 (\pm 7.4) per ha found by Commarmot et al. (2017) in the forest reserve Bettlachstock and higher than the 34.0 (\pm 6.0) stems per ha reported by Brändli et al. (2020). The volume of the standing dead trees is considerably lower in the PNJ when compared to the results of the NFI which gives a value of 21.8 (\pm 4.4) m³/ha (Abegg et al. 2023*b*), the values found in the beech-forests of the forest reserves Bettlachstock (15.9 \pm 3.4 m³/ha, Commarmot et al. 2017) and Sihlwald (9.1 \pm 2.9 m³/ha, Brändli et al. 2020). The volume of dead trees in the PNJ is as well lower than the 31.9 m³/ha reported by Christensen et al. (2005) based on data from sample plot inventories from 16 beech-dominated forest reserves in Europe.

As with standing trees, conifers contribute a considerably higher proportion to both, the volume and the number of standing dead trees. The relatively high number of dead standing trees and the small volume of these trees indicates that most of the dead trees are relatively small and thus contribute only little to the volume (see Figure A7).

The combination of a lower volume of dead standing trees and a comparable number of dead trees reflects the forest structure which is still influenced by former management. Only few large trees which considerably contribute to the volume have died so far.

5.2.3 Tree related microhabitats

The amount of habitat trees is slightly lower than the 57.7 (\pm 7.4) per ha reported by Brändli et al. (2020). This difference can mainly be reltated to the lower values of trees bearing a TreM whilst the number of giants and the number of dead trees with DBH \geq 36 cm is slightly higher than the values provided by Brändli et al. (2020). For a variety of unmanaged beech forests across Europe Vandekerkhove et al. (2018) report a mean value for very large trees (VLT) of 13.9 (\pm 9.1).

The number of TreMs (see Table A4) is slightly lower than the 52.3 (\pm 7.2) per ha found in Sihlwald (Brändli et al. 2020) and considerably lower than the 189.5 (\pm 20.5) reported by Commarmot et al. (2017) for the beech forest in the forest reserve Bettlachstock. Whilst the most frequent TreMs are the same as in Sihlwald (Deadwood in Crown, Bark lession and Crown breakage), this is not the case for Bettlachstock. These differences can probably be explained by topographic features: The forests in Bettlachstock are located on relatively steep slopes and thus tree damages through rockfall are more prevalent than in Sihlwald and PNJ. The cumulative occurence probability of most TreM-types increases with increasing diameter (Courbaud et al. 2022) and depending on site factors densities and occurence probabilities of TreMs differ (Larrieu et al. 2022). In the PNJ, TreM-types with a high probability to occur already at smaller diameters according to Courbaud et al. (2022), such as bark lessions and dead wood in crown, are more frequent whilst TreMs where this probability is higher for higher DBH, such as cavities and hollow stems, are very rare. This reflects the relatively low number of VLTs in the PNJ. Higher numbers of VLTs will result in higher densities of TreMs in the future.

5.2.4 Lying deadwood

Lying deadwood is - together with the standing deadwood - an important habitat for saproxylic species. Larger amounts of deadwood result in an increase of these species (Haeler et al. 2021). The amount of lying deadwood non-significantly differs between the core and the buffer zone, with the latter showing the smaller total amount. The total amount of lying deadwood of 8.0 (\pm 2.8) m³/ha is very low. For mixed conifer forests in the economic region "Western Plateau", the NFI reports 24.3 (\pm 7.9) m³/ha of lying deadwood (Abegg et al. 2023c). The amount of lying deadwood is as well considerably lower than the ones found by Hermann et al. (2012) for six beech dominated forest reserves, which range from 20.1 to 100.5 m³/ha and the 154.5 m³/ha found by Stillhard et al. (2022) in a primeval beech forest in Western Ukraine. While it is not surprising that the values for lying deadwood are lower than those found in forest reserves or primeval forests, the derivation from the mean value reported by the NFI is remarkable. This is an additional indicator of the impact of former management on the current forest composition as is the small amount of lying deadwood in the higher decay classes.

5.2.5 Regeneration

The total number of the trees counted in the regeneration (6973 \pm 1133 per ha) is in the range of the 6196 (\pm 613) trees per ha reported by Brändli et al. (2020) but lower than the 21402 (\pm 4108) reported by Commarmot et al. (2017) for Bettlachstock. Given the stochastic nature of the process of regeneration (also seen in the high SE), the number of trees in the regeneration layer can be considered as average.

The species composition of the regeneration layer shows a similar pattern to the adult trees with a DBH \geq 7.0 cm. Looking at the total of all height classes, the two most important species are silver fir, followed by Norway spruce. This pattern is to be expected given the composition of the adult trees and consequently the availability of seed trees. In the seedling class (10-39.9 cm height) this pattern can be observed, where the two coniferous species, silver fir and Norway spruce, account for about 60% of the total number of trees. However, when compared to the adult trees, we observe a higher proportion covered by broadleaved species already in the saplings (40-129.9 cm height), where broadleaved species dominate with a proportion of > 50%. When looking at the recruits (trees taller than 1.29 to DBH < 7.0 cm) this pattern is even more pronounced. In this class, which consist of trees that have established and of which a larger proportion will survive to become an adult tree compared to the smaller classes, the most important species is beech followed by silver fir. This may indicate that the forest structure favours the more shade tolerant species beech and silver fir. Beech and silver fir are both known to be able to survive for a long time in shade, giving these species an advantage over more light demanding species such as Norway spruce (Petrovska et al. 2021).

6 Conclusion

The SPI 2021 in the PNJ documented the initial state of the forest at the moment of the establishment of the PNJ. It shows that the forest is still strongly influenced by the only recently ceased management. In the future, the naturalness of the forest will increase. As in other forest reserves in Switzerland and Europe basal area will increase, the number of stems will

decrease and the number of VLT will increase. Just as in other reserves, species composition, especially of the larger trees, will only slowly change towards a more natural state and the high proportion of conifer species in large trees may even increase.

Effects of global change will increase the dynamics and consequently accelerate the development of the forests in the PNJ towards more natural species composition through an increase in mortality rates which will affect spruce in particular (Thom and Seidl 2022). This will result in increased light availability allowing an increase in recruitment and growth of other, most likely broadleaved pioneer species. Increased mortality will result in higher levels of standing and lying deadwood as well. In general, these developments will be favourable for the PNJ: The impression of the forest will become "wilder" as traces of previous management disappear and the amount of dead wood increases. The latter will as well serve as important habitat for saproxylic species.

Figure 4: DBH distribution of all living trees with a DBH \geq 12 cm in 1994, 2004 and 2021 for the total perimeter. Database: 669 accessible SPs for 1994 and 2004, 129 SP in 2021.

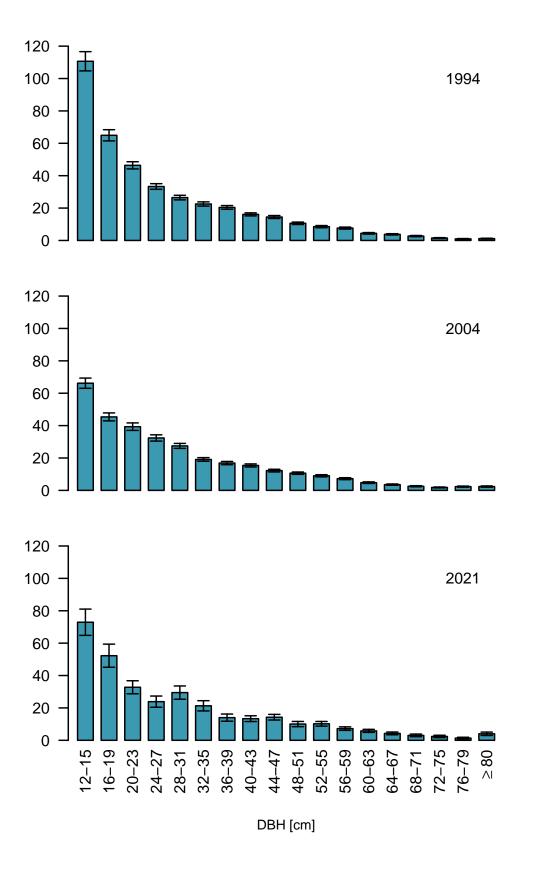


Table 6: Number of trees, basal area and volume of living trees and standing dead trees. Dataset: 129 accessible SPs 2021.

				Living		Dead trees				
Species	Number of stems [N/ha]		á	Basal area [m²/ha]		olume /ha]	Number of stems [N/ha]		Volume [m³/ha]	
		± SE	Ā	\pm SE	Σ	± SE	Ā	\pm SE	χ	\pm SE
Picea abies	144	19	10.5	1.2	149.8	18.6	4	1	0.7	0.3
Abies alba	183	19	10.9	0.9	138.1	11.7	5	3	1.1	0.6
Larix Mill	2	1	0.3	0.2	3.9	2.5	0	0	0.0	0.0
Pseudotsuga menziesii	12	5	1.1	0.4	13.8	5.5	1	1	0.0	0.0
Other conifers	-	-	-	-	-	-	20	3	1.5	0.2
Total conifers	341	24	22.8	1.4	305.6	19.9	31	5	3.3	0.8
Fagus sylvatica	80	11	5.1	0.6	70.8	10.1	1	1	0.3	0.2
Quercus	6	2	0.3	0.1	3.5	1.4	-	-	-	-
Quercus rubra	2	2	0.0	0.0	0.1	0.1	-	-	-	-
Fraxinus excelsior	24	6	1.3	0.3	16.7	4.1	6	2	0.9	0.3
Acer pseudoplatanus	20	4	1.0	0.3	11.6	3.2	1	1	0.0	0.0
Populus	2	1	0.3	0.2	4.6	3.6	-	-	-	-
Populus nigra	0	0	0.1	0.1	0.8	8.0	-	-	-	-
Betula pendula	5	3	0.1	0.1	1.3	0.6	1	1	0.0	0.0
Alnus glutinosa	15	5	0.4	0.1	4.8	1.7	0	0	0.1	0.1
Tilia cordata	4	3	0.1	0.1	0.7	0.5	-	-	-	-
Prunus	6	3	0.1	0.1	1.1	0.6	0	0	0.0	0.0
Salix caprea	9	4	0.2	0.1	1.5	8.0	4	3	0.4	0.3
Sorbus	10	3	0.1	0.0	0.6	0.2	1	1	0.1	0.1
Carpinus betulus	2	1	0.0	0.0	0.3	0.3	-	-	-	-
Other broadleaves	-	-	-	-	-	-	2	1	0.1	0.1
Corylus avellana	7	6	0.0	0.0	0.2	0.1	-	-	-	-
Sambucus nigra	1	1	0.0	0.0	0.0	0.0	0	0	0.0	0.0
Hedera helix	1	1	0.0	0.0	0.0	0.0		-	-	
Total broadleaves	194	19	9.2	0.8	118.6	11.3	18	4	1.9	0.5
Total	535	27	32.0	1.3	424.2	20.4	48	6	5.2	0.9

Figure 5: DBH distribution living trees within the perimeter of the PNJ. Database: Core zone: 72 SP, buffer zone: 59 SP, Total: 129 SP

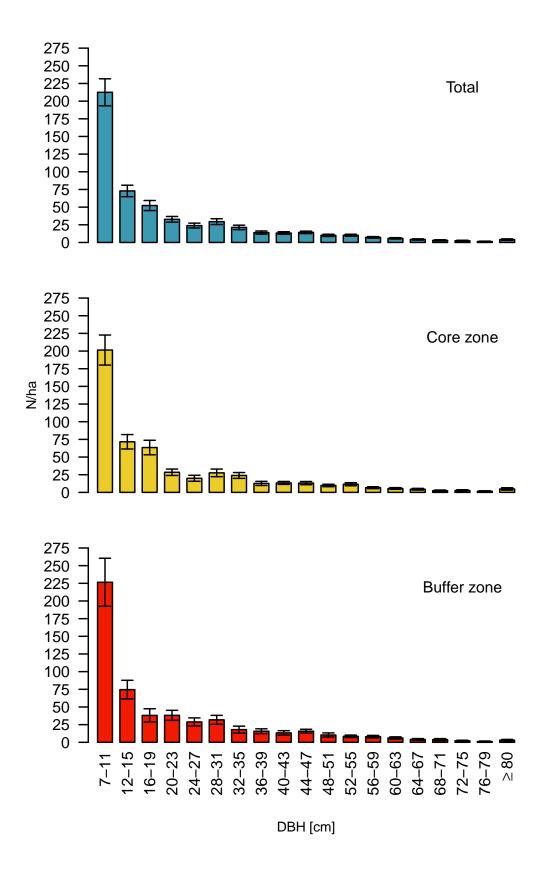


Figure 6: Species shares on basal area $[m^2 ha^{-1}]$ grouped by DBH-classes and perimeter. Dataset: 129 accessible SPs 2021.

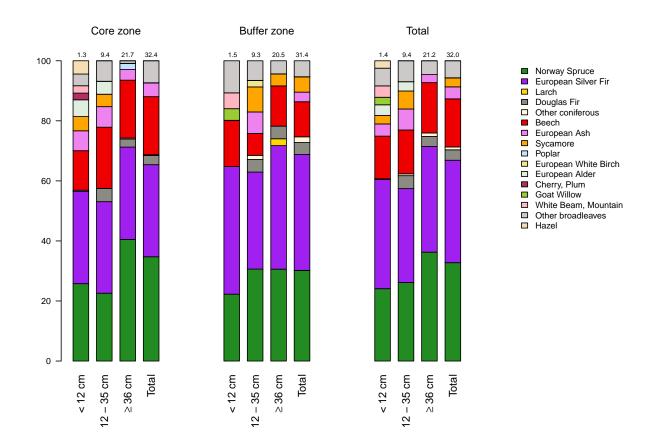


Table 7: Total number of habitat trees per ha. Giants and dead standing trees with a DBH ≥ 36 cm are counted only in the categorie 'giant' or dead standing tree even when when bearing a TreM. Database: Core zone: 72 SP, buffer zone: 59 SP, Total: 129 SP.

	Core	zone	Buffer	zone	Total	
Categorie	Ā	\pm SE	χ	\pm SE	x	\pm SE
Giants (living trees with DBH \geq 80 cm)	5.4	1.8	3.3	1.3	4.5	1.2
Living trees bearing one or more than one TreM	30.6	4.8	30.8	7.7	30.7	4.3
Dead standing trees with DBH \geq 36 cm	2.5	1.0	1.4	1.1	2.0	0.7
Dead standing trees bearing one or more than one TreM	2.1	1.2	1.8	1.2	1.9	0.9
Total habitat trees	40.6	5.3	37.3	8.2	39.1	4.6

Table 8: Lying deadwood [m³/ha], grouped by degree of decay and woodtype in the core and buffer zone and the entire perimeter. Database: Core zone 72 SP, Buffer-zone 59 SP, entire perimeter 129 SP.

Degree of decay	Woodtype	Core	Core zone		zone	To	tal
			\pm SE	- x	\pm SE		\pm SE
fresh	Coniferous Broadleaved	0.5 0.4	0.7 0.6	0.0	0.0	0.3	0.5 0.4
	Total	0.9	0.9	0.0	0.0	0.5	0.7
solid	Coniferous Broadleaved	3.2 1.4	1.8 1.2	3.3	1.8 1.0	3.3 1.2	1.8 1.1
	Total	4.7	2.2	4.3	2.1	4.5	2.1
rotten	Coniferous Broadleaved	1.0 1.4	1.0 1.2	0.7 0.2	0.8 0.4	0.9 0.9	0.9 0.9
	Total	2.3	1.5	0.9	0.9	1.7	1.3
mould	Coniferous Broadleaved	0.5 1.5	0.7 1.2	0.2 0.0	0.4 0.0	0.4 0.8	0.6 0.9
	Total	2.0	1.4	0.2	0.4	1.2	1.1
duff	Coniferous Broadleaved	0.0 0.0	0.0 0.0	0.0 0.2	0.0 0.4	0.0 0.1	0.0 0.3
	Total	0.0	0.0	0.2	0.4	0.1	0.3
Total	Coniferous Broadleaved	5.1 4.8	2.3 2.2	4.2 1.4	2.0 1.2	4.7 3.3	2.2 1.8
	Total	9.9	3.1	5.6	2.4	8.0	2.8

References

- Abegg, M., P. Ahles, B. Allgaier Leuch, F. Cioldi, M. Didion, C. Fischer, A. Herold, R. Meile, B. Rohner, E. Rösler, S. Speich, C. Temperli, and B. Traub, 2023*a*. Swiss national forest inventory Result table No. 1320646. URL
 - https://www.lfi.ch/resultate/resultate-en.php?befNr=96&invNr=550&p=theme&prodItNr=1320646&prodNr=95®ionNr=366&zigrNr=21.
- Abegg, M., P. Ahles, B. Allgaier Leuch, F. Cioldi, M. Didion, C. Fischer, A. Herold, R. Meile, B. Rohner, E. Rösler, S. Speich, C. Temperli, and B. Traub, 2023b. Swiss national forest inventory Result table No. 1330344. URL
 - https://www.lfi.ch/resultate/resultate-en.php?auswNr=434&befNr=96&invNr=550&p=theme®ionNr=366&zigrNr=24&prodNr=95&prodItNr=1330344.
- Abegg, M., P. Ahles, B. Allgaier Leuch, F. Cioldi, M. Didion, C. Fischer, A. Herold, R. Meile, B. Rohner, E. Rösler, S. Speich, C. Temperli, and B. Traub, 2023c. Swiss national forest inventory Result table No. 1359183. URL
 - https://www.lfi.ch/resultate/resultate-en.php?befNr=22&invNr=550&p=theme&prodItNr=1359183&prodNr=95®ionNr=366&zigrNr=215.
- Abegg, M., P. Ahles, B. Allgaier Leuch, F. Cioldi, M. Didion, C. Fischer, A. Herold, R. Meile, B. Rohner, E. Rösler, S. Speich, C. Temperli, and B. Traub, 2023*d*. Swiss national forest inventory Result table No. 1362219. URL
 - https://www.lfi.ch/resultate/resultate-en.php?befNr=96&invNr=550&p=theme®ionNr=366&zigrNr=2&prodNr=95&prodItNr=1362219.
- Abegg, M., P. Ahles, B. Allgaier Leuch, F. Cioldi, M. Didion, C. Fischer, A. Herold, R. Meile, B. Rohner, E. Rösler, S. Speich, C. Temperli, and B. Traub, 2023e. Swiss national forest inventory Result table No. 1370552. URL
 - https://www.lfi.ch/resultate/resultate.php?auswNr=434&befNr=1157&invNr=550&p=theme®ionNr=366&zigrNr=2&prodNr=95&prodItNr=1370552.
- Bersier, A. 1953. Atlas géographique de la Suisse. Feuille Jorat. Notice explicative. Comission géologique suisse. URL https://data.geo.admin.ch/ch.swisstopo.geologie-geologischer_atlas/erlaeuterungen/GA25-ERL-27.pdf.
- Böhl, J., and U.-B. Brändli. 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. European Journal of Forest Research **126**:449–457.
- Bormann, F. H., and G. E. Likens. 1979. Catastrophic Disturbance and the Steady State in Northern Hardwood Forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. American Scientist 67:660–669. URL http://www.jstor.org/stable/27849531.
- Brang, P., S. Hilfiker, U. Wasem, A. Schwyzer, and T. Wohlgemuth. 2015. Langzeitforschung auf Sturmflächen zeigt Potenzial und Grenzen der Naturverjüngung. Schweizerische

- Zeitschrift fur Forstwesen **166**:147–158. URL https://doi.org/10.3188/szf.2015.0147.
- Brändli, K., J. Stillhard, M. Hobi, and P. Brang. 2020. Waldinventur 2017 im Naturerlebnispark Sihlwald. Birmensdorf, Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, Sihlwald, Stiftung Wildnsipark Zürich,.
- Buchet, E. 1925. La dernière revision de l'amenagement des forêts de Lausanne. Journal forestier suisse : organe de la Société Forestière Suisse pages 125–131.
- Christensen, M., K. Hahn, E. P. Mountford, P. Ódor, T. Standovár, D. Rozenbergar, J. Diaci, S. Wijdeven, P. Meyer, S. Winter, and T. Vrska. 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. Forest Ecology and Management **210**:267 282. URL http://www.sciencedirect.com/science/article/pii/S0378112705001180.
- Commarmot, B., J. Wunder, and C. Heiri. 2017. Auswertung der Stichprobeninventur 2014 im Naturwaldreservat Bettlachstock-Hasenmatt. Eidg. Forschungsanstalt WSL, Birmensdorf.
- Courbaud, B., L. Larrieu, D. Kozak, D. Kraus, T. Lachat, S. Ladet, J. Müller, Y. Paillet, K. Sagheb-Talebi, A. Schuck, J. Stillhard, M. Svoboda, and S. Zudin. 2022. Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. Journal of Applied Ecology **59**:492–503. URL https:
 - //besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.14068.
- Direction générale de l'environment. 2013. Guide d'inventaire forestier. Département de la sécurité et de l'environment, Inspection cantonale des fôrets.
- Düggelin, C., M. Abegg, U. B. Brändli, S. Bischof, F. Cioldi, C. Fischer, and R. Meile. 2020. Schweizerisches Landesforstinventar. Anleitung für die Feldaufnahmen der fünften Erhebung 2018–2026. WSL Berichte URL https://www.dora.lib4ri.ch/wsl/islandora/object/wsl%3A23637.
- Haeler, E., A. Bergamini, S. Blaser, C. Ginzler, K. Hindenlang, C. Keller, T. Kiebacher, U. G. Kormann, C. Scheidegger, R. Schmidt, J. Stillhard, A. Szallies, L. Pellisier, and T. Lachat. 2021. Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. Landscape Ecology pages 89–104.
- Heiri, C., U.-B. Brändli, H. Bugmann, and P. Brang. 2012. Sind Naturwaldreservate naturnäher als der Schweizer Wald? Schweizerische Zeitschrift fur Forstwesen 163:210–221. URL https://doi.org/10.3188/szf.2012.0210.
- Hermann, S., C. Malgorzata, and P. Brang. 2012. Totholzvolumen und -qualität in ausgewählten Schweizer Naturwaldreservaten. Schweizerische Zeitschrift für Forstwesen **163**:222–231.
- Hill, A., A. Massey, and D. Mandallaz, 2017. forestinventory: Design-based global and small-area estimations for multiphase forest inventories. R package version 0.2.0.

Idoate-Lacasia, J., J. Stillhard, J. Portier, P. Brang, S. Zimmermann, C. Bigler, H. Bugmann, and M. L. Hobi. under Review. Long-term biomass dynamics of temperate forests in Europe after cessation of management. Forest Ecology and Management.

- Kaufmann, E., 2001. Swiss National Forest Inventory: Methods and Models of the Second Assessment, Chapter estimation of standing timber, growth and cut, pages 162–204. WSL Swiss Federal Research Institute, Birmensdorf, Zürcherstrasse 111, 8903 Birmensdorf.
- Larrieu, L., B. Courbaud, C. Drénou, M. Goulard, R. Bütler, D. Kozák, D. Kraus, F. Krumm, T. Lachat, J. Müller, Y. Paillet, A. Schuck, J. Stillhard, M. Svoboda, and K. Vandekerkhove. 2022. Key factors determining the presence of Tree-related Microhabitats: A synthesis of potential factors at site, stand and tree scales, with perspectives for further research. Forest Ecology and Management 515:120235. URL https://www.sciencedirect.com/science/article/pii/S0378112722002298.
- Mandallaz, D. 2008. Sampling techniques for forest inventories. Chapman and Hall, Boca Raton.
- Moreno, I., and P. Christe. ???? La faune de la zone centrale du Parc naturel périurbaindu Jorat détectée par pièges photographiquesl'année de sa création. Bulletin de la Société Vaudoise des Sciences Naturelles **101**:5–15. URL https://www.e-periodica.ch/cntmg?pid=bsv-002:2022:101::204.
- Petrovska, R., P. Brang, A. Gessler, H. Bugmann, and M. L. Hobi. 2021. Grow slowly, persist, dominate—Explaining beech dominance in a primeval forest. Ecology and Evolution 11:10077–10089. URL
 - https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.7800.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- Stillhard, J., P. Brang, H. Bugmann, and M. Hobi. 2021. Stichprobeninventur 2018 im Naturwaldreservat Bödmerenwald. Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL.
- Stillhard, J., M. L. Hobi, P. Brang, U.-B. Brändli, M. Korol, V. Pokynchereda, and M. Abegg. 2022. Structural changes in a primeval beech forest at the landscape scale. Forest Ecology and Management **504**:119836. URL https://www.sciencedirect.com/science/article/pii/S0378112721009270.
- Stillhard, J., I. Murzynowska, G. Projer, and M. Hobi, 2023. Sample plot inventory data form the Parc Naturel du Jorat. URL https: //www.envidat.ch/dataset/sample-plot-inventory-parc-naturel-du-jorat.
- Sutter, F., and P. Waldner, 2019. LWF Lausanne long-term research site. URL https://www.envidat.ch/dataset/lwf-lausanne-long-term-research-site.
- Thom, D., and R. Seidl. 2022. Accelerating Mountain Forest Dynamics in the Alps. Ecosystems **25**:603–617. URL https://doi.org/10.1007/s10021-021-00674-0.

Vandekerkhove, K., M. Vanhellemont, T. Vrška, P. Meyer, V. Tabaku, A. Thomaes, A. Leyman, L. De Keersmaeker, and K. Verheyen. 2018. Very large trees in a lowland old-growth beech (Fagus sylvatica L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe. Forest ecology and management **417**:1–17.

Appendix

Table A1: Number of stems, basal area and volume of living trees and standing dead trees, Core zone. Dataset: 72 accessible SPs 2021.

			Li	ving tre	es			Dead trees			
Species	Number of stems [N/ha]			Basal area [m²/ha]		Volume [m³/ha]		Number of stems [N/ha]		Volume [m³/ha]	
					· — -						
		± SE	X	\pm SE	. X	± SE	X	± SE	Χ	± SE	
Picea abies	144	28	11.3	1.8	162.0	27.5	3	1	0.5	0.2	
Abies alba	161	21	9.9	1.2	126.9	16.4	2	1	1.1	1.0	
Larix Mill	0	0	0.1	0.1	1.0	1.0	-	=	-	-	
Pseudotsuga menziesii	12	8	1.0	0.6	12.2	7.2	-	=	-	-	
Other conifers	-	-	-	-	-	-	15	4	1.3	0.3	
Total conifers	317	30	22.3	2.0	302.0	29.1	20	4	2.9	1.1	
Fagus sylvatica	88	10	6.3	0.9	87.5	15.4	2	1	0.6	0.4	
Quercus	4	2	0.2	0.1	2.7	1.5	-	-	-	-	
Fraxinus excelsior	31	8	1.5	0.4	19.8	5.3	9	3	1.2	0.5	
Acer pseudoplatanus	19	5	0.5	0.2	4.5	2.2	-	=	-	-	
Populus	3	2	0.5	0.4	7.6	6.5	-	=	-	-	
Betula pendula	1	1	0.0	0.0	0.5	0.5	1	1	0.0	0.0	
Alnus glutinosa	20	8	0.5	0.2	6.9	2.7	1	1	0.2	0.2	
Tilia cordata	7	5	0.2	0.1	1.2	0.9	-	-	-	-	
Prunus	6	5	0.1	0.1	1.3	8.0	1	1	0.0	0.0	
Salix caprea	9	6	0.2	0.1	1.9	1.4	3	3	0.4	0.4	
Sorbus	7	2	0.1	0.0	0.5	0.3	1	1	0.1	0.1	
Other broadleaves	-	-	-	-	-	-	2	1	0.1	0.0	
Corylus avellana	12	10	0.1	0.1	0.3	0.3	-	-	-	-	
Sambucus nigra	1	1	0.0	0.0	0.0	0.0	1	1	0.0	0.0	
Total broadleaves	208	24	10.1	1.0	134.8	16.1	20	5	2.5	0.8	
Total	525	32	32.4	2.0	436.8	31.5	40	6	5.4	1.3	

Figure A1: DBH and height of 425 living trees measured during the SPI in 2021. Dataset: 129 accessible SP 2021.

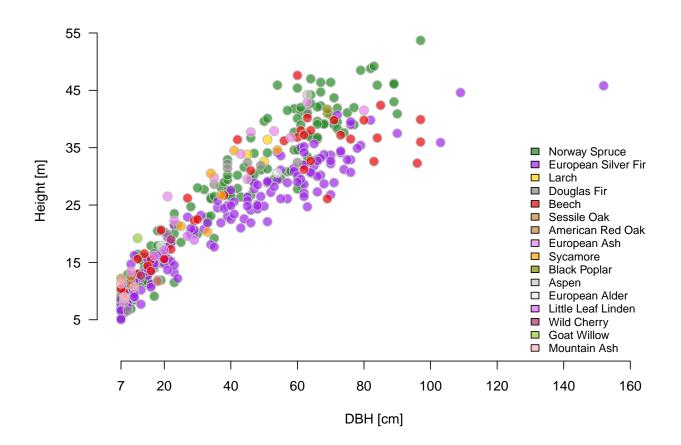


Table A2: Number of trees, basal area and volume of living trees and standing dead trees, Buffer zone. Dataset: 57 accessible SPs 2021.

			Li	ving tree		Dead trees					
Species	Number of stems [N/ha]			Basal area [m²/ha]		Volume [m³/ha]		Number of stems [N/ha]		Volume [m³/ha]	
			$[m^2$								
	Ā	\pm SE	Ā	\pm SE	Ā	\pm SE	Ā	\pm SE	x	\pm SE	
Picea abies	144	25	9.5	1.7	134.4	23.7	6	3	0.9	0.5	
Abies alba	210	35	12.1	1.2	152.1	16.3	9	6	1.2	0.7	
Larix Mill	4	3	0.6	0.4	7.6	5.5	1	1	0.0	0.0	
Pseudotsuga menziesii	13	7	1.3	0.7	15.9	8.6	1	1	0.0	0.0	
Other conifers	-	-	-	-	-	-	26	6	1.7	0.4	
Total conifers	371	38	23.5	1.9	310.0	26.2	44	10	3.8	1.0	
Fagus sylvatica	70	21	3.7	0.8	49.6	11.7	1	1	0.1	0.1	
Quercus	8	4	0.4	0.2	4.5	2.5	-	-	-	-	
Quercus rubra	5	5	0.0	0.0	0.3	0.3	-	-	-	-	
Fraxinus excelsior	15	8	1.0	0.5	12.7	6.6	3	1	0.5	0.4	
Acer pseudoplatanus	21	6	1.6	0.5	20.5	6.5	1	1	0.0	0.0	
Populus	1	1	0.1	0.1	0.8	8.0	-	-	-	-	
Populus nigra	1	1	0.3	0.3	1.8	1.8	-	-	-	-	
Betula pendula	10	7	0.2	0.1	2.3	1.3	1	1	0.0	0.0	
Alnus glutinosa	7	4	0.2	0.1	2.2	1.6	-	-	-	-	
Prunus	6	3	0.1	0.1	1.0	0.8	-	-	-	-	
Salix caprea	10	7	0.1	0.1	0.9	0.7	6	5	0.3	0.3	
Sorbus	15	7	0.1	0.0	0.7	0.3	1	1	0.1	0.1	
Carpinus betulus	4	3	0.1	0.1	0.7	0.6	-	-	-	-	
Other broadleaves	-	-	-	-	-	-	1	1	0.1	0.1	
Corylus avellana	1	1	0.0	0.0	0.0	0.0	-	-	-	-	
Sambucus nigra	1	1	0.0	0.0	0.0	0.0	-	-	-	-	
Hedera helix	3	3	0.0	0.0	0.1	0.1	-	-	-	-	
Total broadleaves	176	30	8.0	1.2	98.2	15.2	14	5	1.1	0.5	
Total	548	45	31.4	1.7	408.2	23.5	59	12	5.0	1.1	

Figure A2: Sample plot design FRM. Light blue: Sample plot with radius of 12.62 m. Blue: Sample plot with radius of 7.98 m. Red: Transects of 15 m each for line intersect sampling of CWD. Yellow: Regeneration subplots

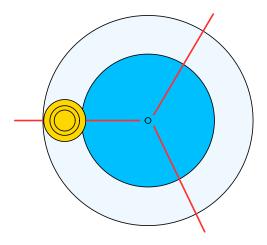


Figure A3: Species shares on number of trees (N ha^{-1}) grouped by DBH-classes and perimeter. Dataset: 129 accessible SP 2021.

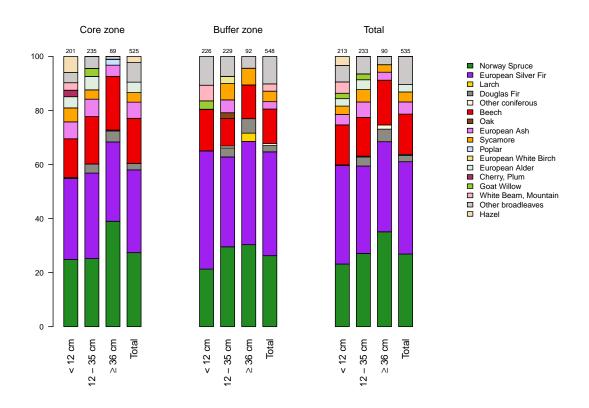


Figure A4: Species shares on volume of trees (m^3 ha^{-1}) grouped by DBH-classes and perimeter. Dataset: 129 accessible SP 2021.

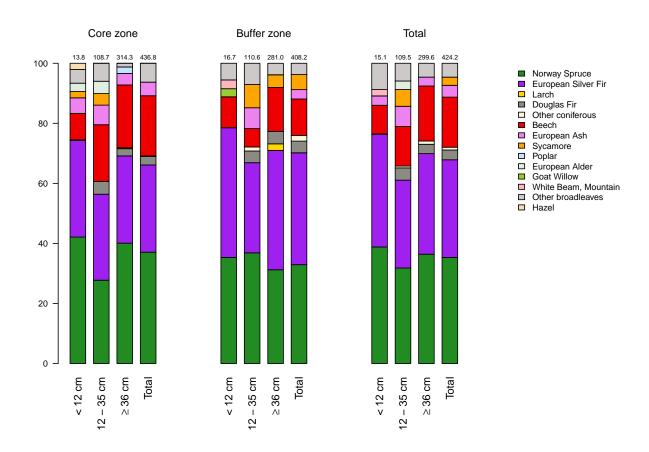


Table A3: Regeneration density per ha by species and height class in the core and buffer zone and the total perimeter. Database: Core zone 72 SP, Buffer zone 59 SP, Total perimeter 129 SP.

Regeneration class	Species	Core	zone	Buffer	zone	Tot	al
			\pm SE		\pm SE		\pm SE
	Picea abies	639	279	1509	1040	1023	484
	Abies alba	1167	381	316	110	791	221
	Fagus sylvatica	139	72	70	49	109	46
	Quercus robur	28	28	-	-	16	16
10 - 39.9 cm height	Fraxinus excelsior	417	268	667	432	527	242
	Acer pseudoplatanus	528	446	281	154	419	257
	Sorbus aucuparia	28	28	-	-	16	16
	Total	2944	795	2842	1190	2899	685
	Picea abies	236	87	333	199	279	100
	Abies alba	792	298	561	209	690	190
	Fagus sylvatica	486	176	439	239	465	144
	Quercus robur	42	24	-	-	23	13
40 - 129.9 cm height	Fraxinus excelsior	444	217	965	728	674	343
	Acer pseudoplatanus	750	435	246	101	527	247
	Alnus glutinosa	83	71	-	-	47	39
	Sorbus aucuparia	181	111	35	25	116	63
	Total	3014	703	2579	824	2822	533
	Picea abies	236	81	114	47	182	50
	Abies alba	326	102	289	100	310	72
	Fagus sylvatica	431	98	351	157	395	88
	Fraxinus excelsior	83	58	26	26	58	34
	Acer pseudoplatanus	181	74	105	57	147	48
0 - 6.9 cm DBH	Betula pendula	-	-	26	15	12	7
0 0.5 0111 0011	Alnus glutinosa	35	35	-	-	19	19
	Prunus avium	14	14	-	-	8	8
	Prunus padus	-	-	26	26	12	12
	Salix caprea	42	26	9	9	27	15
	Sorbus aucuparia	104	59	53	24	81	35
	Total	1451	209	1000	214	1252	151
	Picea abies	1111	325	1956	1226	1484	570
	Abies alba	2285	641	1167	302	1791	384
	Fagus sylvatica	1056	251	860	362	969	212
	Quercus robur	69	46	-	-	39	26
	Fraxinus excelsior	944	453	1658	1141	1260	562
	Acer pseudoplatanus	1458	887	632	245	1093	506
Total	Betula pendula	- ,	<u>-</u>	26	15	12	7
	Alnus glutinosa	118	84	-	-	66	47
	Prunus avium	14	14	-	<u>-</u>	8	8
	Prunus padus	-	-	26	26	12	12
	Salix caprea	42	26	9	9	27	15
	Sorbus aucuparia	312	132	88	38	213	76
	Total	7410	1473	6421	1776	6973	1133

Figure A5: DBH distribution of all living trees with a DBH \geq 12 cm in 1994, 2004 and 2021 for the core zone. Database: 669 accessible SPs for 1994 and 2004, 129 SP in 2021.

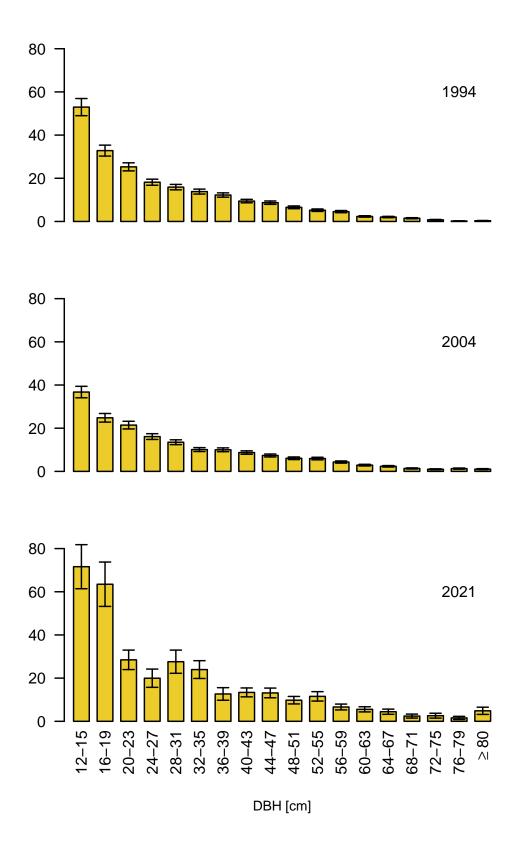


Figure A6: DBH distribution of all living trees with a DBH \geq 12 cm in 1994, 2004 and 2021 for the buffer zone. Database: 669 accessible SPs for 1994 and 2004, 129 SP in 2021.

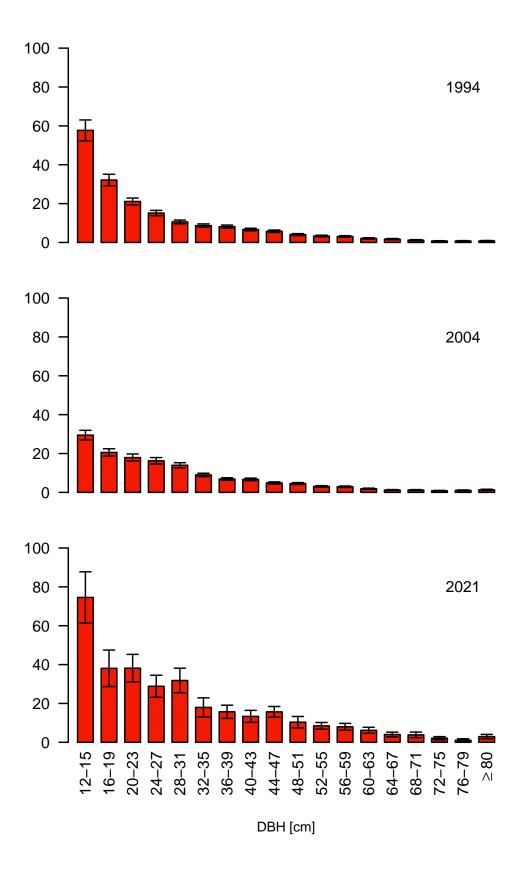


Figure A7: DBH distribution of dead trees 2021 on the total perimeter, the core and the buffer zone. Database: 129 accessible SP 2021.

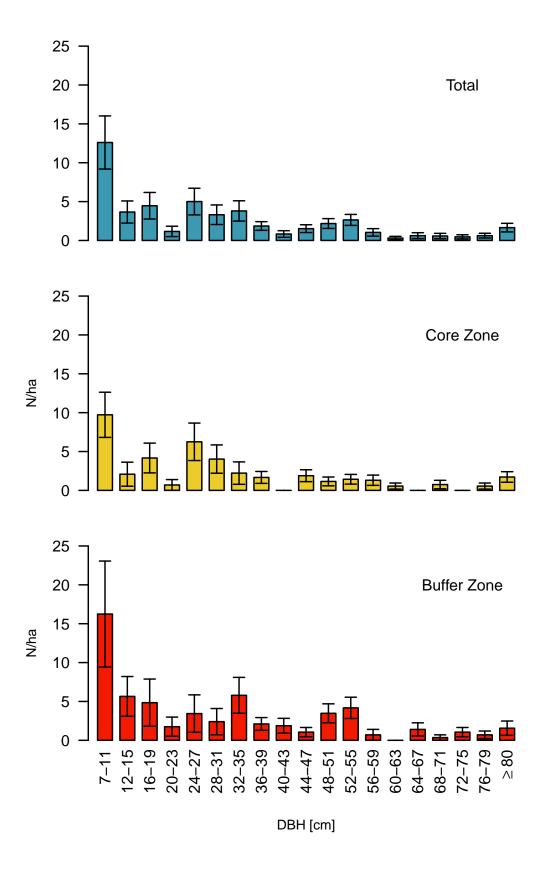


Table A4: Density of trees carrying TreMs per ha. More than one TreM might appear on a tree. Database: Core zone: 72 SP, Buffer zone: 59 SP, Total perimeter: 129 SP.

		Core zone		Buffer zone		Total	
	TreM type	Ā	\pm SE	Ā	\pm SE	χ̄	\pm SE
	Dead wood in crown	17.5	4.9	9.5	6.3	14.0	3.9
	Crown breakage	9.6	3.1	7.3	3.2	8.6	2.2
	Stem breakage	1.9	1.4	0.0	0.0	1.1	0.8
Living trees	Cracks and fissures	0.0	0.0	0.4	0.4	0.2	0.2
	Bark lession	11.1	2.7	13.2	4.1	12.0	2.4
	Cavity with decayed wood	0.3	0.3	0.0	0.0	0.2	0.2
	Holes in stem	0.6	0.4	1.6	1.1	1.0	0.5
	Hollow stem	0.0	0.0	0.0	0.0	0.0	0.0
	Polypores	0.0	0.0	0.0	0.0	0.0	0.0
	Sap flow	4.0	1.5	8.3	3.0	5.9	1.6
	Total TreMs living trees	45.1	7.5	40.2	9.8	42.9	6.0
Dead trees	Cavity with decayed wood	0.0	0.0	0.0	0.0	0.0	0.0
	Holes in stem	3.8	2.0	2.5	1.9	3.2	1.4
	Hollow stem	0.0	0.0	0.4	0.4	0.2	0.2
	Polypores	1.7	1.0	0.9	0.9	1.3	0.7
	Total TreMs dead trees	5.5	2.4	3.7	2.1	4.7	1.6
Total TreMs		50.6	8.4	43.9	10.2	47.6	6.5