Assessment of ungulate effects on trees in the canton of Vaud:

comparison of data from the Swiss NFI2 and NFI4 on ungulate browsing, fraying and bark stripping

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Contents

1. Introduction

1.1. Impact of ungulates on trees

Ungulates, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*), can have a major impact on forest regeneration processes [1]. There are three main types of impacts: browsing, fraying and bark stripping. Bark stripping occurs patchy and is primarily due to red deer on thin-barked trees [1]. Deer usually choose thin stems (< 4 cm diameter, rarely over 10 cm) for fraying [1]. Browsing occurs on trees < 2 m and is the most frequent in Swiss forests [2]. Depending on site conditions and the sensitivity of the affected plant species, it can cause a decrease in height growth or lead to plant death [1, 3, 4]. Thus, browsing can lead to a delay in regeneration processes and, in the long term, a decrease in the number of stems [4]. As some species are preferentially browsed by ungulates, browsing can change the growth rate rank between species [5] and thus the future species composition of a forest, which can result in a decrease in its biodiversity [6, 7] and its resilience, particularly in combination with climate change [8].

In Europe, the ungulate density has increased over the past decades and is likely to continue to rise [9]. The increases in the population sizes of roe deer, red deer and chamois are due to reduced death rates and higher regeneration rates. The death rate of ungulates has decreased because food availability has increased in agricultural areas and their natural predators, wolf and lynx, were then extinct [10] and are still not present throughout the area. The population of red deer has increased and spread, especially in the Jura and the Alps in the region of the canton of Vaud [11].

Since a correlation between ungulate population size and browsing frequency has been observed in many studies [12], an increase in browsing in the last decades most likely also occurred in the canton of Vaud. The Swiss National Forest Inventory (NFI) is the only dataset including assessments of browsing, fraying and bark stripping that is available from the last decades for the whole canton of Vaud.

1.2. Swiss National Forest Inventory

Data on trees has been collected through the Swiss NFI over the last 40 years and throughout Switzerland. The NFI consists of a systematic sampling of trees in plots arranged in a quadratic √2 km grid. At each grid intersection point that lies within a forest, there is one plot. In each plot the trees (≥12 cm diameter at breast height [DBH]), the saplings (height ≥ 130 cm but <12 cm DBH), and the seedlings (10–129 cm height) have been sampled in in circles of different sizes and different ungulate impacts have been assessed.

The aim of the NFI is to give an overview of the condition of the Swiss forest at national level. Therefore, the number of plots is limited per region within the cantons. This means that there may not be enough data on smaller regions to make an accurate analysis of all species and the impacts of ungulates [e.g. 13].

1.3 Results of NFI analyses for Switzerland

Throughout Switzerland and for all the NFI sampling periods, browsing has been found to be much more frequent than fraying and bark stripping [14]. Since NFI2 (1993–1995) there has been an increase in the browsing intensity on silver fir (*Abies alba*) and oak (*Quercus*) over the whole of Switzerland [15]. In NFI4b (first part of NFI4: 2009–2013) an overall increase in browsing was documented in the Jura, in high Alpine regions, and in the southern Alps [15]. Of all the tree species in Switzerland, oak was found to have the highest browsing intensity: it increased from NFI2 to NFI4, at which point about 32% of all oak trees had signs of browsing [16]. For oak, an analysis of the "economic regions" (www.lfi.ch) of Switzerland was made, which indicated that browsing increased the most in the western Jura, western Plateau and southwestern Alps [8]. Further, there has been an increase in oak seedlings in western Switzerland since NFI2, whereas the stem count of saplings stayed the same or even decreased in some regions [8]. This shows that either oak became more established in western Switzerland or the smaller trees could not reach the sapling class due to browsing. Oak is considered sensitive to browsing because it is preferentially browsed, it has average height growth, its ability to react to browsing is low, and its chance of survival is reduced by browsing [8]. Therefore, browsing can lead to a decrease in stem count for oak and to segregation from other species [17]. Other species with a high browsing intensity in Switzerland are maple (*Acer* spp.), rowanberry (*Sorbus aucuparia*) and silver fir (*Abies alba*) [15], for which segregation has been found in some regions using data sources other than NFIs, such as indicator areas [12]. In the western Plateau, which includes part of the canton of Vaud, the browsing intensity on silver fir was lower than in all other economic regions during the NFI1 (1982–1986) and NFI2 (1993–1995) periods (Figure 1) [18]. This trend held until NFI4b (2009–2013), when browsing intensity on silver fir was comparably low in Vaud [15].

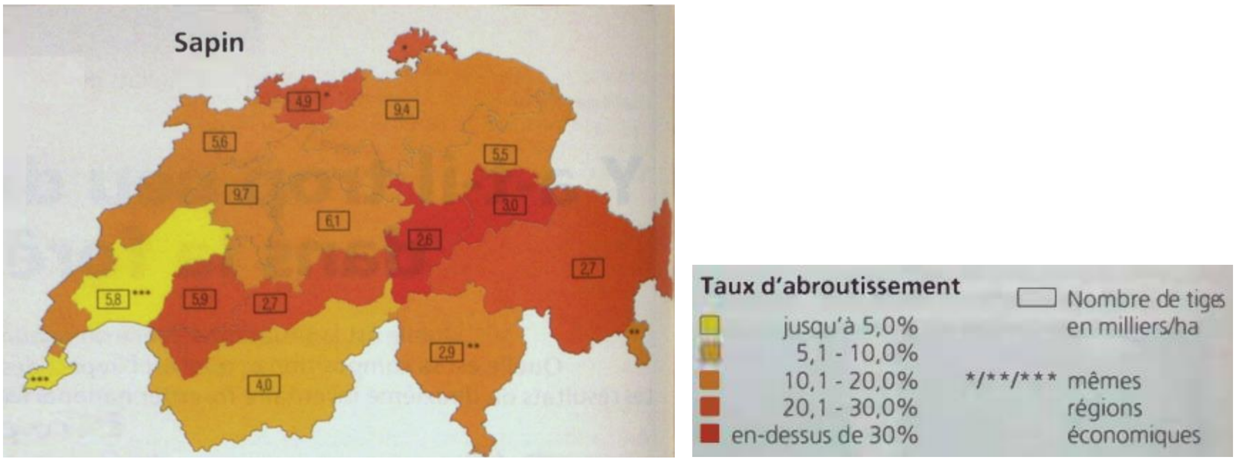


*Figure 1: Browsing intensity [%] and stem count [1000 trees/ha] for silver fir (*Abies alba*) in Switzerland's economic regions following NFI2 (1993–1995). Source: [18].*

1.4 Research goals

The main goal of this report is to identify the frequency of browsing, fraying and bark stripping in the canton of Vaud, to determine which tree species are most affected, and to analyse the development over time using the data from NFI2 and NFI4.

Research goals:

1) To provide an overview of the data on browsing, fraying and bark stripping available from NFI2 and NFI4 for the canton of Vaud
2) To determine the current (NFI4) and past (NFI2) frequency of browsing, fraying and bark stripping on the most frequent tree species for the entire canton of Vaud and for different hunting zones, production regions and altitudinal vegetation belts
3) To assess the development of browsing over time in the canton of Vaud between NFI2 and NFI4, and within NFI4 separately, for the different tree species and for different production regions and hunting zones.
4) To analyse several possible reasons for an increase or decrease in browsing, e.g. ungulate density and/or altitude (a proxy for growth conditions).

2. Methods

2.1 The canton of Vaud

The NFI data in Switzerland is often divided into five production regions: Jura, Plateau, Pre-Alps, Alps and Southern Alps (Figure 2). The canton of Vaud covers four of these production regions: Alps, Pre-Alps, Jura and Plateau. As only small areas of Vaud lie in the Pre-Alps and in the Alps, these production regions were grouped together for the analysis.

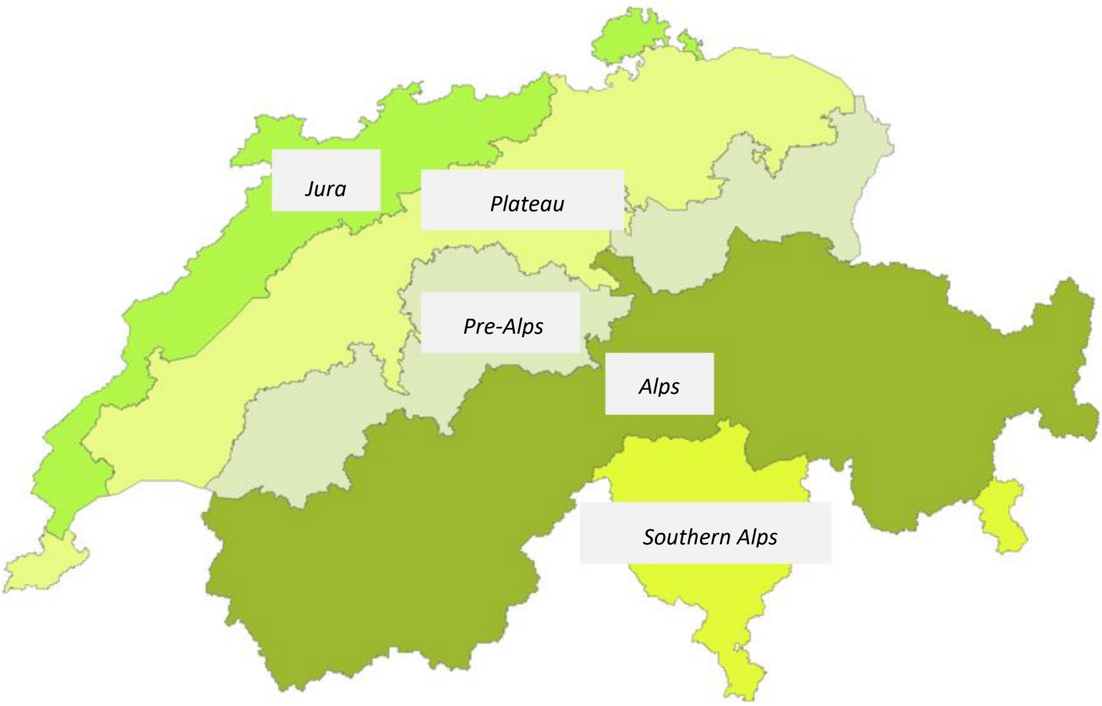


Figure 2: NFI production regions (≠ economic regions) over the whole of Switzerland. Source: NFI (www.lfi.ch).

The canton of Vaud is divided into the three hunting zones Alps, Plain and Jura (Figure 3). The spatial subdivision of these hunting zones is different from that of our grouped NFI production regions. In particular, the lower parts of the production regions Jura and Alps/Pre-Alps lie within the Plain hunting zone. Every hunting zone covers many wildlife sectors (Figure 3). However, these spatial units are very small considering the √2 km grid of the NFI and were thus only used for preparing the hunting data and not as analysis unit.

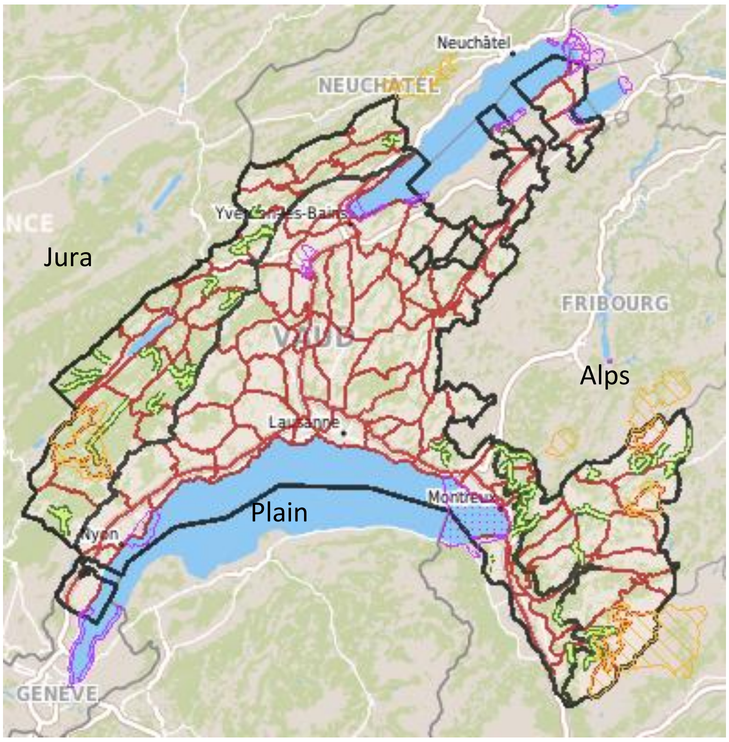


Figure 3: Hunting zones (black) and wildlife sectors (red) in the canton of Vaud. Source: Informations dépourvues de foi publique – Géodonnées Etat de Vaud, Office fédéral de topographie, OpenStreetMap (www.geo.vd.ch).

2.2 NFI field method

All NFI plots were sampled once during each NFI period (NFI1: 1982–1986, NFI2: 1993–1995, NFI3: 2004–2007, NFI4: 2009–2017). In each NFI three datasets were compiled: (1) tree data, in which only trees (≥12 cm DBH) were measured; (2) regeneration plot count data, and (3) regeneration nearest tree data, in which saplings (height ≥ 130 cm but <12 cm DBH) and seedlings (10–129 cm height) were assessed [19, 20]. The tree data was sampled over the whole area of the plot, whereas the regeneration data (plot count data and nearest tree data) was sampled on subplots within the plot. Unfortunately, the sampling methodology of trees <12 cm DBH changed between the NFI periods; this had to be considered when comparing the data on ungulate impacts over time. Concerning tree regeneration, NFI2 and NFI4 were conducted in the most comparable manners [19, 20]. In NFI1 the regeneration subplot was positioned differently (in the plot centre) [21], and in NFI3 plot counting was not used for browsing [22]. For this reason, studies on the development of browsing over time should focus on NFI2 and NFI4 (but see differences in the browsing assessment, section 2.2.2).

Different damage types were assessed in the three NFI datasets (Table 1). For each damage type a binary outcome was observed on the individual tree level, meaning that every tree was assigned as either damaged (browsed, frayed and/or bark stripped) or not.

Table 1: Types of tree damage assessed in each subsample of NFI2 and NFI4

Sample type	Browsing	Fraying	Bark stripping
Tree data NFI2 & NFI4	no	no	yes
Regeneration plot count data NFI2	yes[1]	yes[2]	yes[2]
Regeneration plot count data NFI4	yes	no	no
Nearest tree data NFI4	yes	yes[2]	yes[2]

[1] if fraying was present, browsing was considered unknown.

[2] fraying and bark stripping were not considered separately.

2.2.1 Tree data for assessing bark stripping

In the tree data of both NFI2 and NFI4, the only ungulate impact that was assessed was bark stripping [19, 20]. All trees (≥12 cm DBH) were sampled in a different area depending on their DBH (12 cm to <36 cm DBH in circles 2 acres in area, ≥36 cm DBH in circles 5 acres in area; see black circles in Figure 4). Various tree characteristics were assessed, such as crown shape, social status, the forest layer to which the tree belonged, and damage. For damage, the size, the location on the tree, and the cause were recorded. A tree was counted as bark stripped if (i) wood was exposed, (ii) the damage occurred on the stem, and (iii) the cause was ungulates. However, assessing the cause of damage is not always trivial. Rock fall, for example, may cause wounds that look quite like bark stripping some years later. Therefore, bark stripping can probably only be recognised as such for about one year (but unlike browsing no rate per year can be calculated).

2.2.2 Tree regeneration plot count data for assessing browsing in NFI2 and NFI4 and for assessing fraying/bark stripping in NFI2

For the plot count data, all seedlings (10–129 cm height) and saplings (height ≥ 130 cm but <12 cm DBH) were counted and assessed for damage in a circle of a defined radius [19, 20].

In NF2 there was a hierarchical structure in the regeneration data, from the most severe damage to the least [19]. If a seedling or sapling had a dead treetop, there was no data on fraying or bark stripping. If a seedling or sapling was frayed/bark stripped, there was no data on the browsing of that tree and there was no way to know whether the seedling or sapling was browsed as well as frayed/bark stripped or only frayed/bark stripped. No differentiation was made between fraying and bark stripping [Code 3 “Pflanze gefegt, geschält”, cf. 19].

In the regeneration data from NFI4, only browsing was assessed and only for seedlings. All other damage was only considered for the nearest trees.

Subplot arrangement

For NFI2 two subplots with the same area were made, one 10 m east and one 10 m west of the plot centre [19]. For NFI4 only one subplot, 10 m west of the plot centre, was sampled [20]; see red circles in Figure 4. Thus, during NFI2 more subplots were sampled and consequently more seedlings and saplings were assessed for browsing.

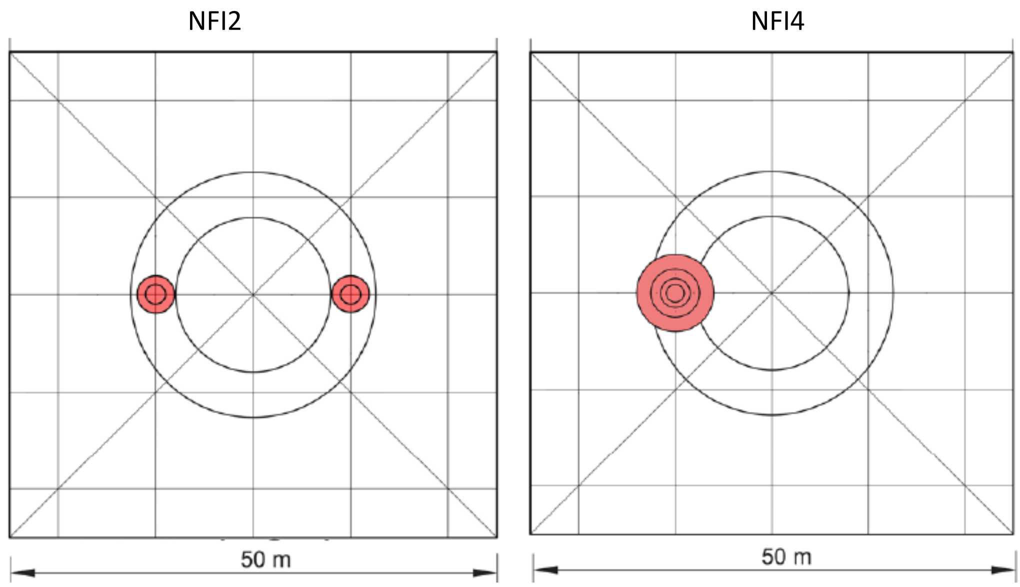


Figure 4: Sample design for an NFI plot: a 50 × 50 m interpretation plot and subplots along an 8 or 12 m radius for the single tree survey. In NFI2, the subplots were located 10 m east and 10 m west of the plot centre and their size was dependent on the tree height class. In NFI4, a single subplot was located 10 m west of the plot centre. Source: [23].

Height classes

In the NFI, young trees are divided into different height classes (Table 2). NFI2 distinguished between seven height classes and NFI4 only between four [19, 20]. In NFI2, more classes were used to be able to compare data with that from NFI1 [21]. To compare data from NFI2 and NFI4, the classes used in NFI2 can easily be pooled into those used in NFI4 (Table 2). In NFI4, only seedlings of classes 1 and 2 were assessed for browsing, as these classes are the most affected. Thus, only the same height classes from NFI2 were considered for the statistical analysis in this study. For fraying and bark stripping, all height classes were sampled in NFI2 and were included in the fraying analysis. Further, dead trees were not included in the analyses of browsing and fraying.

Table 2: Height classes used in NFI2 and NFI4, height classes used to assess browsing and fraying/bark stripping in NFI2, height classes used to assess browsing in NFI4, and height classes included in the browsing analysis of both NFIs and in the fraying/bark stripping analysis of NFI2. Radius of the circular subplots in NFI2 and NFI4.

NFI2 [cm]	NFI4 [cm]	Assessed in NFI2	Assessed in NFI4	Browsing analysis	Fraying/bark stripping analysis of NFI2	NFI2 radius [m]	NFI4 radius [m]
10 – 39 height	**10 – 39 height**	Yes	Yes	Yes	Yes	1.00	0.9
40 – 69 height	**40 – 129 height**	Yes	Yes	Yes	Yes	2.12	1.5
70 – 99 height							
100 – 129 height							
130 height to 3.9 DBH	**130 height to 3.9 DBH** *(0- 3.9 DBH)*	Yes	No	No	Yes	2.12	2.5
4 – 7.9 DBH	**4 – 11.9 DBH**	Yes	No	No	Yes	2.12	4.0
8 – 11.9 DBH							

Subplot area

The radius of the subplot(s) depended on the height class of the sampled seedlings and saplings (Figure 4). The 10–39 cm height class in NFI2 was sampled within a circle with radius 1 m and all larger classes within a circle with radius 2.12m (Table 2). In NFI4, the radius of the subplot was different for each height class, and also compared with those from NFI2 (Table 2). The subplot areas of the two smallest height classes, which were included in the browsing analysis, were therefore larger in NFI2 than in NFI4 (Table 2, Figure 4). Thus, once again more seedlings and saplings could be assessed for browsing in NFI2. The standard error of NFI2 was hence expected to be smaller than that of NFI4. For calculating the “classical browsing intensity” from 10 cm to 129 cm [24], these different areas had to be considered, i.e. seedlings were weighted according to the conversion factor required for a 1 ha area and thus small seedlings had a greater weight than large seedlings.

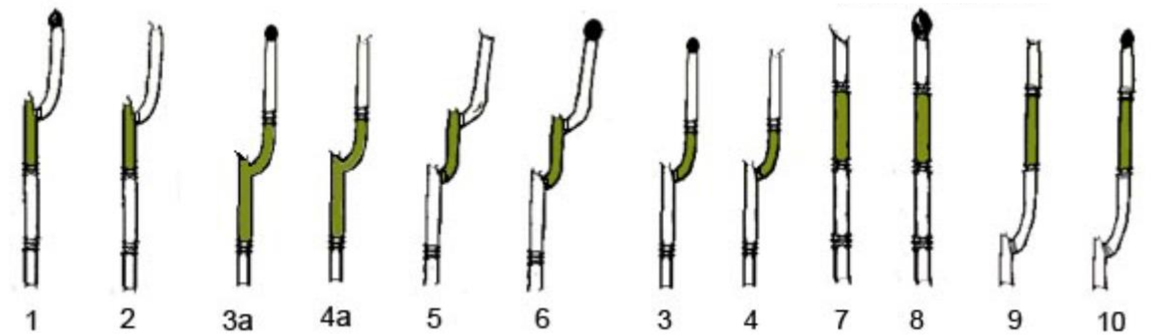
Browsing assessment

Browsing was only assessed along the main stem for both NFI2 and NFI4. All other stems of multi-stemmed trees were excluded from the sampling in NFI2, and the dataset was restricted to the main stem for NFI4 (only the “Hauptlode”).

In NFI1, the browsing of the youngest shoot was assessed [21]. As browsing has seasonal variability, observations made after budburst underestimated the annual browsing rate, while those made shortly before budburst (late winter) overestimated it [23]. For NFI2 the method was therefore adjusted such that the shoot of the previous year was assessed. The idea behind the NFI2 assessment was to capture one whole year, i.e. including summer browsing and the reaction of the tree in the same year. For that reason, two bud scars under the top bud and everything in between had to be undamaged for a tree to be considered not browsed [19]. This method takes: (i) the seasonality of browsing into account better than in NFI1 [23] and (ii) captures any reaction of deciduous trees within the same year (i.e. 3a and 4a in Figure 5).

The annual browsing intensity, however, was in some cases overestimated with this method [25], as images 3 and 4 of Figure 5**Error! Reference source not found.** were not included in the original field sampling manual of NFI2 [19]. In images 3 and 4, the browsing happened in the year before the previous year (see the small bud scars). If these trees were considered to be identical to 3a and 4a, two years would be assessed [25].

For NFI4, the assumption was made that only one shoot is formed per year and that a replacement shoot is formed in the year following the browsing event [20]. Thus, 3 and 4 of Figure 5 were considered clearly equal to 3a and 4a and thus not browsed. As deciduous trees often react in the same year after summer browsing [4], **it was expected that, overall, more trees were assessed as browsed with the method of NFI2 than with that of NFI4**. Thus, only an increase in browsing intensity from NFI2 to NFI4 could be considered a real change. Decreases in browsing were thus hard to interpret, in particular if they were less than about 25% (according to simulations by A.D. Kupferschmid), as they were likely caused by a change in the browsing assessment method.



NFI2	B	B	B	B	B	B	NB	NB	NB	NB	NB	NB
NFI4	B	B	NB	NB	B	B	NB	NB	NB	NB	NB	NB

Figure 5: Different sampling methodologies for assessing browsing in NFI2 and NFI4 with ten examples of trees. The previous year's growth is coloured green. B = browsed, NB = not browsed. Source of the single images: [23].

The methods for assessing browsing applied in NFI2 and in NFI4 clearly are not perfect solutions. However, both methods can be executed within a reasonable time span and show very low variation between observers. **As the NFI4 method was maintained over the years 2009 to 2017, an accurate analysis of the browsing development could be made for this time span.**

To the best knowledge of A. D. Kupferschmid, the browsing assessment in NFI4 is similar to the one used in indicator areas [26]. There, the sampling normally takes place over a short period in early spring, thus probably tending to underestimate summer browsing on deciduous trees that react within the same year.

2.2.3 Nearest tree data for assessing fraying/bark stripping in NFI4

In NFI2 and NFI4, the tree nearest to the subplot centre was sampled separately for four height classes and assessed for damage [20]. The same subplot as used for the plot count data was sampled [20]. Unfortunately, this method did not consider the nearest tree per species, but only per height class regardless of species. Bark stripping and fraying were not considered separately [20]. Browsing was assessed separately, but as browsing was already assessed with the plot count data in NFI4, this nearest tree browsing data was not used.

The height classes of the nearest tree data in NFI4 are the same as in the plot count data (Table 2) [20]. For browsing, only the seedling height classes 10–39 cm and 40–129 cm were sampled. For fraying and bark stripping, the nearest tree of the two sapling classes were also assessed. All dead trees were excluded from the fraying analysis of NFI4.

2.3 NFI plot data for the canton of Vaud

Normally, each NFI plot in Vaud was sampled once in 1993–1994 in NFI2 (none in 1995) and once during the period 2009–2017 in NFI4 (Figure 6). However, there were a few more plots in NFI2 than in NFI4 (Table 3; differences are highlighted in Figure 7), likely due to shifts in the forest boundaries, i.e. some plots were considered forest in NFI2 but not in NFI4.

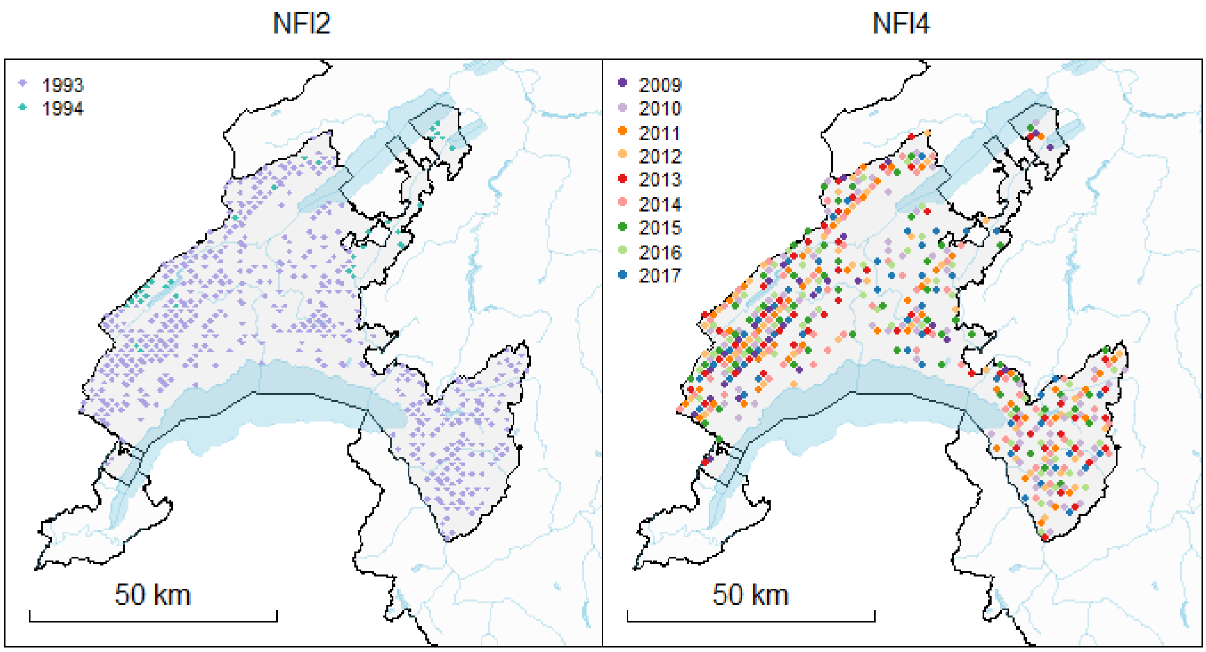


Figure 6: Distribution of NFI plots in the canton of Vaud, indicating the year in which each plot was sampled in NFI2 (1993 or 1994) and NFI4 (2009–2017).

Considered over the whole of Switzerland, one-ninth of the NFI4 plots were sampled per year. This resulted in more-or-less steady numbers in the canton of Vaud and its production regions/hunting zones, with one exception for the Alps/Pre-Alps region and Alps zone, where only one plot was sampled in 2009 and thus more in 2010 (Table 4). During the nine years, a forest and its ungulate population could change considerably. The sampling year within NFI4 was thus integrated into the analysis.

Table 3: Number of NFI plots in the canton of Vaud per production region and hunting zone.

	Production region			Hunting zone			Total
	Alps/Pre-Alps	Plateau	Jura	Alps	Plain	Jura	
NFI2	151	178	217	120	206	220	546
NFI4	145	151	202	117	176	205	498

Table 4: Number of NFI4 plots in the canton of Vaud sampled per year and production region or hunting zone.

	2009	2010	2011	2012	2013	2014	2015	2016	2017
Production region									
Alps/Pre-Alps	1	31	16	14	18	21	13	17	14
Plateau	10	19	15	14	14	21	19	18	21
Jura	18	26	24	22	25	27	25	18	17
Hunting zone									
Alps	1	27	11	8	16	17	11	15	11
Plain	11	24	18	19	17	24	23	17	23
Jura	17	25	26	23	24	28	23	21	18

The plots were quite regularly distributed over the different hunting zones and production regions (Figure 7). Only in the Plateau region and Plain zone were the plots more patchily distributed. This is because the settlement density is much higher in the Plain.

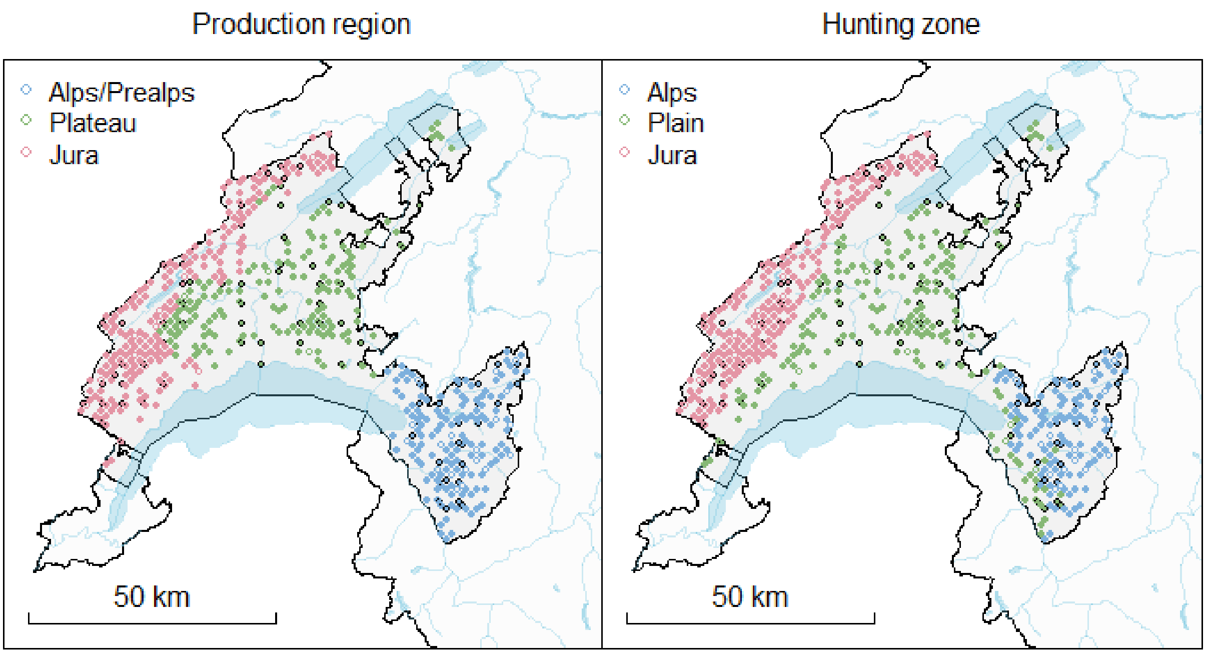


Figure 7: Distribution of the NFI plots in the canton of Vaud over the NFI production regions and the hunting zones. Filled symbols coloured according to the legend represent plots sampled in both NFI2 and NFI4, unfilled symbols with coloured borders represent plots only sampled in NFI4, and symbols with black borders represent plots only sampled in NFI2.

For the descriptive analysis of the NFI data, the hunting zones were considered more accurate than the production regions for the canton of Vaud, as the NFI production regions were intended for the whole of Switzerland. They include more altitudinal vegetation belts, e.g. the Jura, Pre-Alps and Alps all extend to Lake Geneva with the altitudinal vegetation belt "colline/submontane" (Figure 8). The hunting zones consider this altitudinal zonation, classifying these lower areas as Plain. However, as not all tree species are present in any one altitudinal zone, some statistical analyses were made based on the production regions.

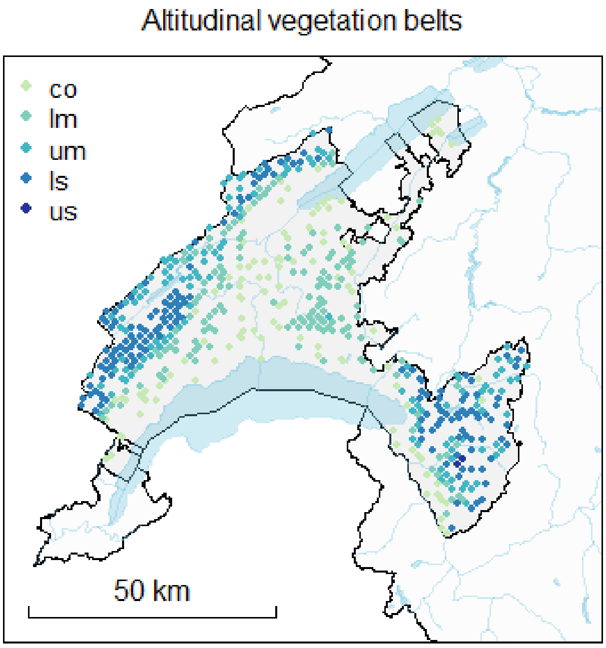


Figure 8: Distribution of the NFI2 plots in the canton of Vaud over the different altitudinal vegetation belts. Abbreviations of altitudinal zones: co = "colline/submontane", lm = "lower montane", um = "upper montane", ls = "lower subalpine", us = "upper subalpine".

The developmental stage of the forests in the plots in the canton of Vaud ranged from young growth to pole timber, then medium timber, then old timber and finally mixed forest (Table 5). All stages were present in each region (Figure 9). However, in NFI2 timber wood was more frequent in the Plateau and Jura regions than were young growth/thicket and mixed forest, while mixed forest was more frequent in the Alps/Pre-Alps region (Table 5). In NFI4, many more mixed forest plots appeared in the Plateau and Jura regions than in NFI2 (Figure 9), at the expense of medium timber (Table 5).

Table 5: Number of NFI plots in the canton of Vaud per forest developmental stage (Total [N]) and in percent per production region.

	NFI2				**NFI4**			
	Alps/Pre-Alps [%]	**Plateau [%]**	**Jura [%]**	**Total [N]**	**Alps/Pre-Alps [%]**	**Plateau [%]**	**Jura [%]**	**Total [N]**
no information	2.0	0.0	0.0	*3*	0.7	1.3	0.5	*4*
young growth / thicket	9.3	9.0	5.1	*41*	11.0	11.9	5.9	*46*
pole timber	9.9	18.0	14.7	*79*	15.9	15.9	7.9	*63*
young timber	15.9	21.9	24.4	*116*	6.2	9.9	15.3	*55*
medium timber	18.5	32.6	27.6	*146*	15.9	13.2	16.8	*77*
old timber	18.5	15.2	14.7	*87*	25.5	29.8	24.3	*131*
mixed	25.8	3.4	13.4	*74*	24.8	17.9	29.2	*122*

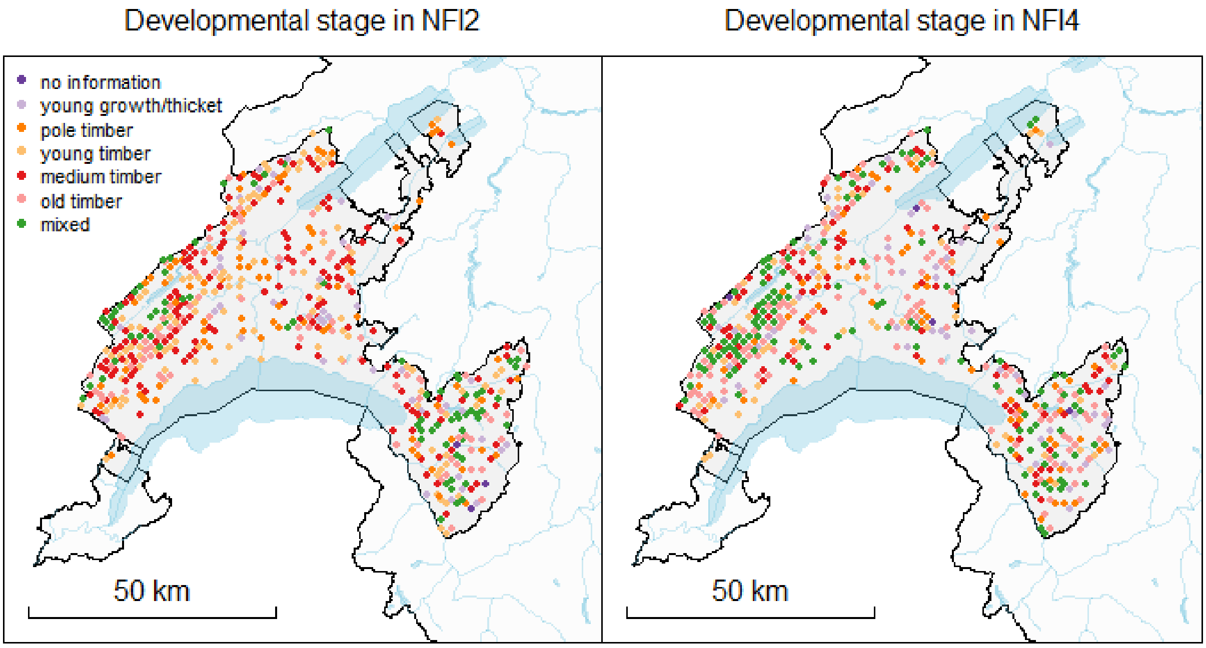


Figure 9: Developmental stages of the forests in the plots over the canton of Vaud in NFI2 and NFI4.

Canopy shading can have an important impact on forest regeneration. In 87% of the NFI4 plots in the canton of Vaud, canopy shading at 130 cm above ground was between 60% and 100% (Figure 10). Many NFI4 plots were very shaded, i.e., values >90% canopy shading at 130 cm appeared in 17% of the plots. They were mostly in the lower regions of the Jura and the Alps, as well as in the Plateau (black points in Figure 10). Overall, canopy shading at 40 cm above ground of <60% appeared much more often at higher altitudes of the Jura than in the other regions (Figure 10). Almost 60% of all pole timber to medium timber had >90% canopy shading at 40 cm above ground, while only 45% of old timber and mixed forest and 30% of young growth/thickets reached this level of shading at 40 cm. Thus, small seedlings are very frequently shaded by the canopy in these plots.

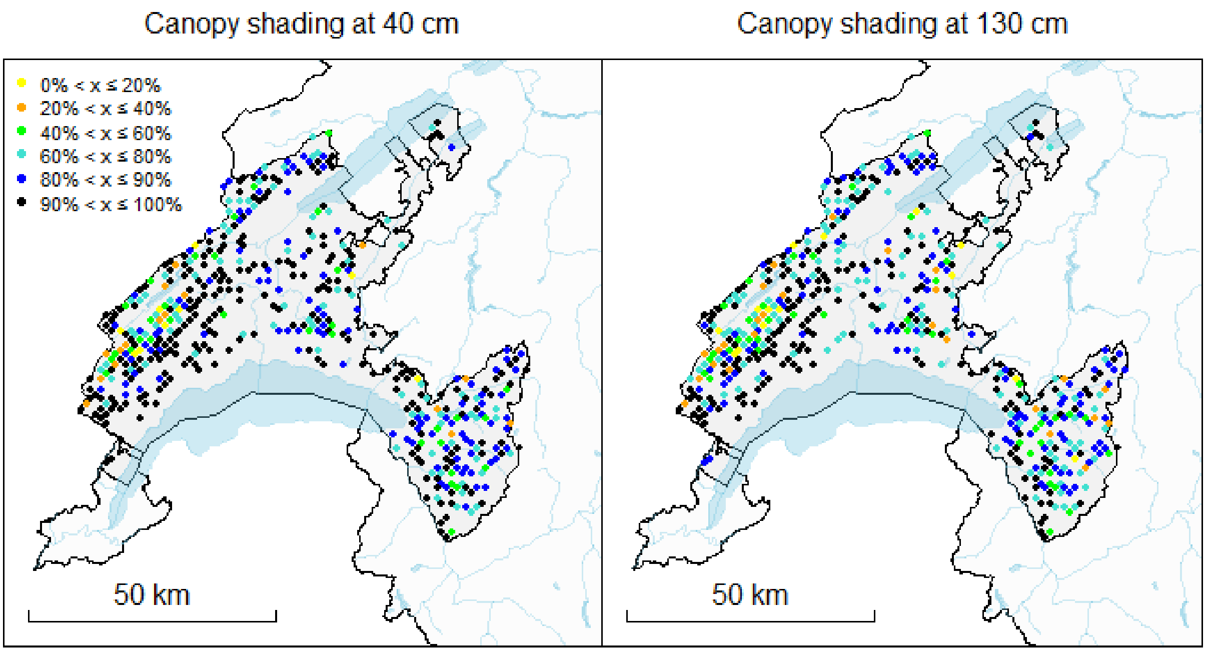


Figure 10: Canopy shading at 40 cm and 130 cm above ground [%] in the NFI4 plots in the canton of Vaud.

2.4 Cantonal data on ungulates

To assess if there was a relationship between the browsing intensity and the population size of ungulates, hunting and perish data from the cantonal authorities was used. The hunting data included the number of animals killed by hunters per year, species and wildlife sector. The perish data indicated the number of animals found dead as roadkill or hunted by wildlife managers per year, species and wildlife sector. The hunting data was available for the whole period (1993–2017), but the perish data only existed from 2008 onwards for every wildlife sector. The considered animals were roe deer, red deer and chamois. The hunting and perish data on wild boar (*Sus scrofa*) were only available starting in the year 1997 and were thus neglected, like in most browsing studies [e.g., 12]. For information on the data preparation, see section 2.5.1.

This data did not show the exact population density of ungulates, but it was the only data available over the whole time span from 1993 to 2017. Estimations from spotlight taxation (kilometric abundance index) were only available for parts of the NFI4 period and not for all wildlife sectors. In addition, they were not comparable between the different hunting zones, due to differences in e.g. roads and visibility (personal communication, Patrick Patthey). Moreover, the procedure for data sampling was not the same for all animals. Thus, this population estimation dataset was not used.

2.5 Statistical analysis

2.5.1 Main variables

For the statistical analysis, five predictors were mainly considered to have an influence on the frequency of ungulate damage: tree species, time, spatial unit, altitude and ungulate density (see below). All other factors that are important for forest regeneration (e.g. climate, soil and light conditions, competition from other vegetation, other damage) and for ungulate damage (e.g. cover, visibility, food availability, distance to paths, disturbance) were not considered in the analysis, because the data was not equally available for both NFI periods and/or the number of plots per classification would have been too small (e.g. forest developmental stage). Some analyses were, however, made with ungulate preference instead of tree species (see below).

The original plan was to either perform a separate analysis for plots with certain characteristics or omit plots with certain characteristics. For example, for estimating the ungulate impact in the canton of St Gallen [27], all plots with >90% canopy shading and/or with >90% of the plot area affected by competition by other vegetation were excluded. As outlined above (Figure 10), with this approach 30–60% of the plots would have been eliminated due to the shading criterion alone. This definitely would have reduced the number of analysed NFI plots too much. Therefore, such plots were not omitted a priori, but this point was considered in the discussion.

Tree species

Different tree species are selected for browsing, fraying and bark stripping. Thus, species is an important variable for assessing ungulate impacts. For the data analysis, only the seven most frequent species or species groups with >100 trees were considered. These species were silver fir (*Abies alba*), maple (*Acer: Acer platanoides*, *Acer pseudoplatanus*, *Acer campestre*, *Acer opalus*), beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), Norway spruce (*Picea abies)*, rowan berry (*Sorbus aucuparia*) and oak (*Quercus: Quercus petrea and Quercus robur*). For all other species, only a descriptive overview was made but the data was not analysed further.

Time

Time was modelled as a categorical predictor with two levels (NFI2 and NFI4) and as a linear predictor within the NFI4 period. The first factor thus showed differences between the two NFIs and the second showed trends within the years 2009–2017.

Spatial unit

Either the production regions or the hunting zones were used. Both spatial unit factors had three levels (Figure 7). When altitude or altitudinal vegetation belt (see section 2.1) was integrated into the model, the production regions were used (see discussion above).

Altitude or altitudinal vegetation belt

Altitude data (in metres above sea level) was available for each NFI plot, i.e. factor z gathered from aerial photographs [19]. Alternatively, the altitudinal vegetation belt was used (Figure 8), which was derived from other NFI attributes (Brändli U.-B. & Keller W. 1985: Die Vegetationshöhenstufen im LFI. Birmensdorf, Eidg. Forschungsanstalt WSL, LFI [unpublished]).

Ungulate density

Not all animals were present in all spatial units. Therefore, the hunting and perish data of the three main ungulates were converted to an ungulate density index (UDI) that considered their body size. The UDI was calculated for each year (y), following [28]:

$$UDI_y = n(red\ deer)_y + \frac{1}{5}n(roe\ deer)_y + \frac{1}{4}n(chamois)_y$$

where n = all animals killed in the corresponding year and hunting zone.

For the number of killed animals, the sum of all animals hunted or killed by other means (perish data) was used. Hunting data was available for the whole period (1993–2017), whereas perish data was only available after 2008. To compensate for this discrepancy, the number of hunted animals was multiplied by an animal-specific factor to reach a corrected UDI. This factor was calculated for each species for the period when both datasets were available.

$$n(before\ 2008)_y = N(hunted\ animals)_y * \left(\frac{N(perish\ data)}{N(hunted\ animals)} + 1\right)$$

$$n(after\ 2008)_y = N(hunted\ animals)_y + N(perish\ data)_y$$

Various areas became game protection areas between NFI2 and NFI4, prohibiting all normal hunting. In such areas, the perish data included shooting by the game guard. Thus, if the perish data was extrapolated from the data after 2008 to the time when hunting was still allowed, this could have led to an overestimation of the number of kills. All analyses were therefore run using the corrected UDI or using an uncorrected UDI (hunting data + perish data). The reason for using both UDI indices was to quantify the influence of the correction factor and thus to determine how sensitive the statistical models were to ungulate density.

The hunting data was dependent not only on the climatic conditions but also on decisions made to increase or decrease the number of ungulates and the success of hunters. To compensate for such variability, a UDI value averaged over three years was also calculated (called UDIrobust in the R code). For example, the average UDI for 2016 was calculated as the mean of the UDIs from 2015, 2016 and 2017.

The ungulate density variable lagged by one year to account for the fact that the previous year's shoot was assessed for browsing. For example, the UDI calculated with the number of animals killed in 2016 (UDI_{2016}) was used for the analysis of the NFI data from 2017, as the shoot assessed in 2017 was actually formed and browsed in 2016.

2.5.2 Descriptive statistics

For each binary outcome – browsing, fraying and bark stripping – the number of trees assessed, the number of trees found to be damaged, and the resulting percentage are presented for: (i) NFI2 and NFI4, (ii) each of the seven common tree species, and (iii) the different hunting zones or production regions.

Note that the plots in which there was protection against ungulate damage of a single seedling or of the whole subplots (i.e. fences) were not excluded from the analysis, as in NFI2 only two plots had protection for one subplot and only one plot had subplots that were both protected. In NFI4, eight nearest seedlings had protection but no information about the plot count data was available.

For calculating the browsing intensity, only seedlings which had information about browsing were included. This excluded all seedlings with a dead treetop, all seedlings which did not form a shoot in the previous year (first year seedlings), and (in NFI2 only) all trees which were frayed.

Browsing intensity was calculated using two different methods:

i) The total number of browsed seedlings of a species and hunting zone was divided by the total number of seedlings of that species and hunting zone (i.e. ratio of mean). This is what is normally done in published NFI analyses [cf., 15, 16] and in the analysis of indicator areas by Dani Rüegg [29]. With the ratio of mean method, all seedlings were counted the same way, thus plots with many seedlings dominated the result.

ii) The percentage of browsed seedlings was first calculated for each plot and species. The mean browsing intensity over all these "plot browsing percentages" was then calculated for every hunting zone or production region (i.e. mean of ratio). In this second method all plots were counted the same way for the browsing intensity, and the resulting values were more representative of the spatial distribution of the browsing percentages.

If the two browsing intensity measures differed widely, this meant that groups of seedlings were browsed differently than single seedlings (for an example see the Appendix 7.1).

As few trees showed signs of bark stripping and few seedlings or saplings showed signs of fraying / bark stripping, no statistical model was calculated for these two damage types and only a descriptive analysis was completed.

2.5.3 Regression analysis for browsing

Mixed effects logistic regression

To examine changes in browsing over time in different regions, for different tree species and different site-specific predictors (altitude and ungulate density), mixed effects logistic regression models were used, i.e. generalised linear mixed models with a Bernoulli conditional distribution and a logit link. Tree species, time and production region or hunting zone were included as fixed effects in every model (Table 6). Additionally, a random intercept for each plot was included in all models to account for the correlation between the outcomes observed on trees within a single plot. Four different models were used, two with interactions between time and species and between time and spatial unit (production region or hunting zone) and two including the height class of the trees (Table 6), also as fixed effects. For each combination of species and spatial unit, the models tested whether there was a change in browsing probability between NFI2 (1993–1994) and the start of NFI4 (2009), or a change within NFI4 (between 2009 and 2017).

*Table 6: Overview of the mixed effects logistic regression models used to assess the **development of browsing over time**. An X indicates that the predictor was included in the model. 'Species' stands for the seven most frequent tree species or species groups. Time NFI2–NFI4 is a categorical predictor with two levels (NFI2 and NFI4) and Time NFI4 is a linear predictor within the NFI4 period (2009–2017). HC = height class.*

Model	Region	Region – HC	Zone	Zone – HC
Fixed effects				
Time NFI2–NFI4	X	X	X	X
Time NFI4	X	X	X	X
Species	X	X	X	X
Production region	X	X		
Hunting zone			X	X
Time NFI2–NFI4 x Species	X	X	X	X
Time NFI4 x Species	X	X	X	X
Time NFI2–NFI4 x Region	X	X		
Time NFI4 x Region	X	X		
Time NFI2–NFI4 x Hunting zone			X	X
Time NFI4 x Hunting zone			X	X
Height class		X		X
Random effect variance				
Plot	X	X	X	X

To test if there was a relationship between browsing probability and altitude and/or ungulate density, several models were used that included different variables estimating ungulate density (Table 7). All models again included tree species and time, as well as the interactions between time and species, as fixed effects. They further included interactions according to the added variables as fixed effects and a random intercept for each plot (Table 7). Variables and interactions with non-significant effects were removed from the model. The best candidate models were selected by using likelihood ratio tests (function *anova*) for differentiation of the models or, in case of unequal N, the lowest Akaike's information criterion [AIC approach, as in 30].

In addition, a model integrating the production regions and the altitude as fixed effects were formed (Table 7). This was not done for hunting zones, as there was no hunting zone that included all altitudinal belts (Figure 8).

Table 7: Overview of the mixed effects logistic regression models used to assess the difference in browsing probability with altitude and/or approximate ungulate density. An X indicates that the predictor was included in the final model and an (X) that it was tested but not significant and thus omitted. 'Species' stands for the seven most frequent tree species or species groups.

Model	**Altitude – UDI**	**Altitude – uncorrectedUDI**	**Altitude – averagedUDI**	**Altitude – Deer**	**Region – Altitude – UDI**
Fixed effects					
Time NFI2–NFI4	X	X	X	X	X
Time NFI4	X	X	X	X	X
Species	X	X	X	X	X
Production region					X
Time NFI2–NFI4 x Species	X	X	X	X	X
Time NFI4 x Species	X	X	X	X	X
Time NFI2–NFI4 x Region					X
Time NFI4 x Region					X
Altitude	X	X	X	X	X
Altitude x Species	(X)	(X)	(X)	(X)	(X)
UDI	UDI	Uncorrected UDI	Averaged UDI	Deer	UDI
UDI x Species	(X)	(X)	(X)		(X)
Altitude x UDI	(X)	(X)	(X)		(X)
Red deer				X	
Roe deer				X	
Chamois				X	
Random effect variance					
Plot	X	X	X	X	X

All plots available in NFI2 and/or NFI4 were considered in the statistical analysis. We did not omit all plots which were only sampled in one NFI (Figure 7), as this would have reduced the dataset and led to the exclusion of valuable information about browsing. We also did not resample NFI2 data to match the sample size of NFI4. An equal number of sample plots would not mean an equal sample size, as the subplot areas were not of equal size within and between the two NFIs (Table 2) and two subplots were sampled in NFI2 but only one in NFI4 (Figure 4). Further, a reduction to only one subplot in NFI2 would have reduced the NFI2 dataset to about half its original size. As we used conditional models that considered the differences between NFI2 and NFI4 over spatial and temporal scales, there would have been no advantage of such efforts to improve comparability artificially. Indeed, we would have lost precision by enlarging the variability within NFI2.

Mixed effects logistic regression for ungulate preference

The above statistical analyses were performed by reducing the tree species list to species that were frequent (i.e. >100 seedlings assessed for browsing during each NFI). A model including all tree species was not possible. However, an ungulate preference was assigned to each tree species. This was done in two ways:

i. The browsing preference data first published in [7] and complemented by [31, 32] was used. Thus, "++" was assigned as 5, "+" as 4, "+/-" as 3, "-/=" as 2, and "–" as 1, i.e. tree species with a value of 1 were considered "unpalatable" and those with 5 "highly palatable and preferentially browsed". All the tree species which were not classified within these publications were omitted from the analysis, including *Aesculus hippocastanum*, *Ailanthus altissima*, *Pyrus communis*, *Pyrus pyraster* and *Malus sylvestris*, as well as all species classified as shrubs in NFI4 (e.g. *Ilex aquifolium*, *Laburnum anagyroides*, *Crataegus monogyna*, *Berberis vulgaris*, *Buxus sempervirens*, *Amelanchier ovalis*, *Lonicera* spp., *Cornus sanguinea*, *Cornus mas*, *Corylus avellana*, *Sambucus nigra*, *Sambucus racemose*, *Rhamnus cathartica*, *Ligustrum vulgare*, *Euonymus* spp., *Rhamnus frangula*, *Viburnum lantana*, *Viburnum opulus*, *Prunus spinosa*, *Prunus mahaleb*, *Crataegus* spp. and *Liriodendron tulipifera).*

ii. Ungulate preferences estimated for the canton of Vaud by Mrs Meylan (forestry specialist in charge of phytosociology and forest inventories, Vaud; received 28 January 2022) were used.

- **Douglas**: Il n'a pas de valeur. Il est effectivement bien plus attractif pour la frayure que pour l'abroutissement. Toutefois, on pourrait lui mettre une **valeur 1,** comme pour l'épicéa.
- **If**: nous sommes d'accord avec la **valeur 5**.
- **Mélèze**: nous lui mettrions une **valeur 4**.
- **Pin sylvestre**: nous lui mettrions une **valeur 4**.
- **Charme**: nous lui mettrions une **valeur 5**.
- **Chênes**: nous lui mettrions une **valeur 5**.
- **Hêtre**: On pourrait même mettre la **valeur 5**, dans les zones où il y a du cerf!
- **Merisier**: nous lui mettrions une **valeur 5**.
- **Noyer**: nous lui mettrions une **valeur 1**.
- **Robinier**: Il n'a pas de valeur, mais nous n'avons pas d'avis.
- **Tilleuls**: Si le hêtre a une valeur de 3, on devrait être au-dessus pour les tilleuls. Nous lui mettrions une **valeur 5**.

If not mentioned above, the ungulate preference values from (i) were used. However, due to the comment on "Tilleuls" (*Tilia*), beech was assigned a value of 4. In addition, all *Pinus* were assigned the value 4, not only *Pinus sylvestris*. This adjusted ungulate preference was called "Appétence".

These ungulate preference estimates were integrated into the model as a fixed numeric count variable, not as a categorical variable as the influence on the browsing probability was assumed to increase with browsing preference value. In addition, as done for tree species, interactions between ungulate preference and the time NFI2–NFI4 and between preference and the time within NFI4 were added (Table 8). All the ungulate density estimates from above (Table 7) were tested, but for simplicity only the models (Table 8) and results for UDI are shown.

Table 8: Overview of the mixed effects logistic regression models used to assess the change in browsing probability with altitude and/or approximated ungulate density for different classes of ungulate preference. An X indicates that a predictor was included in the final model and an (X) that it was tested but not significant and thus omitted. Models were run for all tree species that could be classified (see text).

Model	Preference	Appétence
Fixed effects		
Time NFI2–NFI4	X	X
Time NFI4	X	X
Preference	Ungulate preference	Appétence
Production region	(X)	(X)
Time NFI2–NFI4 x Preference	X	X
Time NFI4 x Preference	X	X
Time NFI2–NFI4 x Region	(X)	(X)
Time NFI4 x Region	(X)	(X)
Altitude	X	X
Altitude x Preference	(X)	(X)
UDI	UDI	UDI
UDI x Preference	(X)	(X)
Altitude x UDI	(X)	(X)
Random effect variance		
Plot	X	X

In these models of ungulate preference, a variable for the forest developmental stage in the corresponding plot per year was also included, i.e. a different stage was possible for a plot in NFI2 compared with in NFI4. In addition, the models were rerun including only the NFI4 period and including canopy shading at 40 cm or shading at 130 cm as an additional variable (not shown in Table 8).

Hypothesis testing and odds ratios

To test whether the browsing probability changed significantly over time for some combinations of predictors (tree species and spatial unit), hypothesis testing was applied based on the fixed effects and their variance-covariance matrix, adjusted for multiple comparisons using the Benjamini-Hochberg method [33]. Comparisons between percentages (e.g. the change in browsing percentage from one year to another) are reported as odds ratios (OR).

If, for example, the overall browsing intensity in 2009 was 12.5%, i.e. 1/8 of all seedlings, then the odds of a seedling being browsed would be 1:7 (odds(1:7)=1/7). This means that one out of eight seedlings would be browsed, but seven not. Correspondingly, if the browsing intensity in 2017 was 30%, i.e. 3/10, the odds would be 3:7 (odds(3:7)=3/7). The change between 2009 and 2017 could then be assessed using the odds ratio: odds(2017)/odds(2009)= odds(3:7) / odds(1:7) = $(\frac{3}{7})/(\frac{1}{7}) = 3$. In this example, the chance of a seedling being browsed in 2017 was thus 3 times higher than in 2009.

A decrease in the observed browsing percentage between NFI2 and NFI4 (time NFI2–NFI4) might be caused by differences in the sampling procedure (see browsing assessment in section 2.2.2). Therefore, a one-sided test for this contrast was performed and only an increase in the observed browsing percentage was interpreted as evidence for an increase in the true browsing percentage. The other analyses were performed using two-sided tests.

Several variables were included in the models, and the differences between the predicted browsing and the observed browsing, i.e. unpredicted browsing hotspots (or low points), were represented in the random intercepts. By plotting these plot-level random intercepts, areas in which unmeasured processes caused a higher (or lower) browsing than expected became apparent.

Implementation (software and packages)

All analyses were performed in the R programming language [34], version 4.1.2 (2021-11-01) using base packages and the following analysis-specific packages: *data.table* to prepare the data [35]; *glmmTMB* to fit generalised linear mixed effects models [36]; *multcomp* for hypothesis tests adjusted for multiple comparisons [37]; and *sf* for geo-spatial plots [38], using publicly available geo-spatial data from swisstopo.

3. Results

3.1 Fraying and bark stripping

3.1.1 Bark stripping on trees ≥12 cm DBH

A total of 6977 trees were assessed for bark stripping in NFI2 and 6747 in NFI4. In NFI2, no single tree ≥12 cm DBH was found that was damaged by bark stripping. In NFI4, three spruce trees had signs of bark stripping. Therefore, the intensity of bark stripping of trees ≥12 cm DBH was almost 0.0% in canton of Vaud for both NFIs. Two of the three damaged trees in NFI4 were in the same plot in the production region Alps and one was in the Jura. All of them belonged to the upper montane altitudinal vegetation belt.

3.1.2 Fraying and bark stripping on trees <12 cm DBH

For fraying and bark stripping, a descriptive analysis was made separately for the different height classes, as the sampled area was different for every height class (Table 2). As sampling in NFI2 and NFI4 followed different methods, a direct comparison was not possible. Only results for the seven most frequent tree species are reported here (Table 9, Table 10). For results for all species, see Table 16 andTable 17 in the Appendix).

In NFI2, all the main tree species had quite large samples, except in the largest height class, where only spruce and beech had >100 saplings (Table 9). However, oak had fewer than one hundred seedlings and saplings in each individual height class and rowan berry in the smallest seedling class and the largest sapling class. Oak had the largest number of assessed trees in the smallest seedling class, whereas all the other main tree species had the largest number in height class 40–129 cm (Table 9).

Overall, in NFI2 the percentage of frayed or bark-stripped seedlings or saplings was between 0% and 4.9% (Table 9). Only one spruce was found to be frayed/bark stripped in the smallest seedling class and only one silver fir in the sapling class 4–11.9 cm DBH. In height class 40–129 cm, fraying/bark stripping increased for silver fir, spruce, maple and ash, with up to 1.2% of the spruce seedlings damaged. Fraying and bark stripping was most frequent overall in the DHB class 0- 3.9 cm. Only spruce was frayed/bark stripped less often than in the large seedling class. None of the very few oak trees had signs of fraying or bark stripping in NFI2.

In NFI2 there were generally more seedlings and saplings with a dried treetop than with fraying or bark stripping. However, the reason for the dried treetops was not known, and in some cases it could have been caused by ungulates.

In NFI4, the number of sampled seedlings and saplings was considerably lower than one hundred per species and height class (Table 10). The reason for this was that only the nearest seedling and sapling per height class, irrespective of the tree species, was assessed for fraying/bark stripping (see section 2.2.3). Over one hundred trees were sampled only for beech in two height classes (Table 10), and the corresponding results were thus expected to be more reliable.

In NFI4, the largest fraying/bark stripping percentage was 6.5% for rowan berry in height class 0–3.9 cm DBH. No seedlings were frayed/bark stripped in the smallest height class. In height class 40–129 cm only one spruce was found with signs of fraying/bark stripping. As in NFI2, the largest fraying/bark stripping percentages appeared in the DBH class 0–3.9 cm, where only for oak and beech was no sapling frayed/bark stripped. In the DBH class 4–11.9 cm only one maple, one beech and one spruce were frayed/bark stripped.

Table 9: Number of seedlings and saplings per height or DBH class in NFI2 that were not frayed or bark stripped (NOT), were frayed or bark stripped (FB), or had a dried treetop and thus no information was available about fraying (D). The total number of trees (T) and the percentage of frayed and bark-stripped trees (P=FB/(FB+NOT)) are given, separately for the seven most frequent tree species. Note that here the plot count data of two subplots per plot were used (in contrast to the corresponding Table 10 for NFI4).

NFI2	***Abies alba***	***Picea abies***	***Acer* spp.**	***Fagus sylvatica***	***Fraxinus excelsior***	***Sorbus aucuparia***	***Quercus* spp.**
Height class 10–39 cm							
NOT	181	201	440	1227	611	72	93
FB	0	1	0	0	0	0	0
D	1	3	9	5	9	1	2
T	182	205	449	1232	620	73	95
P [%]	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Height class 40–129 cm							
NOT	302	583	441	1934	626	176	21
FB	3	7	2	0	1	0	0
D	5	19	18	36	26	4	1
T	310	609	461	1970	653	180	22
P [%]	1.0	1.2	0.5	0.0	0.2	0.0	0.0
DBH class 0–3.9 cm							
NOT	120	227	213	996	335	96	26
FB	3	1	11	3	11	4	0
D	1	3	8	10	17	4	0
T	124	231	232	1009	363	104	26
P [%]	2.4	0.4	4.9	0.3	3.2	4.0	0.0
DBH class 4–11.9 cm							
NOT	74	161	37	108	35	20	19
FB	1	0	0	0	0	0	0
D	0	1	2	0	4	0	0
T	75	162	39	108	39	20	19
P [%]	1.3	0.0	0.0	0.0	0.0	0.0	0.0

Table 10: The number of seedlings and saplings per height or DBH class in NFI4 that were not frayed or bark stripped (NOT) or were frayed or bark stripped (FB). The total number of trees (T) and the percentage of frayed and bark-stripped trees (P=FB/(FB+NOT)) are given, separately for the seven most frequent tree species. Note that here the nearest seedling and sapling per height class and subplot were assessed, irrespective of tree species.

NFI4	*Abies alba*	*Picea abies*	*Acer* spp.	*Fagus sylvatica*	*Fraxinus excelsior*	*Sorbus aucuparia*	*Quercus* spp.
Height class 10–39 cm							
NOT	40	45	47	99	60	59	14
FB	0	0	0	0	0	0	0
T	40	45	47	99	60	59	14
P [%]	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Height class 40–129 cm							
NOT	23	68	40	126	37	32	3
FB	0	1	0	0	0	0	0
T	23	69	40	126	37	32	3
P [%]	0.0	1.4	0.0	0.0	0.0	0.0	0.0
DBH class 0–3.9 cm							
NOT	31	47	35	112	19	29	1
FB	2	1	1	0	1	2	0
T	33	48	36	112	20	31	1
P [%]	6.1	2.1	2.8	0.0	5.0	6.5	0.0
DBH class 4–11.9 cm							
NOT	53	81	24	70	19	9	2
FB	0	1	1	1	0	0	0
T	53	82	25	71	19	9	2
P [%]	0.0	1.2	4.0	1.4	0.0	0.0	0.0

3.2 Browsing

3.2.1 Descriptive results

3.2.1.1 Overview of available data

A total of 6908 living seedlings (tree height <130 cm) were assessed for browsing in NFI2 and 4104 in NFI4 (Table 11). Thus, more seedlings were sampled in NFI2 in total, as well as in each seedling height class. In height class 10–39 cm the difference was small, while in height class 40–129 cm the difference was >2500 seedlings. Accordingly, the number of effectively observed browsed seedlings in NFI2 was greater than in NFI4, and the difference was also larger in height class 40–129 cm than in the smaller height class. For the hunting zones (as well as the NFI production regions), many more seedlings were sampled in the Jura and the Plain (Plateau) than in the Alps (Pre-Alps/Alps) in both NFI2 and NFI4 (Table 11).

Table 11: Overview of the browsing data. The number of trees not browsed, number of trees browsed, NA values (seedlings with a dead treetop or seedlings that were frayed/bark stripped in NFI2), and total number of trees sampled for browsing in NFI2 and NFI4. Counts are separated into height class 10–39 cm and height class 40–129 cm and into individual production regions and hunting zones.

	NFI2				**NFI4**			
	Not browsed	**Browsed**	**NA**	**Total**	**Not browsed**	**Browsed**	**NA**	**Total**
Total	6220	688	153	6908	3692	412	180	4104
Height class 10–39 cm	2596	229	31	2856	2338	129	63	2620
Height class 40–129 cm	3624	459	122	4205	1354	193	117	1664
Production region								
Alps/Pre-Alps	491	176	34	701	422	74	19	515
Plateau	2592	253	75	2920	1287	102	96	1485
Jura	3137	259	44	3440	1983	236	236	2284
Hunting zone								
Alps	306	121	24	451	284	60	11	355
Plain	2678	270	79	3027	1573	145	84	1802
Jura	3236	297	50	3583	1835	207	85	2127

For five out of the seven main tree species with >100 seedlings in NFI2 and NFI4 (Table 12), the number of sampled seedlings was also greater in NFI2 than in NFI4. For rowan berry only two seedlings more were sampled in NFI2 than in NFI4, while oak was sampled almost twice as often in NFI4 as in NFI2 (Table 12). Despite the change in method, it can be assumed that rowan berry and oak became more frequent. By far the most frequent tree species in both inventories was European beech (Table 12).

As ungulates prefer to browse certain species, there was a large difference in the number of browsed seedlings observed per species. Notably, fewer browsed beech seedlings were found in NFI2 than in NFI4, though many more beech seedlings were found overall in NFI2 (Table 12). For ash, in contrast, the number of browsed seedlings was large in NFI2 but much lower in NFI4. For both coniferous tree species (silver fir and spruce) the number of browsed seedlings observed was rather low in both NFI2 and NFI4. Only two oak seedlings were found to be browsed in NFI2, compared with 70 in NFI4 (Table 12).

Table 12: Overview of the number of browsed seedlings per main tree species. The number of seedlings not browsed, number of seedlings browsed, NA values (seedlings with a dead treetop or seedlings that were frayed/bark stripped in NFI2), and total number of seedlings for NFI2 and NFI4.

	NFI2				**NFI4**			
Tree species	**Not browsed**	**Browsed**	**NA**	**Total**	**Not browsed**	**Browsed**	**NA**	**Total**
Abies alba	457	26	9	492	200	13	4	217
Picea abies	733	11	30	814	418	4	5	427
Acer spp.	635	246	29	910	605	112	24	741
Fagus sylvatica	3122	39	41	3203	1796	84	102	1982
Fraxinus excelsior	983	254	36	1273	375	46	32	453
Sorbus aucuparia	138	110	5	253	162	83	6	251
Quercus spp.	112	2	3	117	136	70	7	213

3.2.1.2 Spatial distribution of tree regeneration

In this section, the spatial distribution of seedlings per species and height class is described.

Norway spruce

The number of plots with spruce differed strongly between the height classes (Figure 11, Figure 12). Many more plots had one (or more) seedling in height class 40–129 cm than in the smaller height class in both NFIs. In addition, in both NFIs there were more plots with spruce seedlings in both height classes in the higher altitudinal vegetation belts.

In height class 10–39 cm in NFI2, 14% of the plots had one (or more) spruce seedling in the Jura hunting zone, while this value was 8% in the Alps and 6% in the Plain. For height class 40–129 cm in NFI2, 32% of the plots had spruce seedlings in the Alps, 28% in the Jura, and 20% in the Plain (Figure 11).

In height class 10–39 cm in NFI4, 14% of the plots had one (or more) spruce seedling in the Alps and in the Jura, while this value was 8% in the Plain. For height class 40–129 cm in NFI4, the equivalent numbers were 27% for the Alps, 20% for the Jura and 11% for the Plain (Figure 12). Thus, the percentages of plots with large spruce seedlings decreased slightly from NFI2 to NFI4 (Figure 11, Figure 12). It has to be taken into account, however, that the area sampled was smaller in NFI4 than in NFI2 (sampled surface per one subplot and one instead of two subplots, see section 2.2.2).

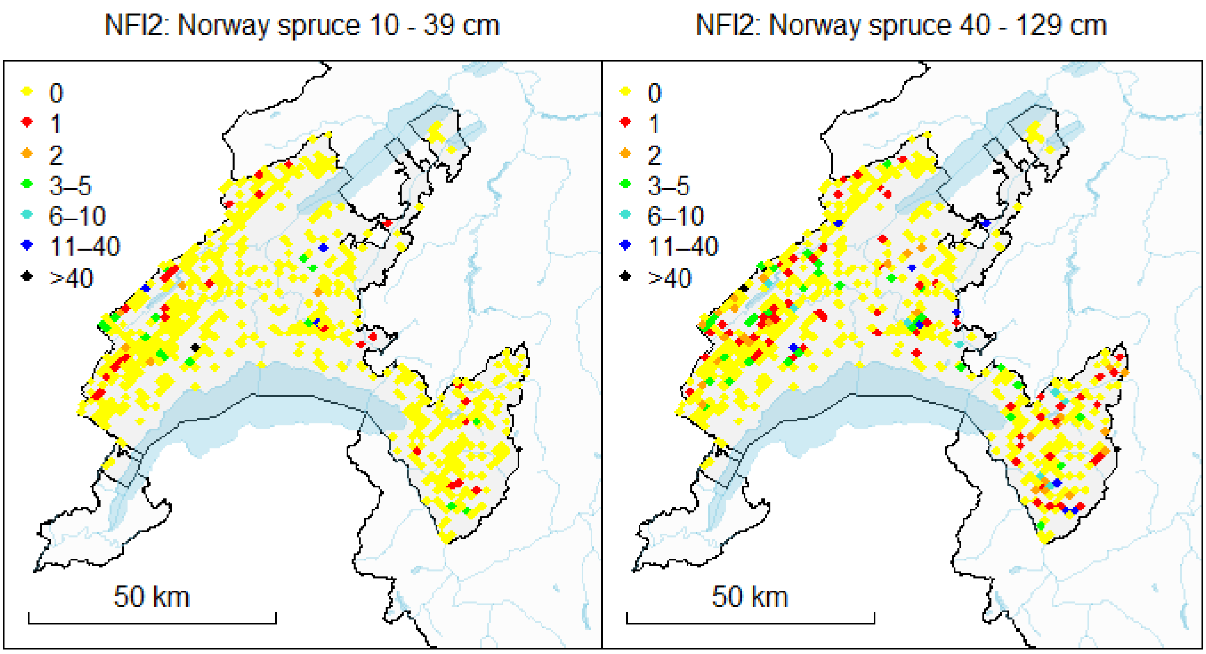


*Figure 11: Number of spruce (*Picea abies*) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

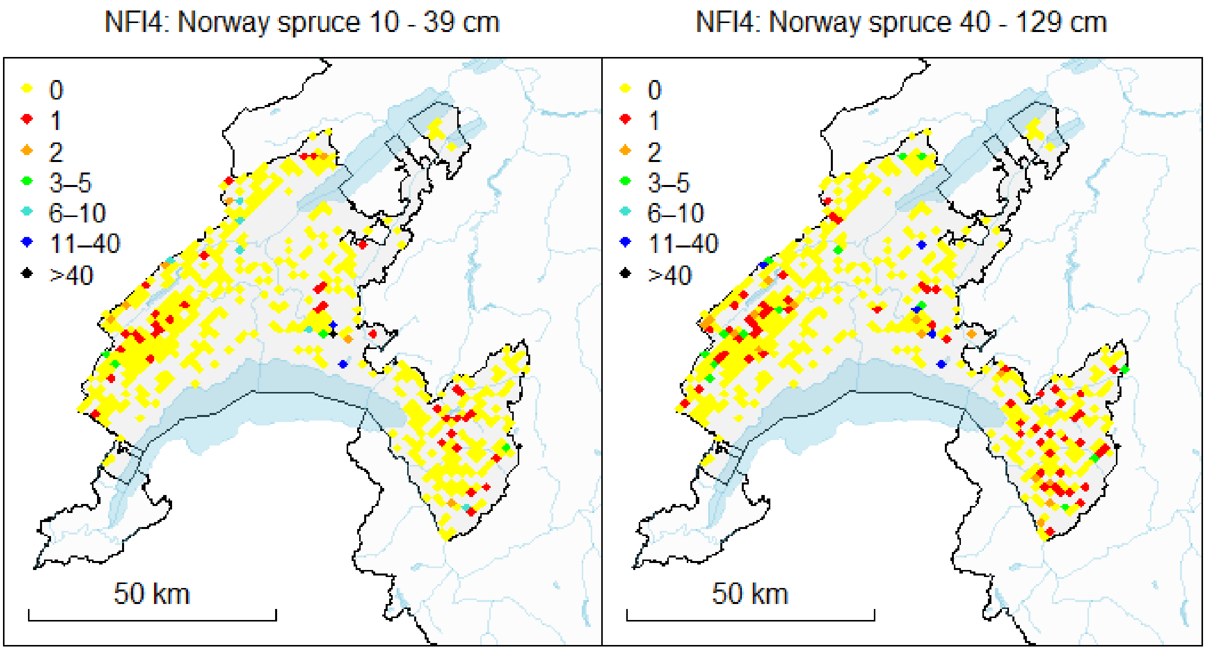


*Figure 12: Number of spruce (*Picea abies*) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

Silver fir

Most plots in the canton of Vaud did not have any silver fir seedlings in either NFI2 or NFI4, in either height class (Figure 13, Figure 14). The percentage of plots with silver fir seedlings was lower in the Alps (A: 6% small seedlings, 12% large seedlings) than in the Jura (J: 15%, 16%) and Plain (P: 15%, 19%) in NFI2. In contrast, in NFI4 the Plain had the fewest plots with small silver fir seedlings (P=9%, A=12%, J=16%), while the Jura and the Alps had the fewest large silver fir seedlings (P=11%, A=8%, J=7%).

In NFI2, the lower montane altitudinal vegetation belt had the most plots with silver fir seedlings (22% small seedlings, 26% large seedlings), followed by the upper montane (12%, 14%), the lower subalpine (6.4%, 14%) and the colline/submontane belt (11%). This situation was similar in NFI4 and for height class 10–39 cm, but in that case it was the upper montane belt that had the most seedlings (21%), followed by the lower subalpine (13%), the colline/submontane (10%), and the lower montane belt (8%). In contrast, for NFI4 height class 40–129 cm, the percentage of plots with silver fir seedlings was around 9–10% for most altitudinal vegetation belts, except the upper montane with 6%.

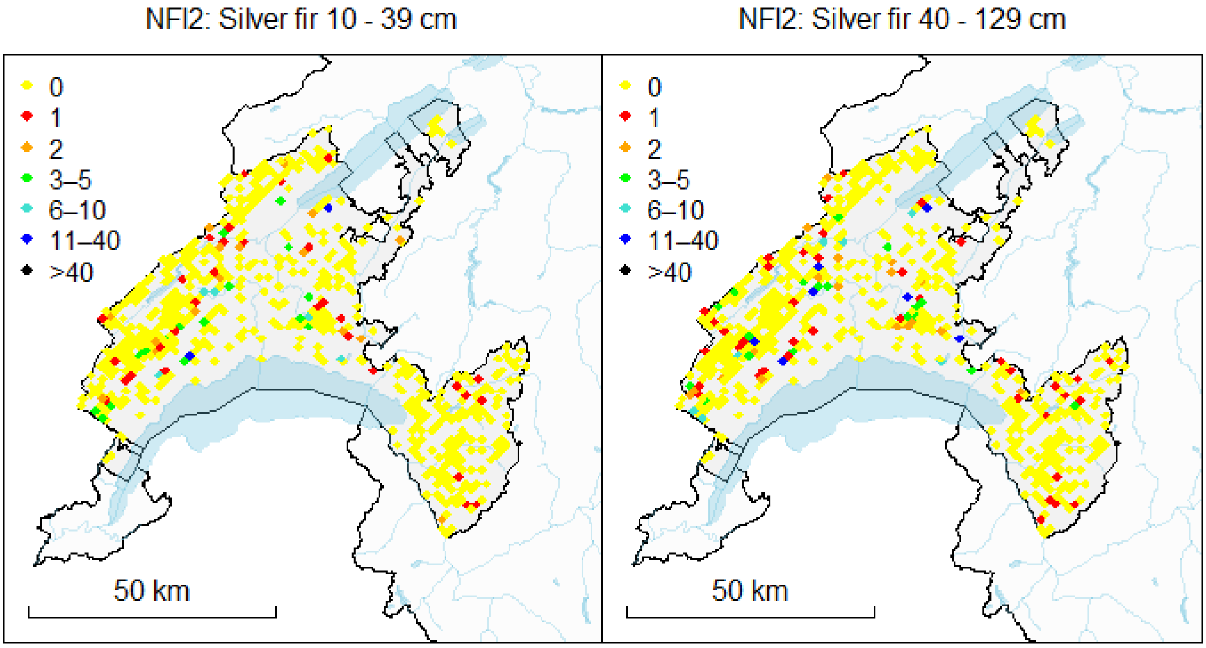


*Figure 13: Number of silver fir (*Abies alba*) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

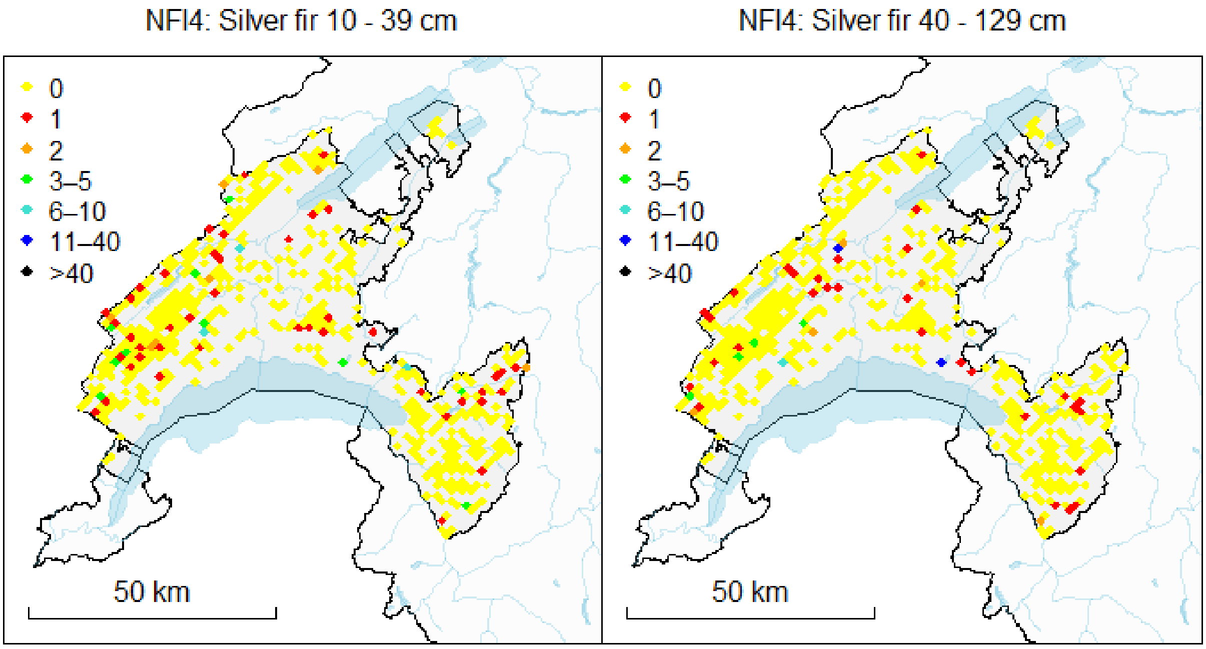


*Figure 14: Number of silver fir (*Abies alba*) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

Beech

There were many more plots with one (or more) beech seedling than with any of the other species (Figure 15, Figure 16). Generally, the Jura had more plots with beech seedlings than the Plain and considerably more than the Alps, in both NFIs and both height classes. For example, in the larger height class in NFI2 49% of the plots in the Jura had beech seedlings, 33% in the Plain, and only 5% in the Alps.

Over all hunting zones, there were slightly more plots with beech seedlings in height class 40–129 cm than in the smaller height class in both NFI2 and NFI4.

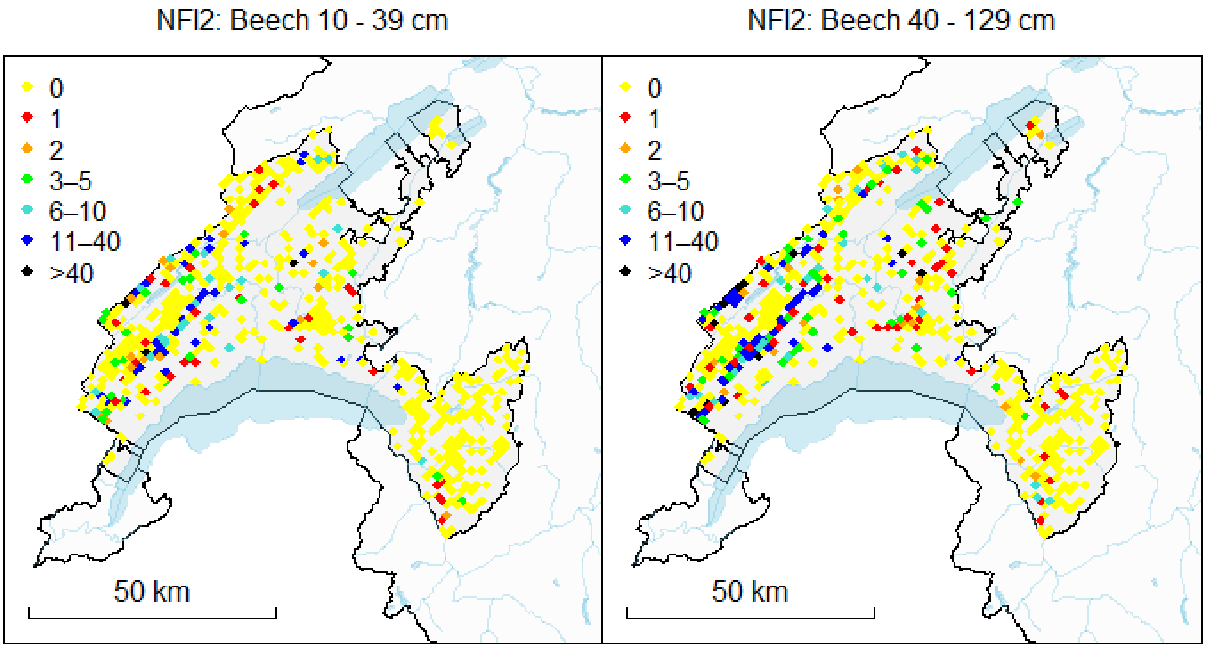


*Figure 15: Number of beech (*Fagus sylvatica*) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

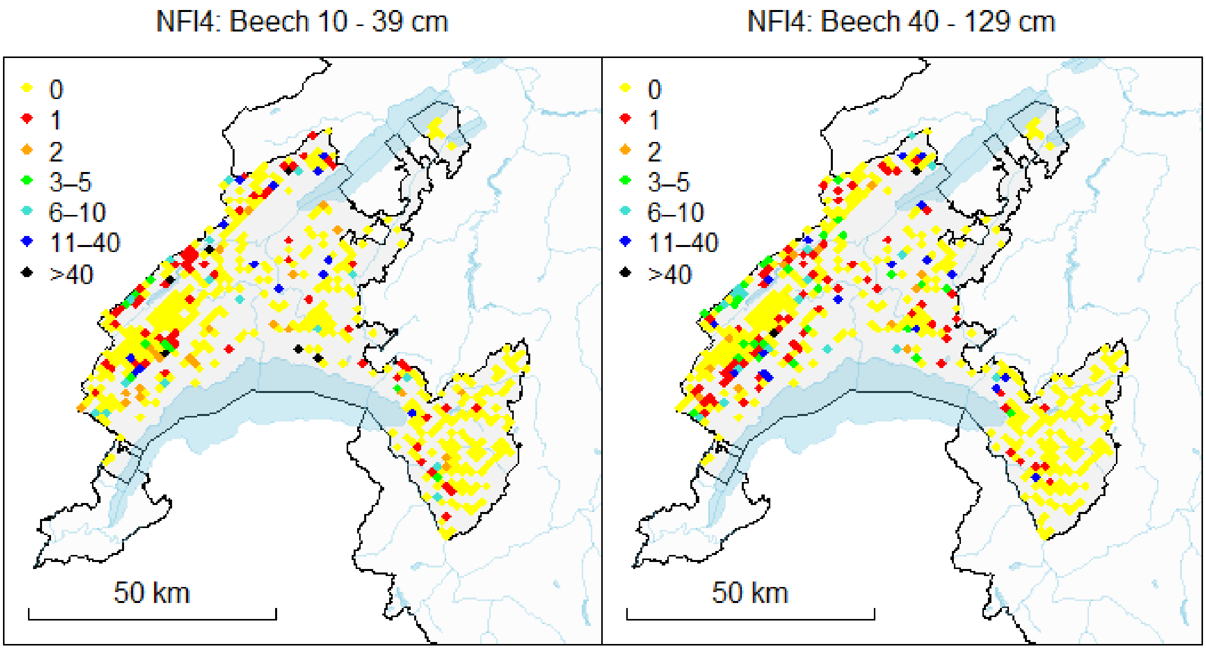


*Figure 16: Number of beech (*Fagus sylvatica*) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

In NFI2, the lower montane altitudinal vegetation belt had the highest percentage of plots with beech seedlings (28% small seedlings, 42% large seedlings), followed by the colline/submontane and upper montane (26–27%, 36%), and finally the lower subalpine (13%, 20%). In contrast, in NFI4 the upper montane belt (36% small seedlings, 40% large seedlings) had a similar percentage of plots with beech seedlings than the lower montane belt (34%, 38%), but more than colline/submontane (19%, 28%) and the lower subalpine (14%, 15%).

Maple

In both NFIs, the percentage of plots with maple seedlings in height class 10–39 cm was around 14–19% in all altitudinal vegetation belts (Figure 17, Figure 18). In contrast, the percentage of large maple seedings was highest in the colline/submontane belt (31%) in NFI2, followed by the lower montane (22%) and finally the upper montane and lower subalpine belts (20%). In NFI4, however, the percentage was highest in the lower subalpine belt (16%), followed by the two montane belts (12%) and finally the colline/submontane belt (8%).

The Jura (25%) had a greater percentage of plots with small maple seedlings than the Plain (15%) and the Alps (8%) in NFI2. The same was found for the large maple seedlings in NFI4 (J=16%, P=11% and A=9%) and there was a trend in the same direction in NFI2 (J=26%, P=24% and A=14%). In contract, there was an equal percentage of plots with small maple seedlings in all hunting zones in NFI4 (15–16%).

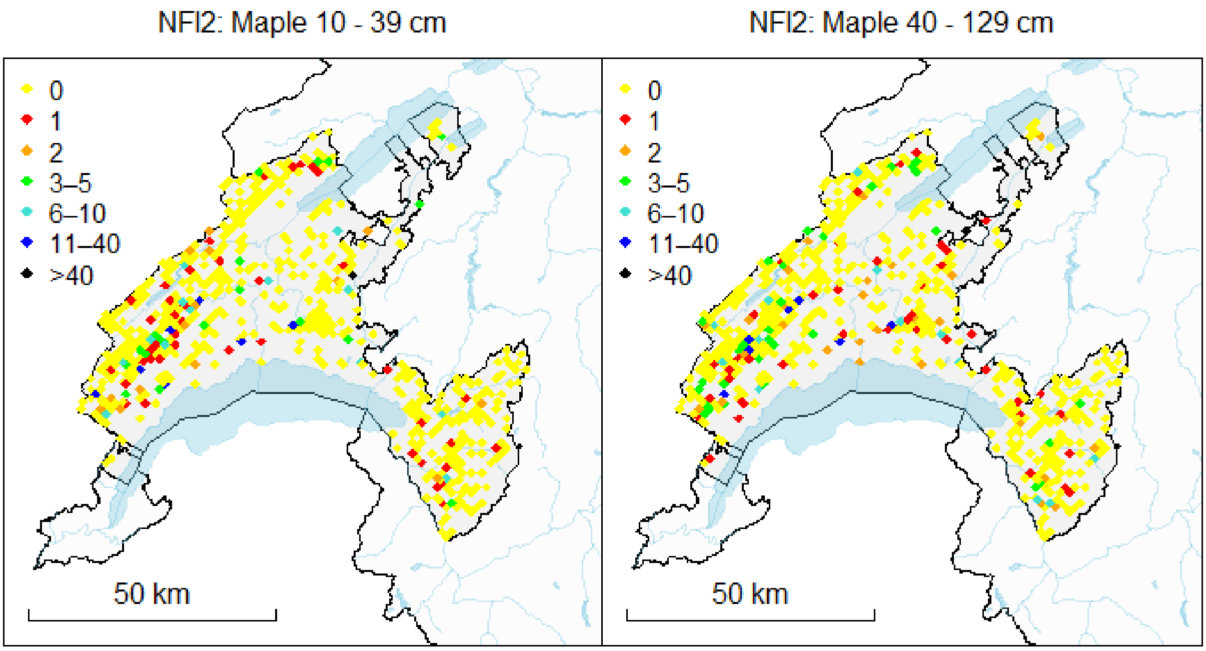


*Figure 17: Number of maple (*Acer *spp.) seedlings per plot (different colours) in the canton of in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

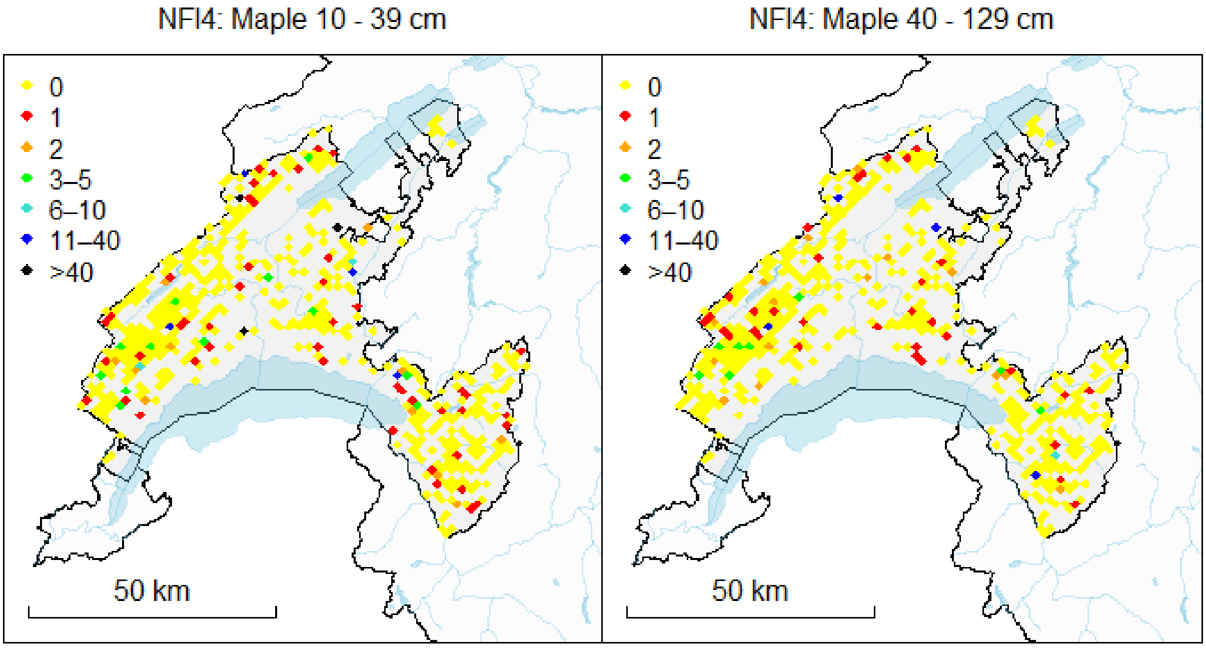


*Figure 18: Number of maple (*Acer *spp.) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

Ash

In both NFIs, the lower the altitudinal belt, the greater the percentage of plots found to have one (or more) ash seedling, for both small and large seedlings (Figure 19, Figure 20). More plots with ash seedlings appeared in the Plain in both NFI2 and NFI4, though considerably fewer in the larger height class in NFI4 (19% vs 28–31%). The Jura and the Alps had more-or-less similar percentages of plots with ash seedlings in NFI2 (6-7%), while in NFI4 fewer ash seedlings were found in the Jura (6% small seedlings, 3% large seedlings) compared with in the Alps (11%, 6%; Figure 19, Figure 20).

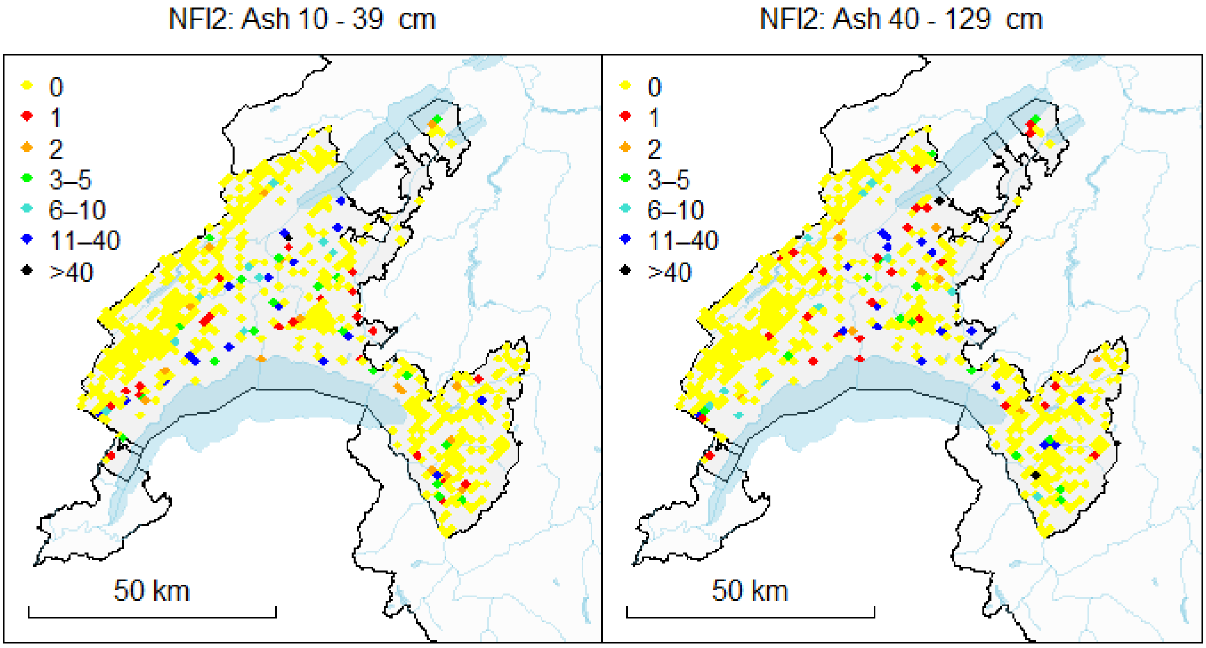


*Figure 19: Number of ash (*Fraxinus excelsior*) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

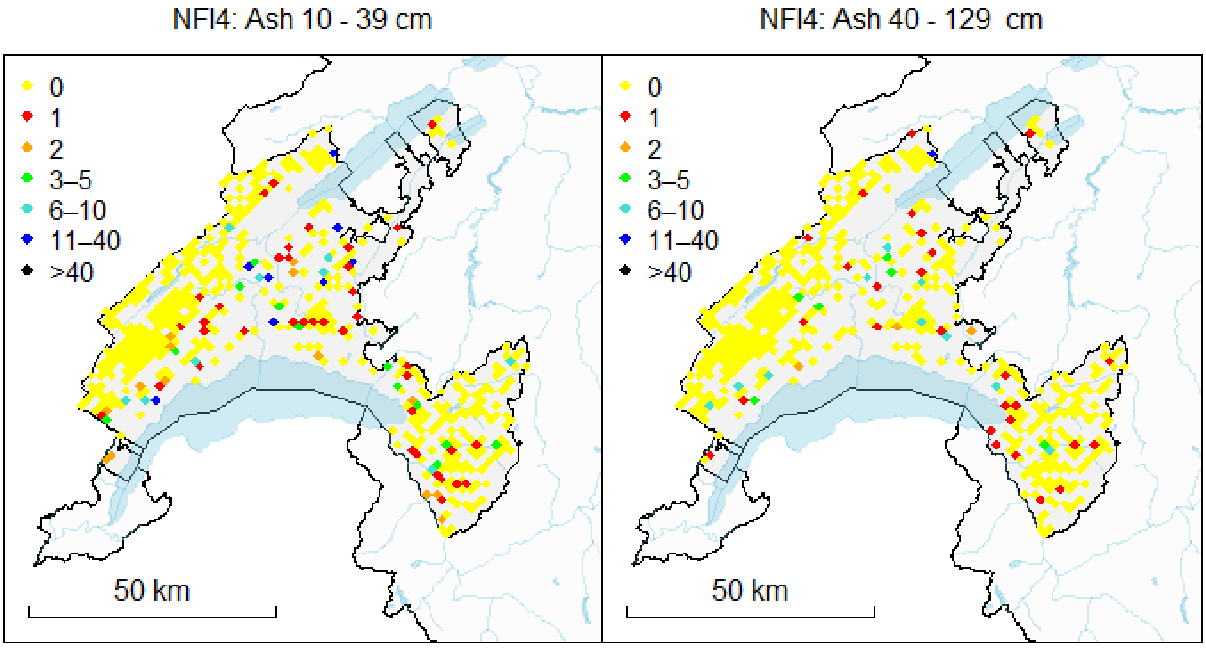


*Figure 20: Number of ash (*Fraxinus excelsior*) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

Rowan berry

In both NFI2 and NFI4, few plots in the canton of Vaud included rowan berry, and most of the plots with rowan berry had few seedlings (Figure 21, Figure 22). The higher the altitudinal vegetation belt, the greater percentage of plots found with rowan berry, in both NFIs and in both height classes. Only in NFI4 and height class 40–129 cm were there few plots with rowan berry in the colline/submontane belt. Consequently, in both NFIs there were only a few plots in the Plain with rowan berry (2–3%). The Alps and the Jura had an equal percentage of small seedlings (NFI2: 9%, NFI4: 18–19%), whereas the Alps had fewer large seedlings compared with the Jura in NFI2 (14% vs 21%) and more in NFI4 (15% vs 11%). In NFI2 a greater percentage of plots were found with one (or more) rowan berry in height class 40–129 cm than with seedling(s) in the smaller height class, while the opposite was found in NFI4.

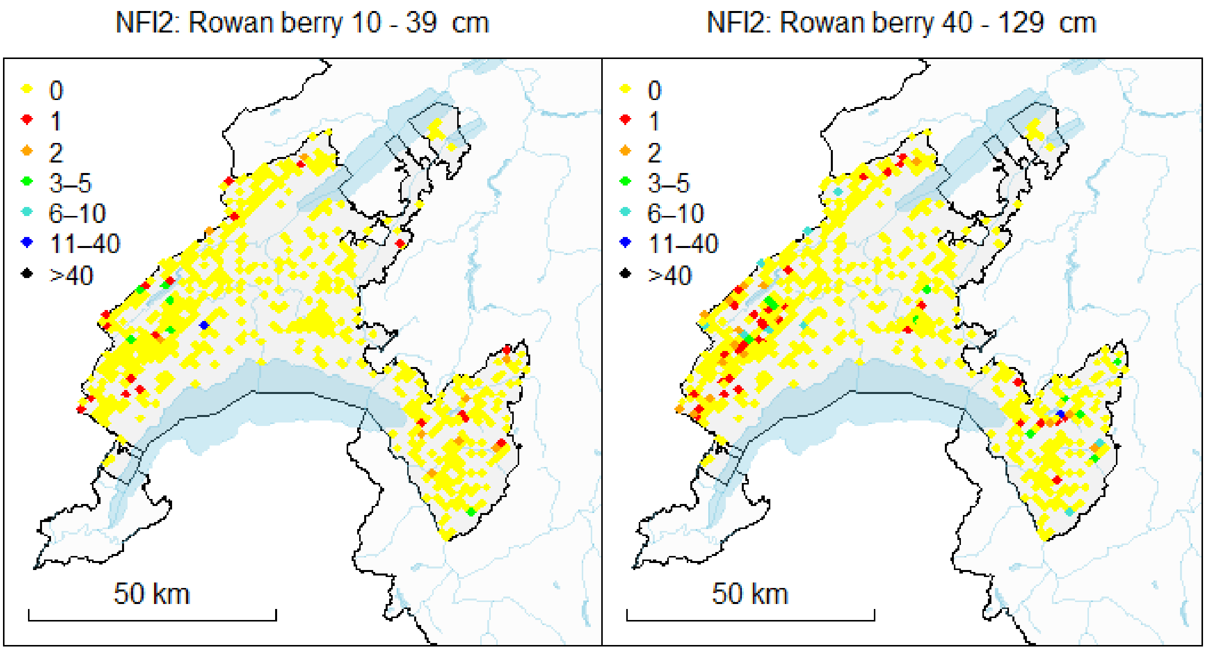


*Figure 21: Number of rowan berry (*Sorbus aucuparia*) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

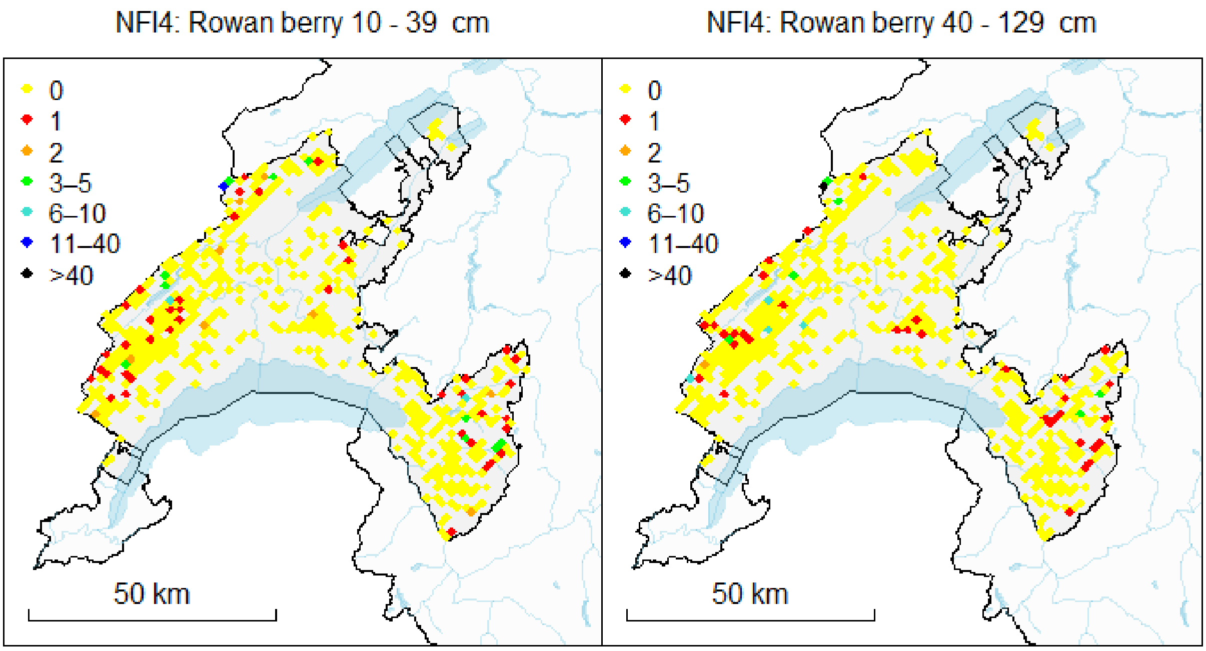


*Figure 22: Number of rowan berry (*Sorbus aucuparia*) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

Oak

Oak grew in very few of the plots in the canton of Vaud, all of which were in the colline/submontane or lower montane altitudinal vegetation belt in both NFIs and both height classes (Figure 23, Figure 24).

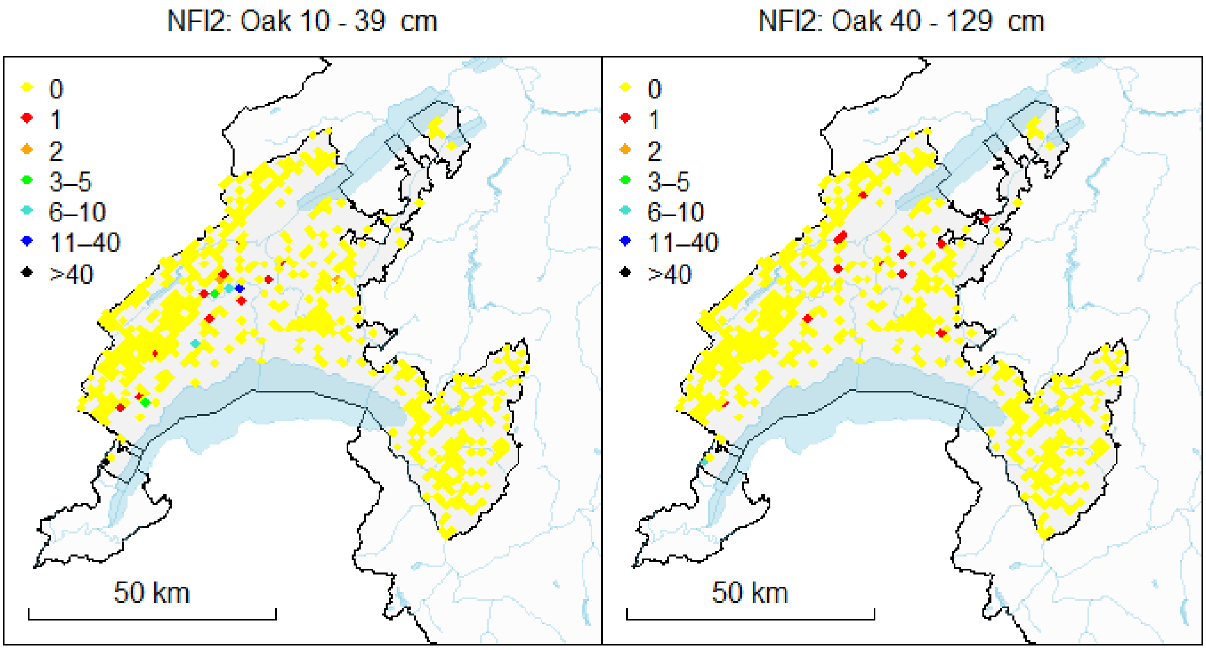


*Figure 23: Number of oak (*Quercus *spp.) seedlings per plot (different colours) in the canton of Vaud in NFI2, shown separately for height classes 10–39 cm and 40–129 cm.*

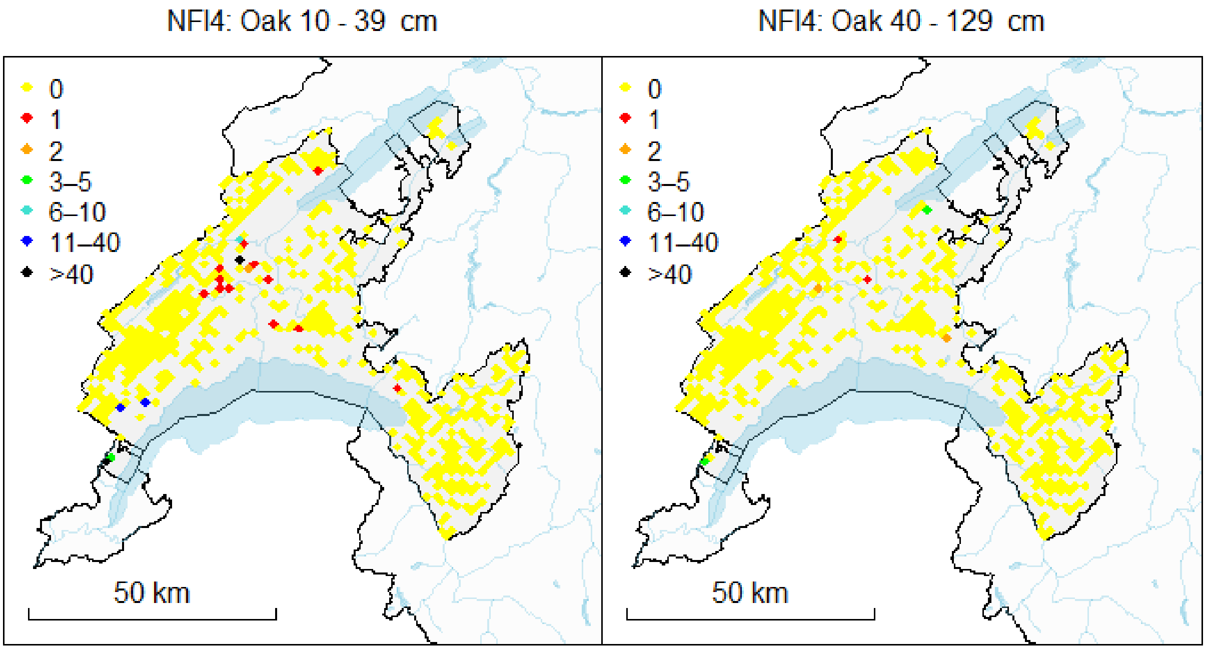


*Figure 24: Number of oak (*Quercus *spp.) seedlings per plot (different colours) in the canton of Vaud in NFI4, shown separately for height classes 10–39 cm and 40–129 cm.*

The colline/submontane belt tended to have a greater percentage of plots with oak (3–11%) than the lower montane (2%-7%). In both NFI2 and NFI4, there were a greater percentage of plots with oak seedlings of height class 10–39 cm than with seedlings in the larger height class. In NFI4 there were almost no plots with large oak seedlings.

There were a greater percentage of plots with oak seedlings in the Plain (3–9%) than in the Jura (0–2%) and no oak seedlings were found in plots in the Alps. In one area in the southwestern part of Vaud near Lake Geneva, 1–2 plots with >40 oak seedlings were found. These plots thus had a large proportion of canton's sampled oak seedlings (Figure 23, Figure 24). This area belongs to the Jura production region but to the Plain the hunting zone. As a result of these few but densely populated plots, >100 oak seedlings were found. However, the few plots with oak seedlings meant that the corresponding results from statistical models have to be interpreted with great caution.

3.2.1.3 Browsing intensity per height class

In height class 10–39 cm, browsing intensity differed widely between the seven main tree species (Table 13). It was very low in NFI2 for silver fir (4.4%) and beech (1.1%), with slightly higher values in NFI4 (6.7% and 3.3%, respectively), whereas for spruce it was very low in both NFIs (1.1% and 1.5%, respectively). For ash the browsing intensity was 15.4% in NFI2 and 11.2% NFI4. For maple, it was 18.2% in NFI2 and only 6.3% in NFI4. The browsing intensity of rowan berry was by far the highest in NFI2 (58%) and was still high in NFI4 (33%). For oak the browsing intensity was very low in NFI2 (1.1%) but the largest out of the seven main species in NFI4 (35.4%, Table 13).

*Table 13: Overview of the browsing data for height class 1039 cm per main tree species. The number of browsed seedlings, total number of seedlings (excluding seedlings with NA for browsing), and browsing intensity (BI=[number of browsed seedlings/total]*100) are given for NFI2 and NFI4.*

	NFI2			NFI4		
Tree species	**Browsed**	**Total**	**BI [%]**	**Browsed**	**Total**	**BI [%]**
Abies alba	8	181	4.4	8	119	6.7
Picea abies	3	201	1.5	2	192	1.0
Acer spp.	80	440	18.2	35	560	6.3
Fagus sylvatica	13	1227	1.1	36	1096	3.3
Fraxinus excelsior	94	611	15.4	16	143	11.2
Sorbus aucuparia	42	72	58.3	40	120	33.3
Quercus spp.	1	93	1.1	68	192	35.4

The browsing intensity of beech was much higher (13.4% vs 1.1%) for height class 40–129 cm than for height class 10–39 cm in NFI2, and approximately double in NFI4 (6.1% vs 3.3%; Table 14). Large maple seedlings had one of the highest browsing intensities in NFI2 and the highest in NFI4 (49.0%) and was much more frequently browsed than in height class 10–39 cm. Rowan berry and ash were browsed with a similar frequency in the two height classes. In contrast, oak was browsed much more often in height class 10–39 cm (35.4%) than in height class 40–129 cm (14.3%) in NFI4 (Table 14), but note that very few oak seedlings were observed in height class 40–129 cm.

*Table 14: Overview of the browsing data for height class 40–129 cm per main tree species. The number of browsed seedlings, total number of seedlings (excluding seedlings with NA for browsing), and browsing intensity (BI=[number of browsed seedlings/total]*100) for NFI2 and NFI4.*

	NFI2			NFI4		
Tree species	**Browsed**	**Total**	**BI [%]**	**Browsed**	**Total**	**BI [%]**
Abies alba	18	302	6.0	3	94	5.3
Picea abies	8	583	1.4	2	230	0.8
Acer spp.	166	441	37.6	77	157	49.0
Fagus sylvatica	26	1934	13.4	48	784	6.1
Fraxinus excelsior	160	626	25.6	16	143	11.2
Sorbus aucuparia	96	176	54.5	43	125	34.4
Quercus spp.	1	21	4.8	2	14	14.3

3.2.1.4 Browsing intensity per hunting zone

To assess browsing intensity the mean of ratio (MoR) and the ratio of mean (RoM = classical browsing intensity) were calculated using the two methods described in section 2.5.2. The calculations were done for the hunting zones (Table 15) and the NFI production regions (Appendix), with the two seedling height classes pooled together.

Over all hunting zones and for both NFI2 and NFI4, spruce had one of the lowest browsing intensities (from 0.7% to 5.1%; Table 15). Beech had similarly low browsing intensities, except in the Alps in NFI2, where it was one of the highest (MoR 33.3%, RoM 51.2%; but note that these values were based on a small number of assessed seedlings). However, the values for beech were slightly higher in NFI4 than in NFI2 in the Plain and the Jura, suggesting an increase in browsing over time.

Maple and rowan berry had the highest browsing intensities overall. Maple MoR was highest in the Alps and the Jura (MoR of 28.2–52.6%), whereas values were slightly lower in the Plain (MoR around 24%). The results obtained by the two calculation methods differed drastically for maple, with considerably lower RoM values than MoR values (Table 15). This implies that maple seedlings in plots with many maple seedlings in the Plain were much less often browsed than maple seedlings in plots with few maple seedlings. The MoR and RoM of rowan berry were high in the Alps and the Jura in both NFIs (30.2–50.7%) and the MoR was high in the Plain for NFI2. All of the few rowan berry seedlings found in the Plain in NFI4 were, in contrast, not browsed. Ash had a high MoR in the Alps in NFI2 (42.9%). In the Jura, in NFI2 in the Plain and in NFI4 in the Alps, ash MoR values were 16.7–27.8%, while MoR was only 9.2% in the Plain in NFI4 (Table 15).

Silver fir also had high MoR and RoM values in the Alps in NFI2 (MoR 30.1) but much lower values in NFI4, and lower values in all other hunting zones in both NFI's (2.5–16.5%). In the Plain the browsing intensity values for silver fir were considerably lower in NFI2 than in NFI4 (Table 15), suggesting a significant increase in browsing over time. Oak had a much higher browsing intensity in the Plain in NFI4 than in NFI2 (Table 15). For oak, the browsing intensities in the Jura had a very large standard error, due to few oak occurrences, and in the Alps no oak seedlings were found in either NFI.

Table 15: Browsing percentages: mean of ratio (MoR), standard error (SE) and ratio of mean (RoM = classical browsing intensity) in NFI2 and NFI4 for the seven main tree species per hunting zone. Values in italics and a smaller font size are based on a total of <20 actually assessed seedlings (i.e. not extrapolated). Values in bold are based on >200 actually assessed seedlings, and those in bold italics are based on 100–200 actually assessed seedlings.

Hunting zone	**NFI2**			**NFI4**		
	MoR [%]	**SE**	**RoM [%]**	**MoR [%]**	**SE**	**RoM [%]**
Alps						
Abies alba	30.1	11.5	30.9	9.5	6.6	7.8
Picea abies	***5.1***	***3.4***	***2.0***	2.6	2.6	1.0
Acer spp.	37.3	10.4	52.6	31.4	8.9	31.5
Fagus sylvatica	*33.3*	*17.8*	*51.2*	0.0	0.0	0.0
Fraxinus excelsior	***42.9***	***12.1***	***28.0***	16.7	11.2	16.7
Sorbus aucuparia	30.2	8.3	42.6	36.1	8.5	40.7
Quercus spp.	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
Plain						
Abies alba	**2.5**	**1.7**	**2.2**	***16.5***	***6.6***	***8.9***
Picea abies	**1.3**	**0.9**	**0.9**	**1.6**	**1.6**	**0.7**
Acer spp.	**24.1**	**5.1**	**9.5**	**23.5**	**6.7**	**3.1**
Fagus sylvatica	**1.2**	**1.0**	**0.5**	**4.9**	**2.0**	**3.0**
Fraxinus excelsior	**21.0**	**3.6**	**16.4**	**9.2**	**3.0**	**10.1**
Sorbus aucuparia	38.0	18.2	18.3	*0.0*	*0.0*	*0.0*
Quercus spp.	***0.1***	***0.1***	***16.4***	***14.5***	***7.5***	***37.2***
Jura						
Abies alba	***10.0***	***2.5***	***6.0***	7.2	4.1	3.6
Picea abies	**1.2**	**0.8**	**2.0**	***2.1***	***2.0***	***1.5***
Acer spp.	**37.4**	**4.6**	**27.7**	**28.2**	**5.9**	**16.2**
Fagus sylvatica	**3.8**	**1.4**	**1.2**	**7.8**	**2.1**	**4.4**
Fraxinus excelsior	***27.8***	***9.3***	***17.7***	26.3	9.8	10.7
Sorbus aucuparia	***41.8***	***6.0***	***50.7***	***38.5***	***6.3***	***33.4***
Quercus spp.	*20.0*	*20.0*	*6.5*	*33.3*	*33.3*	*6.7*

3.2.1.5 Tree density compared with browsing intensity

For each of the seven main tree species, the tree density per hectare and the browsing intensity were calculated for NFI2 and NFI4, separately for each production region and hunting zone.

Norway spruce

For spruce, only the Plain hunting zone (Plateau production region), had a much higher tree density in NFI4 than in NFI2 (Figure 25). The browsing intensity showed no difference between NFI2 and NFI4 in the individual hunting zones/production regions or in the whole canton of Vaud. The estimation error was clearly lower for NFI2 than for NFI4, due to the greater number of seedlings assessed in NFI2 (Table 12 to Table 14).

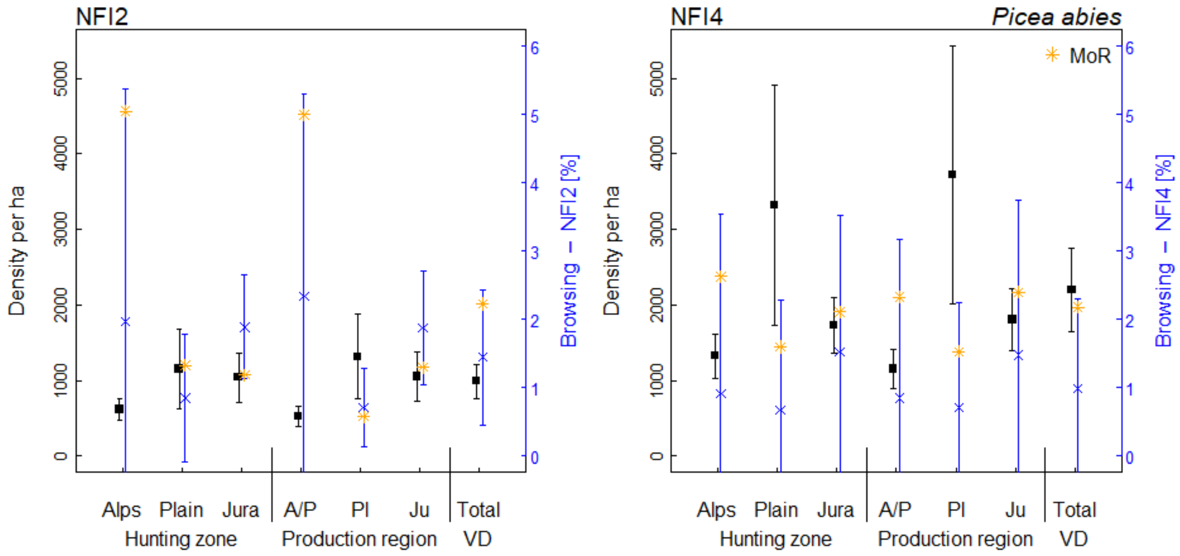


Figure 25: Spruce (Picea abies) *density per ha (black), ratio of mean [%] (blue), and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone (A=Alps, P=Plain, J=Jura) and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

Silver fir

The density of silver fir seedlings in NFI2 was highest in the Plain zone (Plateau region), followed by the Jura, and lowest in the Alps zone (Alps/Pre-Alps region) the number was the lowest (Figure 26). In NFI4, the density of fir seedlings was much higher than in NFI2 in the Jura and the Alps (Alps/Pre-Alps), and thus values for the whole canton of Vaud increased over time.

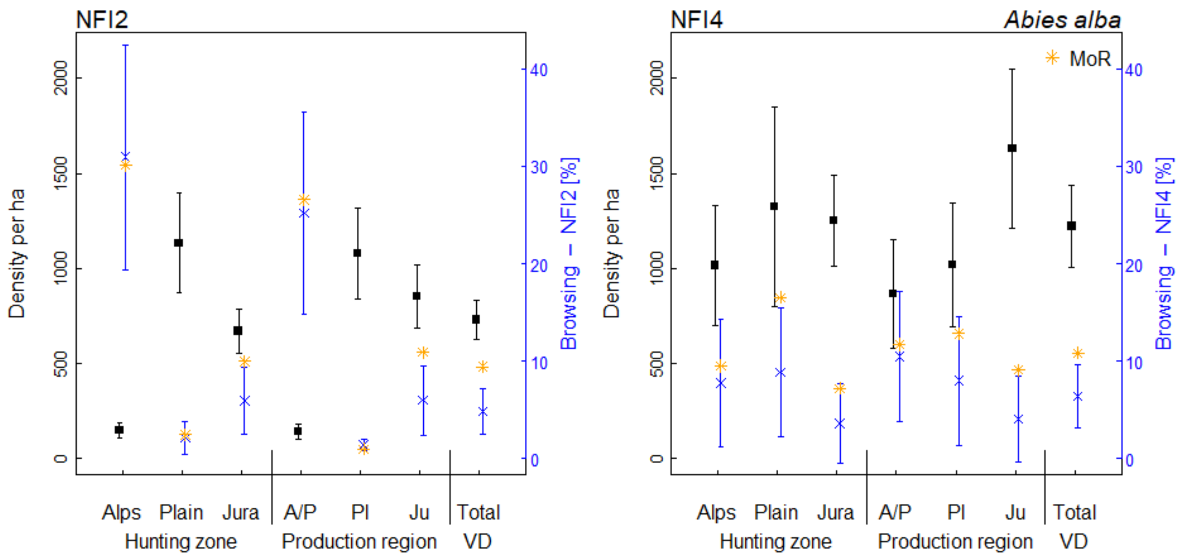


Figure 26: Silver fir (Abies alba) *density per ha (black), ratio of mean [%] (blue) and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

In NFI2, the browsing intensity on silver fir was highest in the Alps (Alps/Pre-Alps), much lower in the Jura, and lowest in the Plain (Plateau). However, in the Alps the density was very low in NFI2, and overall only 26 silver fir were actually assessed in the forest. In NFI4, no clear differences between the browsing percentages in the different regions were visible. The browsing intensity intended to crease over time in the Plain (Plateau). The browsing intensity of the whole canton of Vaud was approximately the same in both NFI2 and NFI4.

Beech

For beech, the tree densities were lowest in the Alps zone (Pre-Alps region), followed by the Plain (Plateau), and the Jura had the largest values in both NFI2 and NFI4 (Figure 27). In NFI4, however, the differences between the regions were much larger. Thus, the tree densities in the Plain, in the Jura and over the whole canton of Vaud were higher in NFI4 than in NFI2.

The browsing intensity on beech was quite low for all regions and in total in both NFI2 and NFI4. Only the Alps hunting zone had a larger value in NFI2. However, only even plots in the Alps included beech in NFI2 (Figure 15, Figure 16), with a total of 18 actually sampled beech seedlings in this zone, seven of which were browsed. Thus, this browsing intensity cannot be considered representative. It is included for completeness, as none of the 75 actually sampled beech seedlings was browsed in the Alps during the NFI4 period.

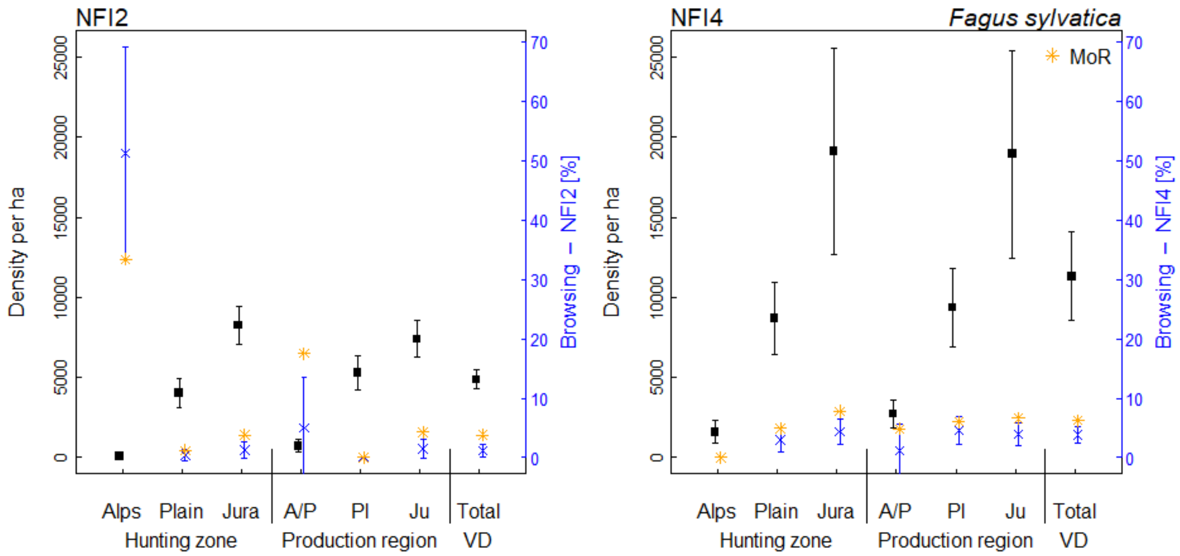


*Figure 27: Beech (*Fagus sylvatica*) density per ha (black), ratio of mean [%] (blue) and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

Maple

For maple the tree densities were higher in NFI4 than in NFI2 in all regions (Figure 28). In both NFIs the Alps zone (Alps/Pre-Alps region) had the lowest density of maple. The Plain (Plateau) had about the same density as the Jura in NFI2, whereas in NFI4 the median was higher but there was also large variability. The maple density for the whole canton of Vaud was also higher in NFI4 than in NFI2.

There was a large difference between the browsing intensity on maple calculated with RoM and the one based on MoR (Figure 28). MoR was quite similar among the hunting zones/production regions. Only in the Plain were the values slightly lower. This indicates that there must have been some plots with more maple seedlings than on average in the Alps, and that these maple seedlings were browsed more often than on average (higher RoM). In contrast, in the Plain the plots with more maple seedlings seemed to have less browsing than on average (lower RoM in Figure 28). The browsing intensity tended to be the highest where the tree density was lowest (Alps or Alps/Pre-Alps in NFI2 and NFI4), whereas the highest tree density corresponded to the lowest browsing intensity (Plain or Plateau in NFI2).

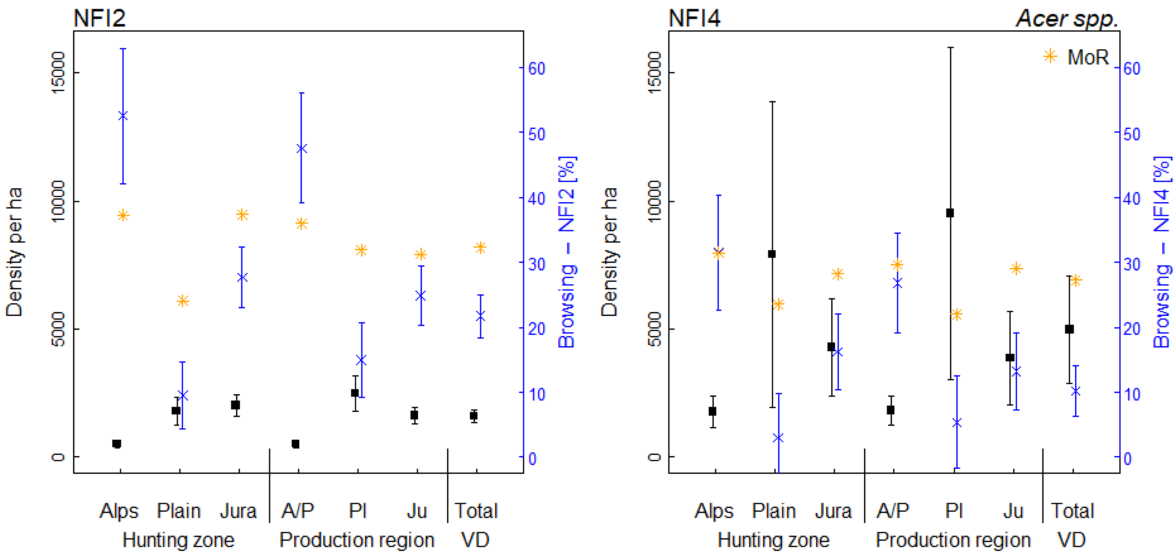


*Figure 28: Maple (*Acer spp.*) density per ha (black), Ratio of Mean [%] (blue) and Mean of Ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

Ash

Ash had the highest tree densities in the Plain zone (Plateau region) in both NFI2 and NFI4 (Figure 29). The Alps (Alps/Pre-Alps) had similar values as in the Jura in both NFI2 and NFI4. In both regions the values in NFI4 were slightly higher than in NFI2, whereas in the Plain (Plateau) the densities stayed approximately the same.

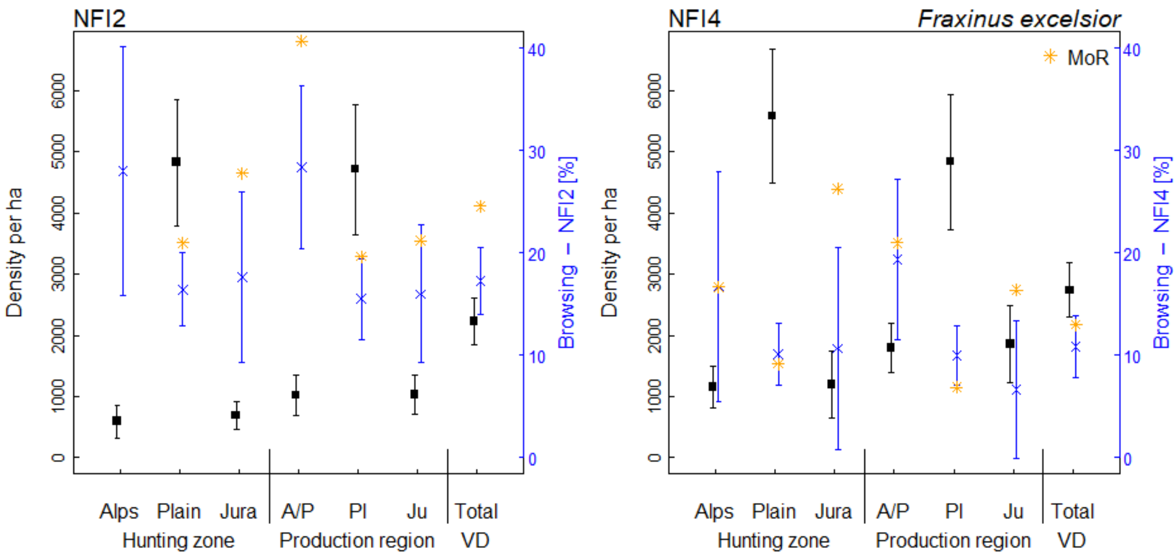


*Figure 29: Ash (*Fraxinus excelsior*) density per ha (black), ratio of mean [%] (blue) and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

The browsing intensity on ash tended to be highest in the Alps (Alps/Pre-Alps) in both NFIs. The browsing intensities were similar in the Jura and the Plain (Plateau). In NFI2 the browsing intensities in all regions tended to be slightly higher than in NFI4 (but possibly due to method differences). In some regions the MoR was larger than the RoM. Again, regions with high tree densities had lower browsing intensities and vice versa.

Rowan berry

Rowan berry had large differences in the tree density between NFI2 and NFI4, with overall higher values in NFI4 (Figure 30). The tree density in both NFI2 and NFI4 was lowest for the Plain zone (Plateau region), and similar for both the Alps (Alps/Pre-Alps) and the Jura. In NFI4, however, the difference between the Plain (Plateau) and the other regions was much larger. The value for Vaud as a whole was also much higher for NFI4 than for NFI2.

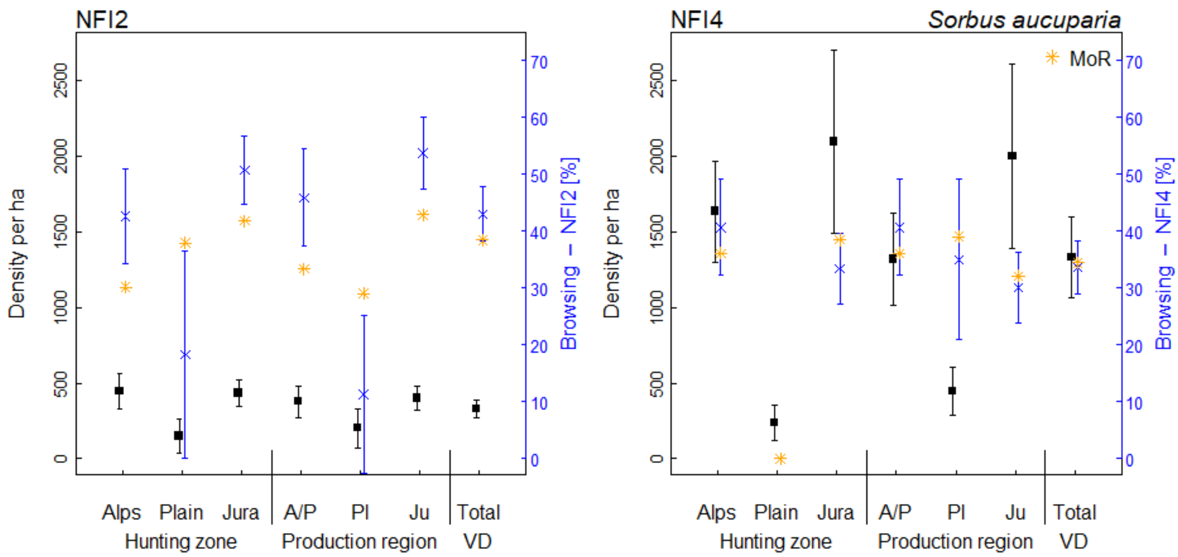


*Figure 30: Rowan berry (*Sorbus aucuparia*) density per ha (black), ratio of mean [%] (blue) and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

For rowan berry, the browsing intensity differed strongly between the two calculation methods. RoM was higher in the Jura and Alps (Alps/Pre-Alps) than in the Plain for both NFIs and higher than in the Plateau in NFI2. All 17 actually sampled rowan berry seedlings in the Plain hunting zone in NFI4 had no browsing, while 10 out of 28 in the Plateau production region were browsed in NFI4. As these are very few seedlings, the browsing percentages should be interpreted with much care. In NFI4 the MoR values were similar to the RoM values and the trends were about the same. In NFI2, however, the MoR values for the Jura and the Alps (Alps/Pre-Alps) were lower than the corresponding RoM values. Thus, the more densely regenerated plots probably had more browsing. Over the whole canton of Vaud, there was no detectable change in the browsing intensity on rowan berry over time.

Oak

The oak densities were low in all regions in NFI2 and small differences were found between the regions (Figure 31). In NFI4, the Plain had a much higher value than in NFI2 and compared with the other hunting zones. As these few plots were in the Jura production region (Figure 23, Figure 24), the Jura had by far the highest tree density. The total tree density was higher in NFI4 than in NFI2 (Figure 31).

The browsing intensity on oak differed across zones/regions and between the NFI2 and NFI4. Due to the small numbers of oak seedlings actually sampled in the NFI, only the browsing intensities in the Plain should be interpreted. In NFI2 browsing was practically absent for oak, while in NFI4 around every third oak was browsed in the Plain and thus in the whole canton of Vaud.

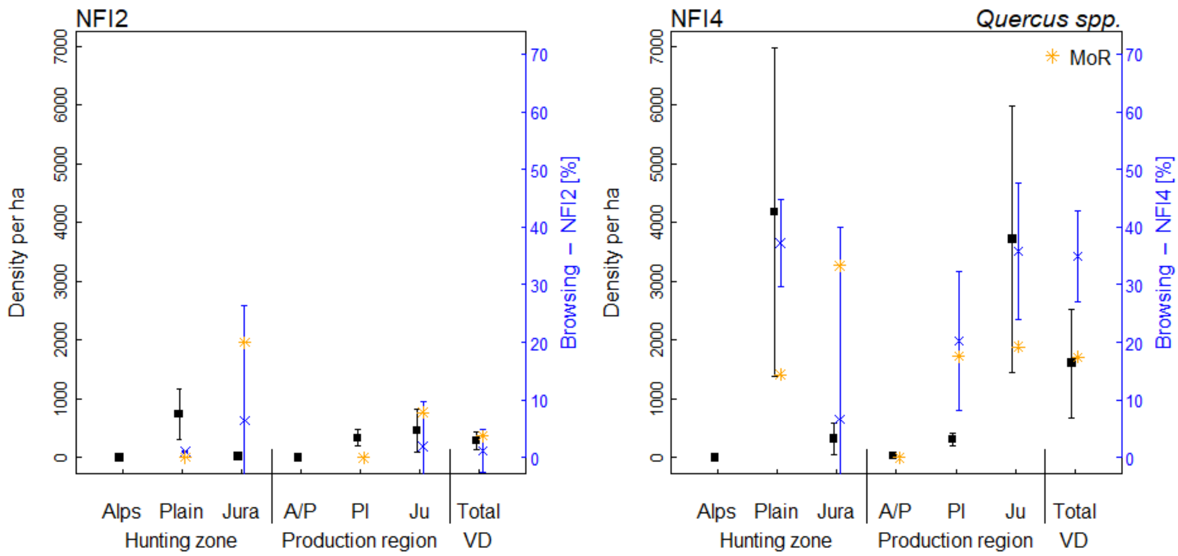


Figure 31: Oak (Quercus spp.*) density per ha (black), ratio of mean [%] (blue) and mean of ratio [%] (orange) of the browsing percentages in NFI2 and NFI4, separated by hunting zone and production region (A/P=Alps/Pre-Alps, Pl=Plateau, Ju=Jura) and for the whole canton of Vaud (Total VD). RoM and MoR have the same scale (blue).*

3.2.1.6 UDI data compiled per NFI plot

UDI development over time

Before analysing the relationship between UDI and browsing intensity, it was first determined whether there was a change in UDI over time. Please note that each plot was only sampled once per NFI period, thus the plots sampled in 2010 differed from those sampled in 2011, and so on.

The means of the UDI and the uncorrected UDI (Figure 32, red line) were similar between NFI2 and NFI4. The uncorrected UDI for the Alps decreased between NFI2 and NFI4, whereas it tended to increase in the Plain (Figure 32, left). Within NFI4 – with the data per NFI plot and sampling year – no significant trend was observed for any hunting zone (Figure 32, right).

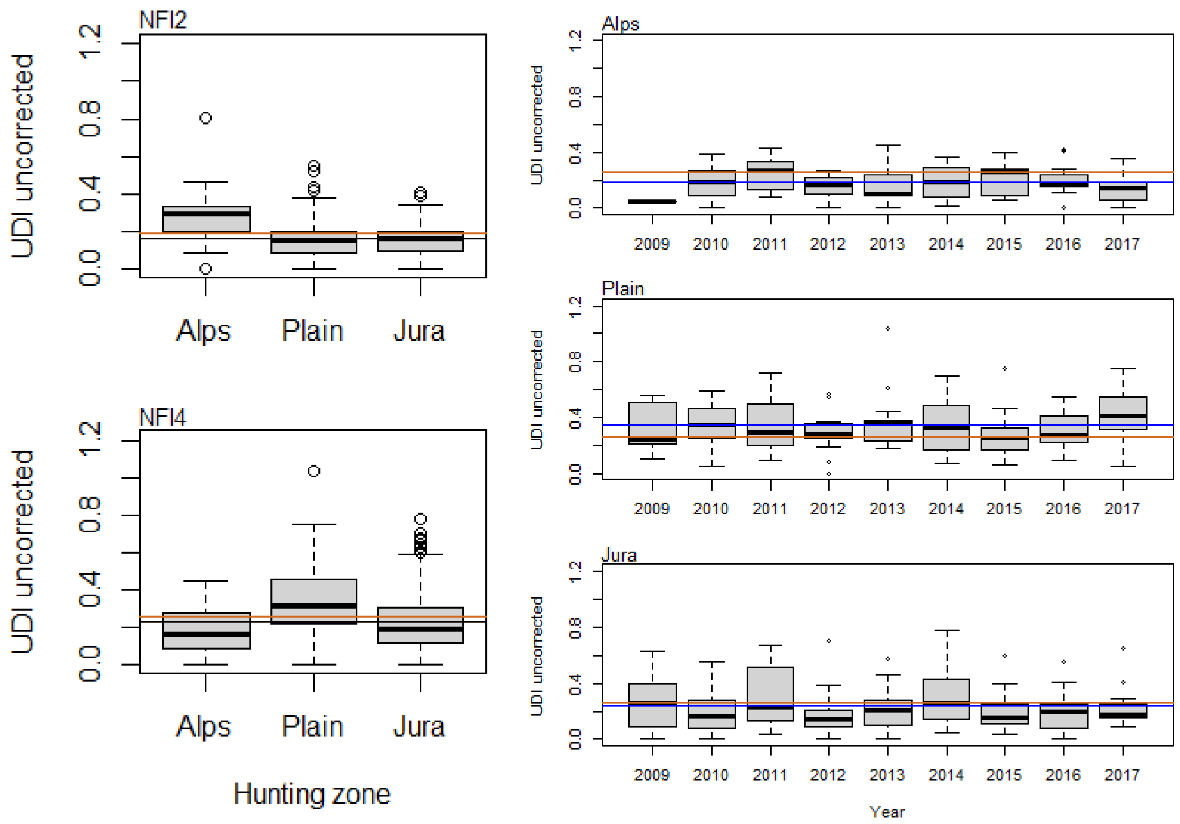


Figure 32: Uncorrected ungulate density index (UDI) for the different hunting zones, compared (left) between NFI2 and NFI4 and (right) within NFI4. The mean uncorrected UDI (orange line) and median uncorrected UDI (black line) in NFI2 and NFI4 are given. The mean uncorrected UDI per hunting zone is given for the data within NFI4 (right, blue lines).

Maps of UDI per NFI plot

For NFI2, the maps of UDI values corrected with perish data from NFI4 and those showing the uncorrected UDI values differed strongly (Figure 33). In contrast, the uncorrected UDI values and three-year-averaged UDI values were very similar per plot. It was therefore crucial to decide whether to analyse with uncorrected or corrected data. Overall, there was more hunting in the Alps and thus higher UDI values. In the Jura there were sectors with more hunting and sectors with less. In the Plain UDI values were generally lower, perhaps with the exception of areas south of Lake Neuchâtel.

The UDI distribution during NFI4 (Figure 34) differed strongly from that in NFI2 (Figure 33). In particular, in the Plain there were many more plots with UDI >0.2 per km^2. This probably reflects a real increase in ungulate densities over time. The increase in hunting/kills was particularly high in the southwestern parts of the Plain. In contrast, in the Alps the UDI values decreased overall in comparison to NFI2. However, large protection areas with no hunting permitted had been established. The maps of the UDI and the average UDI did not differ strongly (Figure 34). Thus, the kills did not vary much from year to year (Figure 32). Note, however, the picture we see in both figures are "artificial" constructs, as the NFI4 plots were sampled between 2009 and 2017, and thus the registered kills were actually for the corresponding years per plot. These results are therefore only a very rough approximation and should not be used for ungulate management purposes but only for analysing NFI regeneration data.

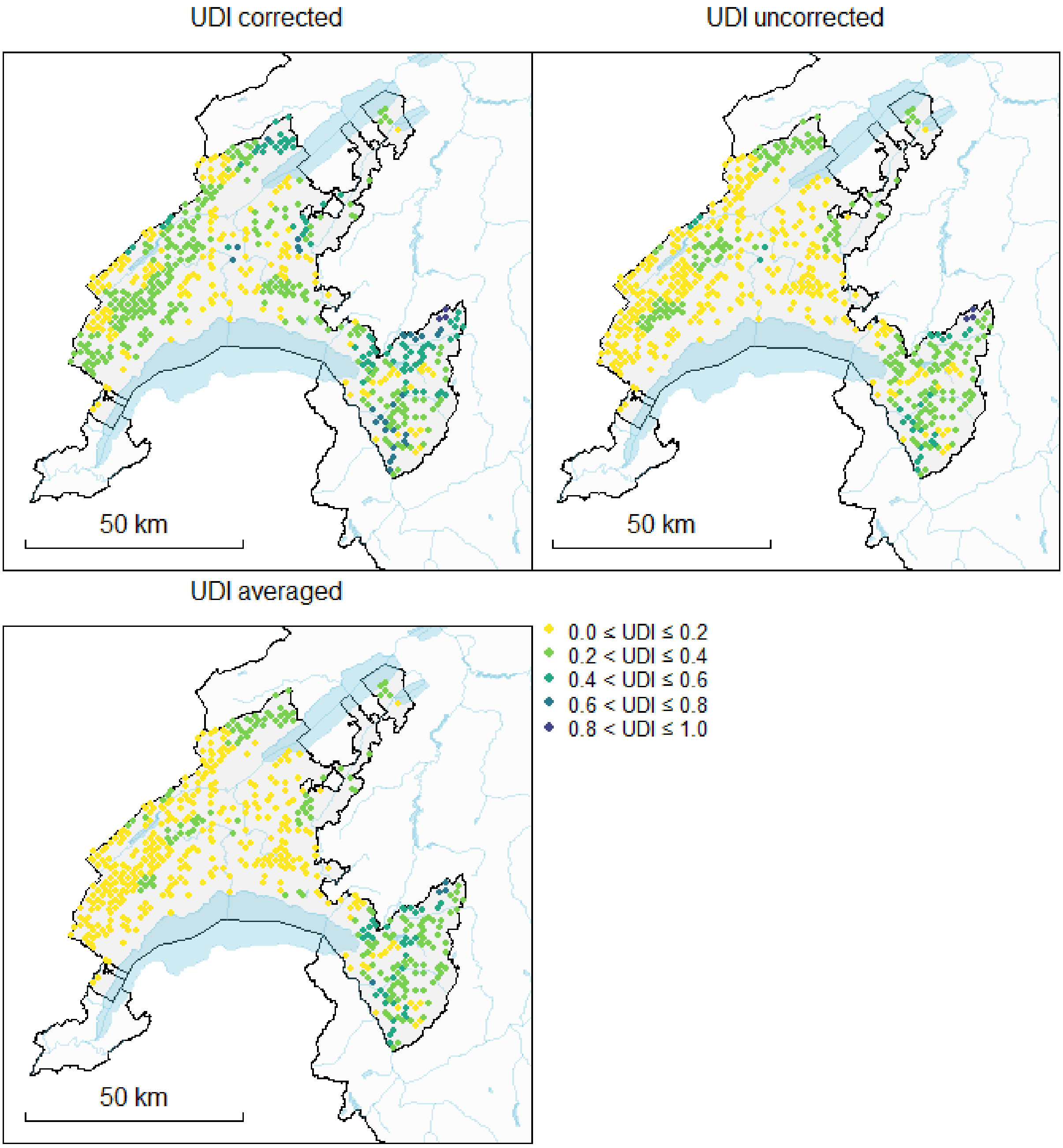


Figure 33: Ungulate density index (UDI) per km² in NFI2: UDI values corrected with perish data from NFI4 (left); uncorrected UDI values (centre); and three-year-average, uncorrected UDI values (right) for each plot in the canton of Vaud. The values correspond to the year in which the assessed shoot (i.e. previous year's shoot) was formed.

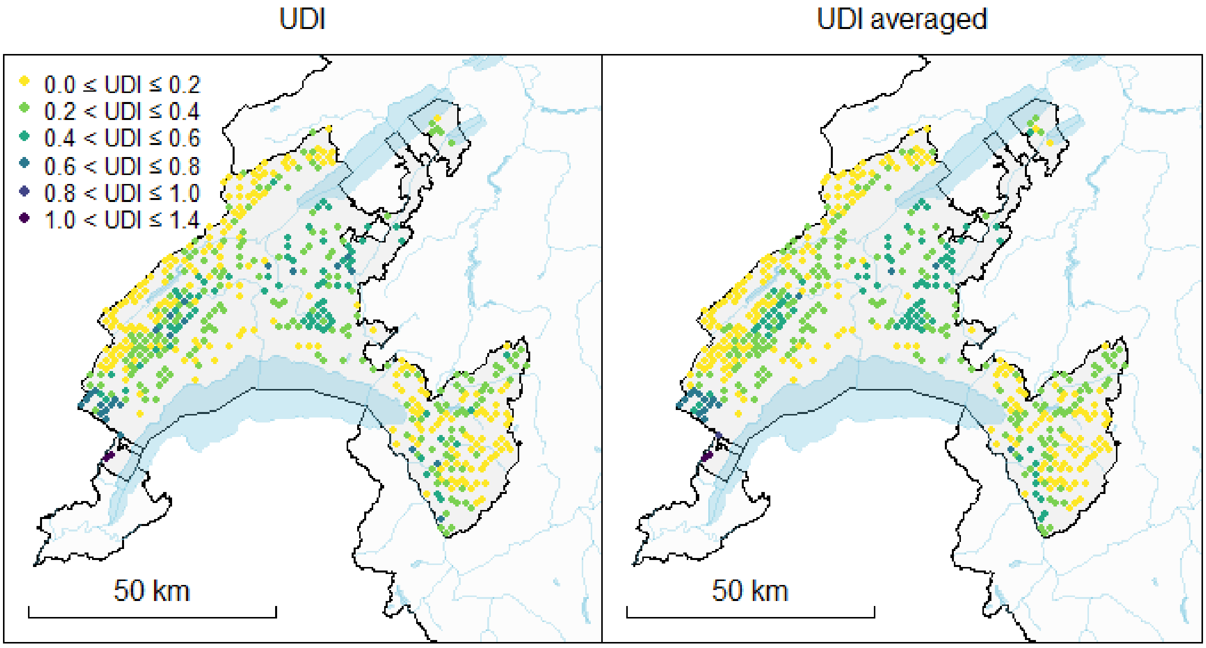


Figure 34: Ungulate density index (UDI) per km² in NFI4, calculated using hunting and perish data per year (left) or averaged over three years (right) for each plot in the canton of Vaud. Note that the values correspond to the year in which the assessed shoot (i.e. previous year's shoot) was formed, i.e. between 2008 and 2016, depending on the sampling year per plot.

Maps of red deer killed per NFI plot

Red deer kills only appeared in one part of the Jura in NFI2 (Figure 35), whereas in the Plain and the Alps no plots had a density of killed red deer >0.02 per km^2. During NFI4, there were many more kills of red deer in the Jura and the Alps. The calculated densities of red deer kills during NFI4 were highest at the upper altitudes but still low in the Plain. However, in the southwestern parts of the Plain (Jura in the protection region), there were also many red deer kills and thus high approximated density values.

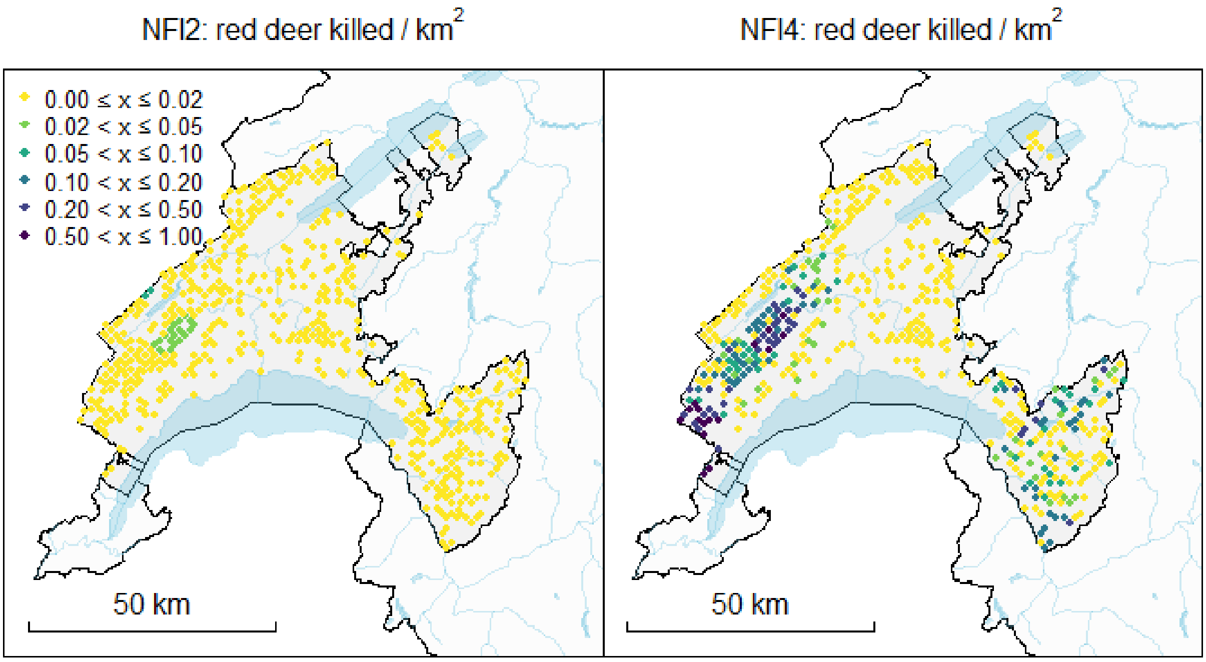


Figure 35: Numbers of red deer killed per km² in plots in the canton of Vaud in NFI2 and NFI4. Note that the colours are differently distributed to the ones in the previous panels for the UDI.

Maps of roe deer killed per NFI plot

Roe deer (Figure 36) were much more frequent than red deer (Figure 35). In NFI2 the densities approximated by the kills (hunting and perish data) were highest in the Jura, while in NFI4 the Plain had the highest roe deer kills.

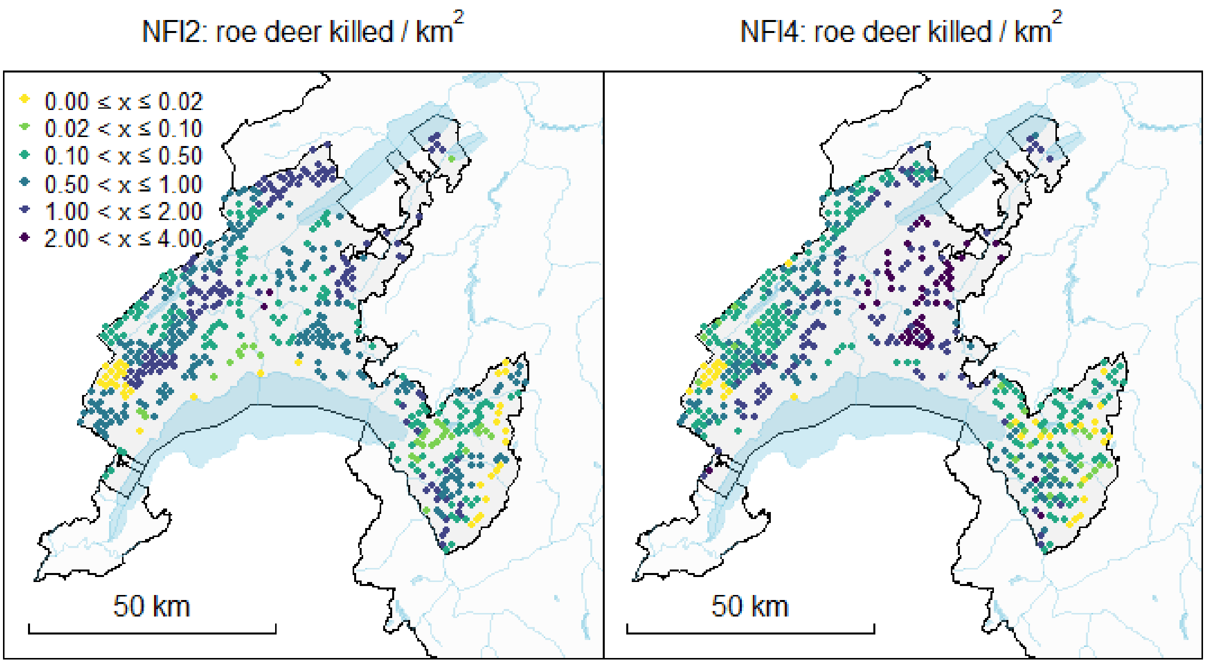


Figure 36: Numbers of roe deer killed per km² in plots in the canton of Vaud in NFI2 and NFI4. Note that the colours are distributed differently compared with earlier figures.

Maps of chamois killed per NFI plot

The density of chamois was highest in the Alps in NFI2 and NFI4 (Figure 37). In the Plain the density was very low in both inventory periods.

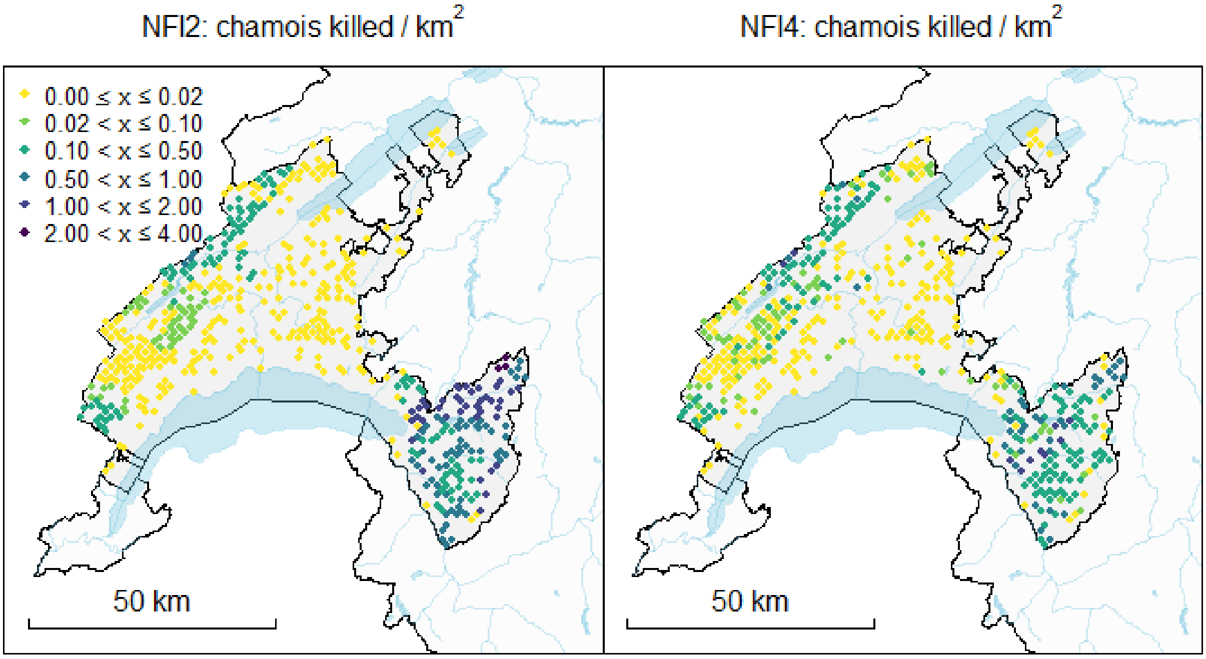


Figure 37: Numbers of chamois killed per km² in plots in the canton of Vaud in NFI2 and NFI4. The colour scale is the same as that for roe deer (Figure 36).

Based on these animal "densities" per NFI plot, the UDI, the uncorrected UDI, the uncorrected three-year-averaged UDI, or the three density values for roe deer, red deer and chamois were used in the statistical models.

3.2.2 Modelling results

3.2.2.1 Development over time

The mixed effects logistic regression models described in section 2.5.3 were used to evaluate the development of browsing over time (Table 6). The models including NFI production region had a better fit (Region model: AIC 4920) than the models with hunting zone (Zone model: AIC 4940), probably due to a better distribution of the different species within the regions. The results from models including production region are therefore presented first below.

Production regions

In Figure 39, the trends in browsing probability per tree species predicted by the Region model (Table 6) are shown. There were large differences in the predicted browsing probabilities between the tree species. Spruce and beech were overall the least browsed, followed by silver fir, and the deciduous species ash, maple, oak and rowan berry were the most browsed.

For each combination of species and region, the models tested whether there was a change in browsing probability between NFI2 (1993–1994) and the start of NFI4 (2009), or a change within NFI4 (between 2009 and 2017). A decrease in the observed browsing probability between NFI2 and NFI4 might be explained by differences in the sampling procedure. Therefore, a one-sided test was used for this contrast, and only an increase in the observed browsing percentage was interpreted as evidence for an increase in the true browsing percentage. **The tests provided evidence for an increase in browsing between 1993–1994 and 2009 for beech and maple in the Plateau region (Figure 38).** These changes were significant at the 95% level when adjusting for multiple testing using the Benjamini-Hochberg procedure. Theoretically this would also be the case for oak and rowan berry in the Plateau, but remember the small data basis (Appendix Table 21, thus the large confidence band in Figure 39). This increase in the browsing on deciduous species in the Plateau between NFI2 and the start of NFI4 was also clearly visible in Figure 39. As browsing was overestimated in NFI2 compared with in the NFI4 assessment, at least a trend towards an increase was expected also for species–region combinations with estimated odds ratios >1, i.e. for spruce and silver fir in the Plateau and for beech in the Jura and Alps/Pre-Alps and oak in the Jura (Figure 38).

Within NFI4 (between 2009 and 2017), a significant decrease in browsing was observed for maple and ash in the Plateau region (Figure 38). This decrease in browsing during the NFI4 period was also highly visible in Figure 39. Theoretically, this would also be the case for rowan berry in the Plateau, but remember the small data basis (thus the large confidence band in Figure 39). A significant increase in browsing during NFI4 was not observed for any species–production region combination. In the Jura, silver fir and beech had, however, high estimated odds ratios (Figure 38) and slight positive trends were visible (Figure 39).

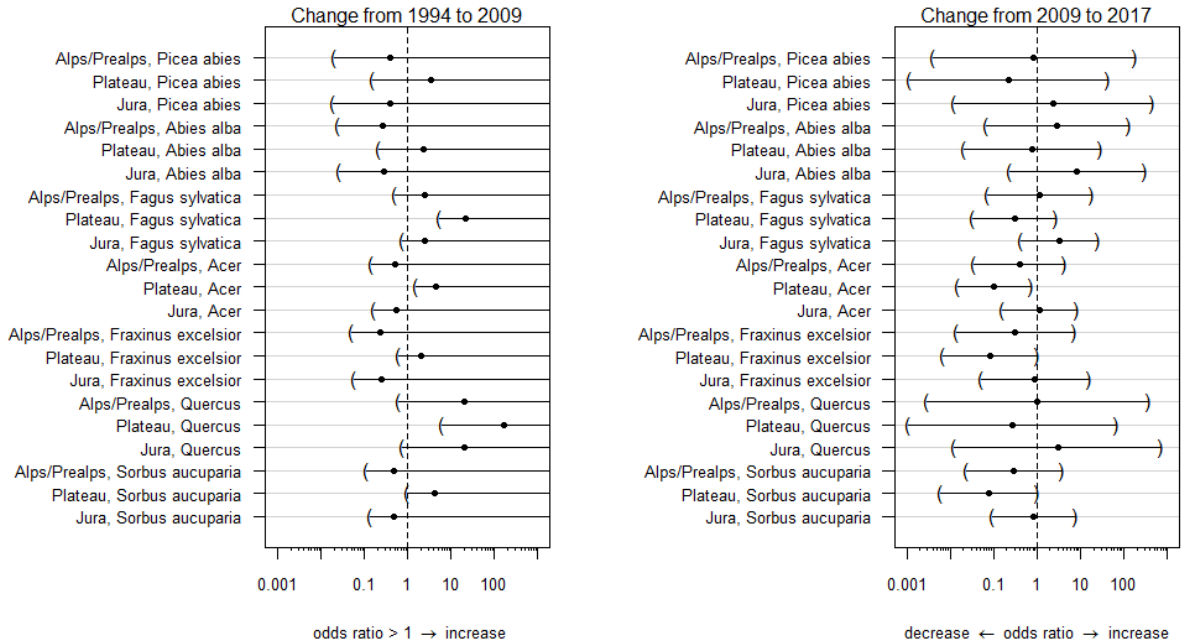


Figure 38: Change in browsing probability between NFI2 (1993–1994) and the beginning of NFI4 (2009), as well as within NFI4 (2009–2017), per production region and tree species (Region model). The dots show the odds ratio for browsing, and the intervals are simultaneous 95% confidence intervals within NFI4 and one-sided confidence intervals for comparisons between NFI2 and NFI4, corrected using the Benjamini-Hochberg procedure for false discovery rate. An odds ratio >1 corresponds to an increase in browsing probability between NFI2 and NFI4 or within NFI4.

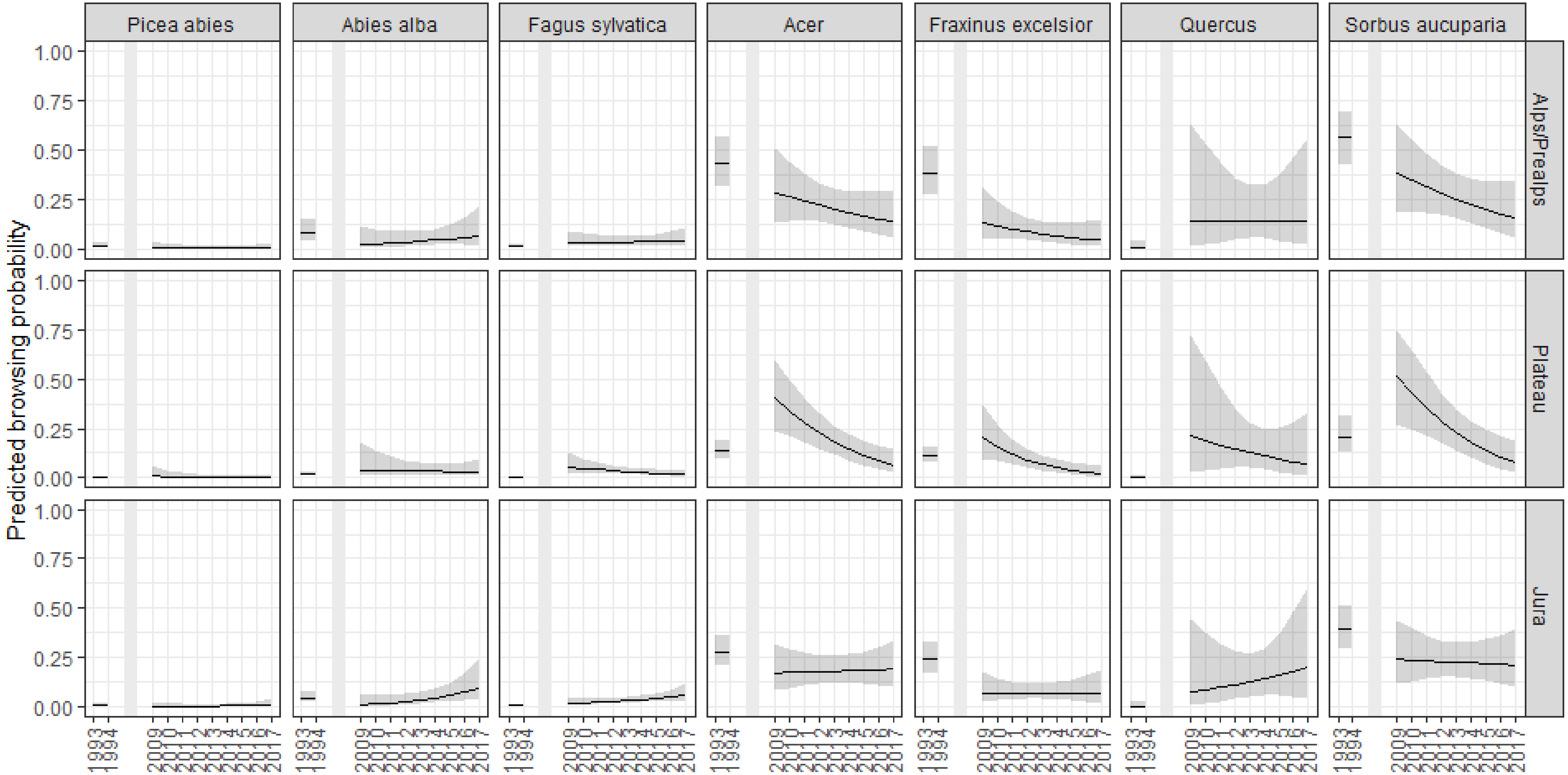


Figure 39: Predicted browsing probability over time, separated by production region and tree species (Region model), with a 95% confidence band shown in grey. Note that the time axis has a jump between NFI2 and NFI4.

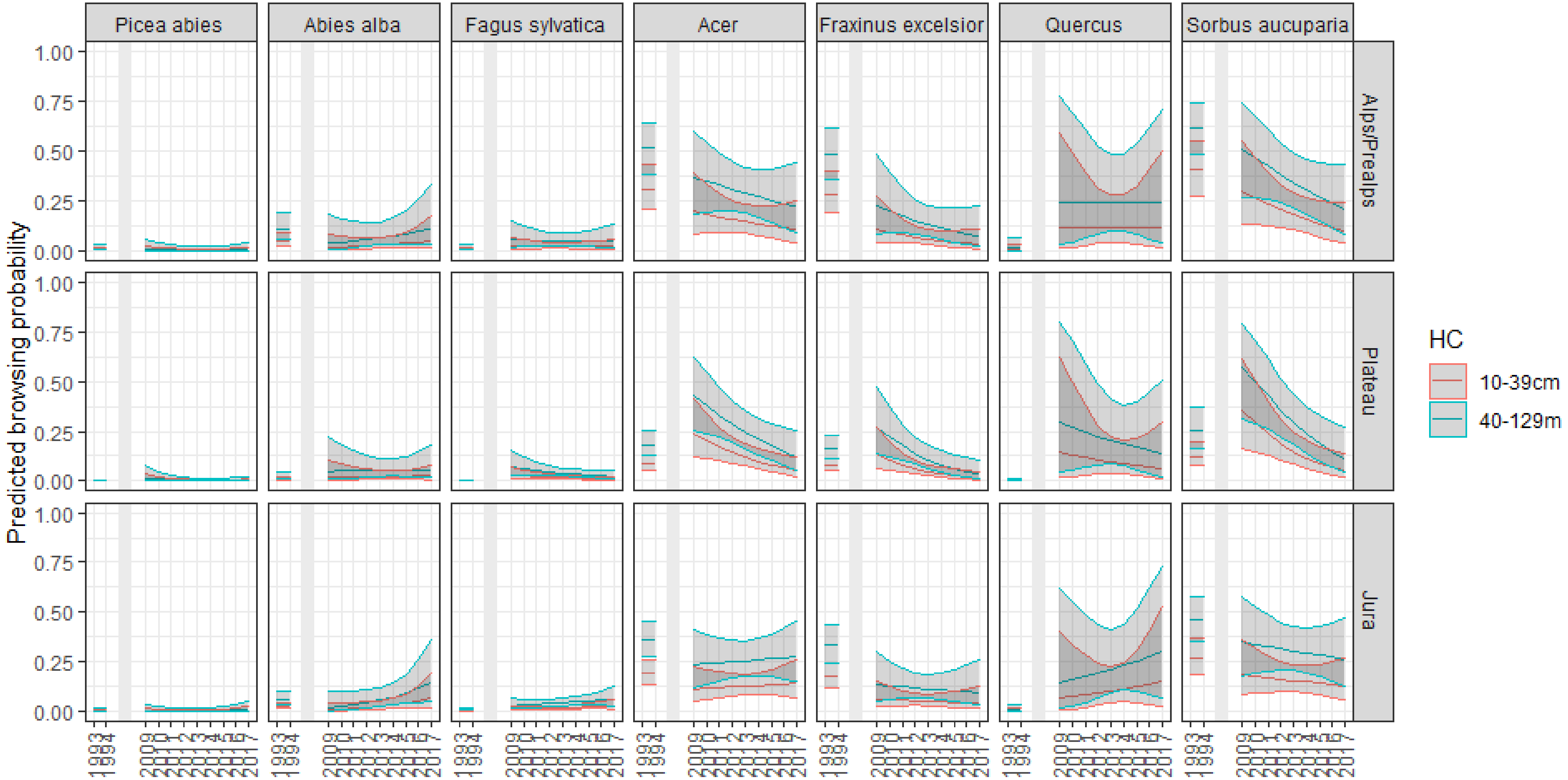


Figure 40: Predicted browsing probability over time, separated by production region, tree species and height class (RegionHC model), with 95% confidence bands shown in grey for height class 10–39 cm (red outline) and height class 40–129 cm (blue outline). Note that the time axis has a jump between NFI2 and NFI4.

The model fit was better when height class was integrated into the model, i.e. the AIC of the Region–HC model was 4840, while the AIC of the Region model was 4920. However, basically the same results were obtained (Figure 40). Seedlings in height class 40–129 cm simply had significantly higher browsing probabilities than those in height class 10–39 cm (Figure 40).

Hunting zones

A complementary analysis was done using hunting zones instead of the NFI production regions. **With the Zone model, the differences between NFI2 and the start of NFI4 were significant for beech in the Jura and Alps and oak overall**. In addition, there was a trend towards an increase (estimated odds ratios >1) in beech in the Plain and in maple and ash in the Alps and Jura (Figure 41).

Within NFI4 (between 2009 and 2017), a significant decrease in browsing was observed for ash in the Alps and Jura (Figure 41, Figure 42). Browsing on maples in the Alps also decreased over the years. A significant increase in browsing during NFI4 was not observed for any species or hunting zone. In the Plain, silver fir and beech had high estimated odds ratios, with 95% confidence intervals that were close to 1 (Figure 41), and slight positive trends were visible (Figure 42).

As in the Region–HC model, the Zone-HC model (AIC 4940) had a better model fit than the Zone model (AIC 4849), and the large seedlings had significantly higher browsing probabilities (Figure 43).

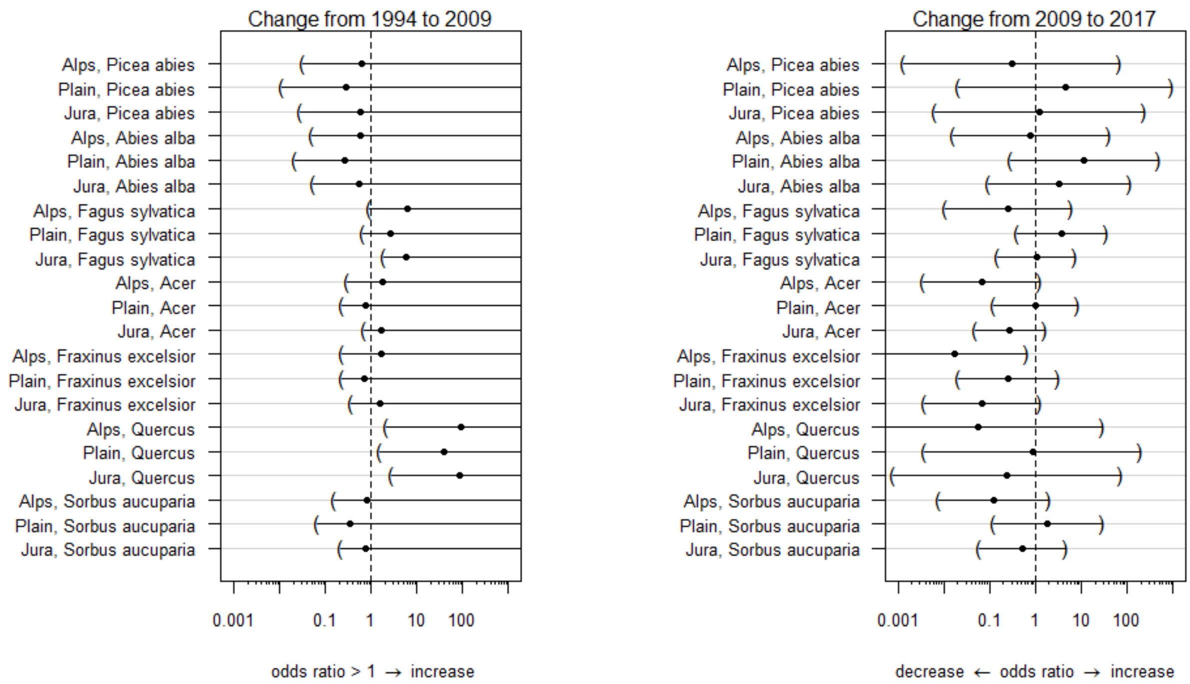


Figure 41: Change in browsing probability between NFI2 (1993–1994) and the beginning of NFI4 (2009), as well as within NFI4 (2009–2017), per hunting zone and tree species (Zone model). The dots show the odds ratio for browsing, and the intervals are simultaneous 95% confidence intervals within NFI4 and one-sided confidence intervals for comparisons between NFI2 and NFI4, corrected using the Benjamini-Hochberg procedure for false discovery rate. An odds ratio >1 corresponds to an increase in browsing probability between NFI2 and NFI4 or within NFI4.

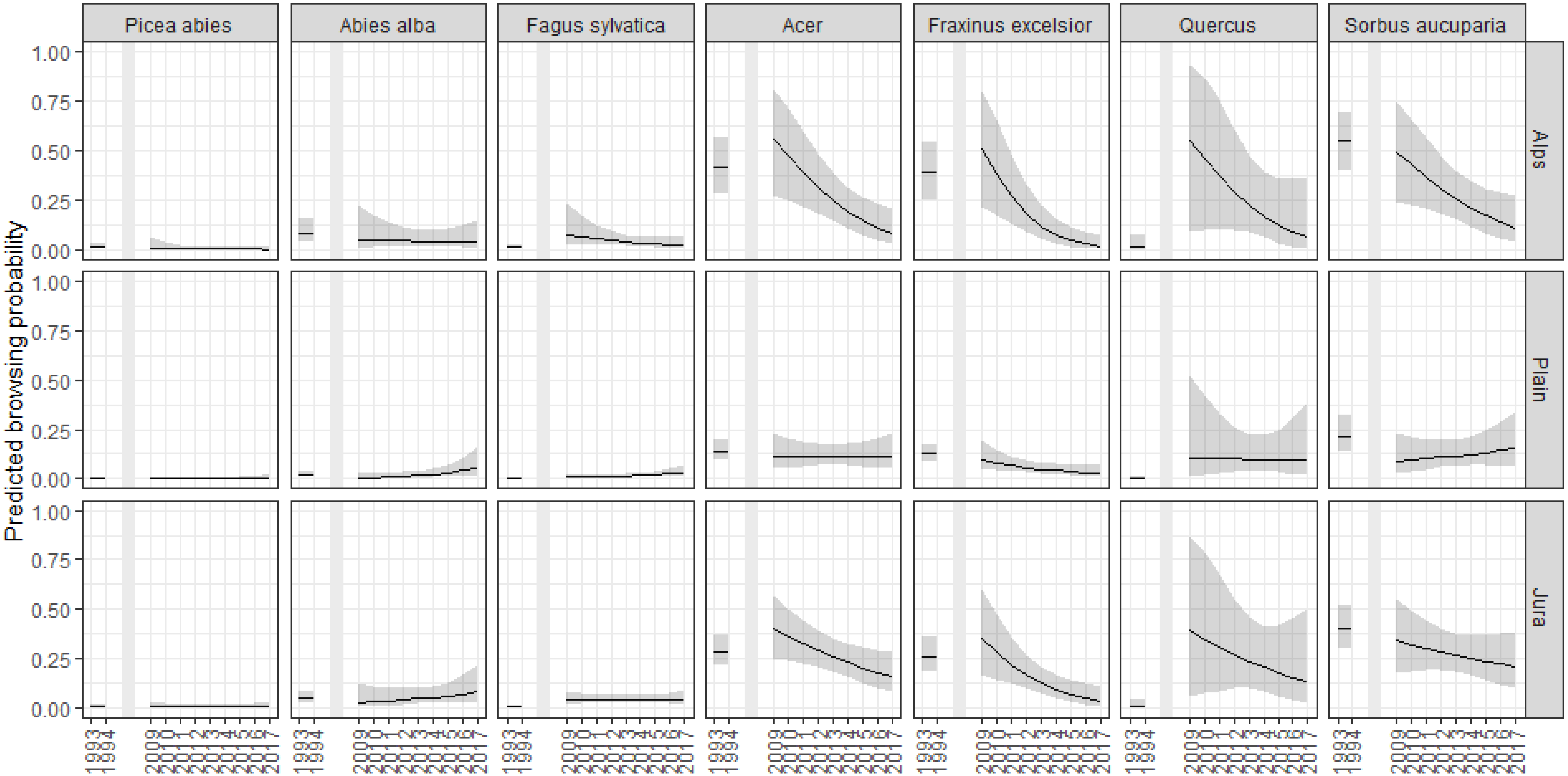


Figure 42: Predicted browsing probability over time, separated by hunting zone and tree species (Zone model), with a 95% confidence band shown in grey. Note that the time axis has a jump between NFI2 and NFI4.

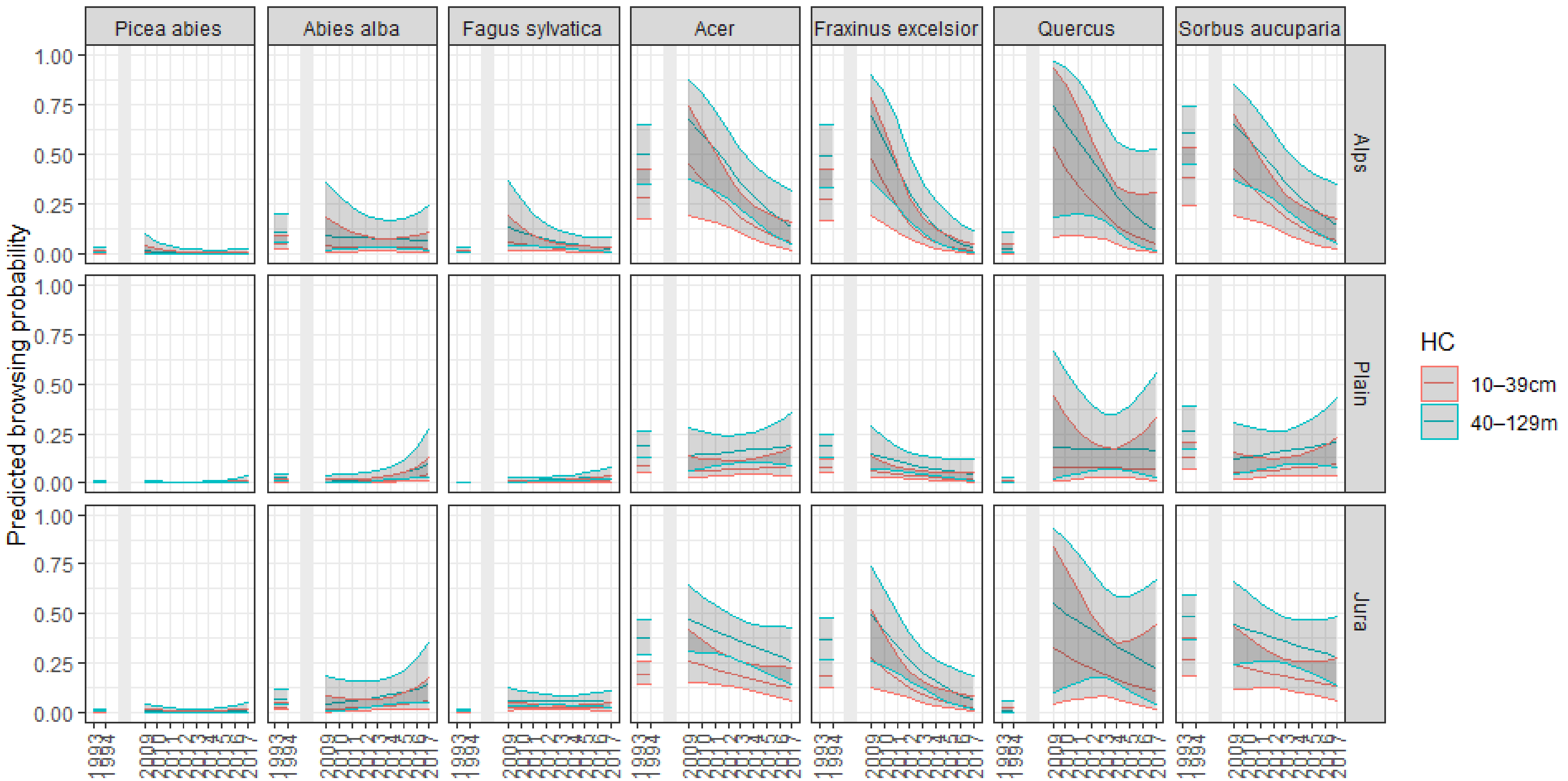


Figure 43: Predicted browsing probability over time, separated by hunting zone, tree species and height class (Zone–HC model), with 95% confidence bands shown in grey for height class 10–39 cm (red outline) and height class 40–129 cm (blue outline). Note that the time axis has a jump between NFI2 and NFI4.

3.2.2.2 Model with UDI and altitude

To assess if there was a relationship between browsing probability and UDI and/or altitude, different mixed effects logistic regression models were used (section 2.5.3, Table 7). The differences between using UDI, uncorrected UDI and average UDI were very small, i.e. with a difference <2.5 AIC. To show that the statistical models were very robust with respect to their predictions, regardless the exact value of UDI taken, the predicted browsing probability was plotted once using the UDI (Figure 44) and once using the average UDI (Figure 45). The important outcomes remained the same for all these models:

i) the higher the UDI value, the higher the predicted browsing probability
ii) the higher the altitude, the higher the predicted browsing probability

There were no significant interactions between UDI value and tree species, between altitude and tree species, or between UDI value and altitude. **Thus, the influences of UDI and altitude seemed to be independent from each other and from the main tree species effects.**

Instead of UDI values, the approximate densities of red deer, roe deer and chamois were integrated into the model (Altitude-Deer model, Table 7). This model performed just as well as the models with UDI values (same AIC) but used two degrees of freedom more (as it required three instead of one variable for the ungulates). However, red deer had the highest estimates (± standard error), with 2.8 ± 0.6, followed by chamois with 0.8±0.3 and roe deer with 0.7±0.1. The weighting of one red deer equals four chamois or five roe deer in the UDI calculations therefore seemed appropriate, although it probably slightly underestimated roe deer densities (a factor of four might have been better).

Further, the model was run for only beech and spruce to see if there was a possible "confounding effect" of the other species that are preferentially browsed. Again, UDI value and altitude had a positive effect on the browsing percentage of these two species. Finally, a model excluding these two species (spruce and beech) that are browsed less often was also run. The same result was found, i.e. there was a higher browsing percentage with increasing altitude and higher UDI value. Thus, altitude and UDI were both very important variables, irrespective of the tree species analysed.

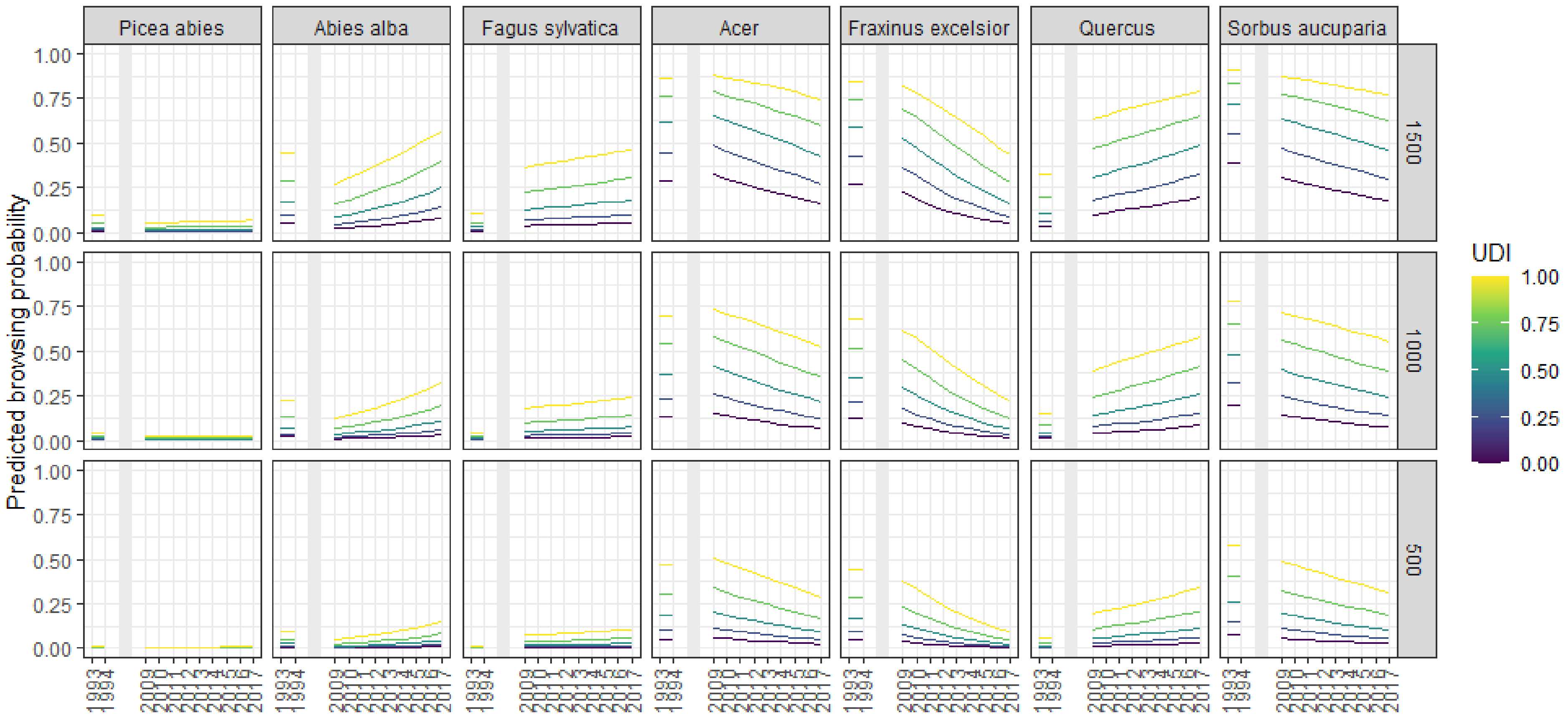


Figure 44: Predicted browsing probability over time, separated by tree species, altitude (bottom panels 500 m a.s.l., middle panels 100 m a.s.l., top panels 1500 m a.s.l.) and ungulate density (UDI, represented by different colours) based on the Altitude–UDI model.

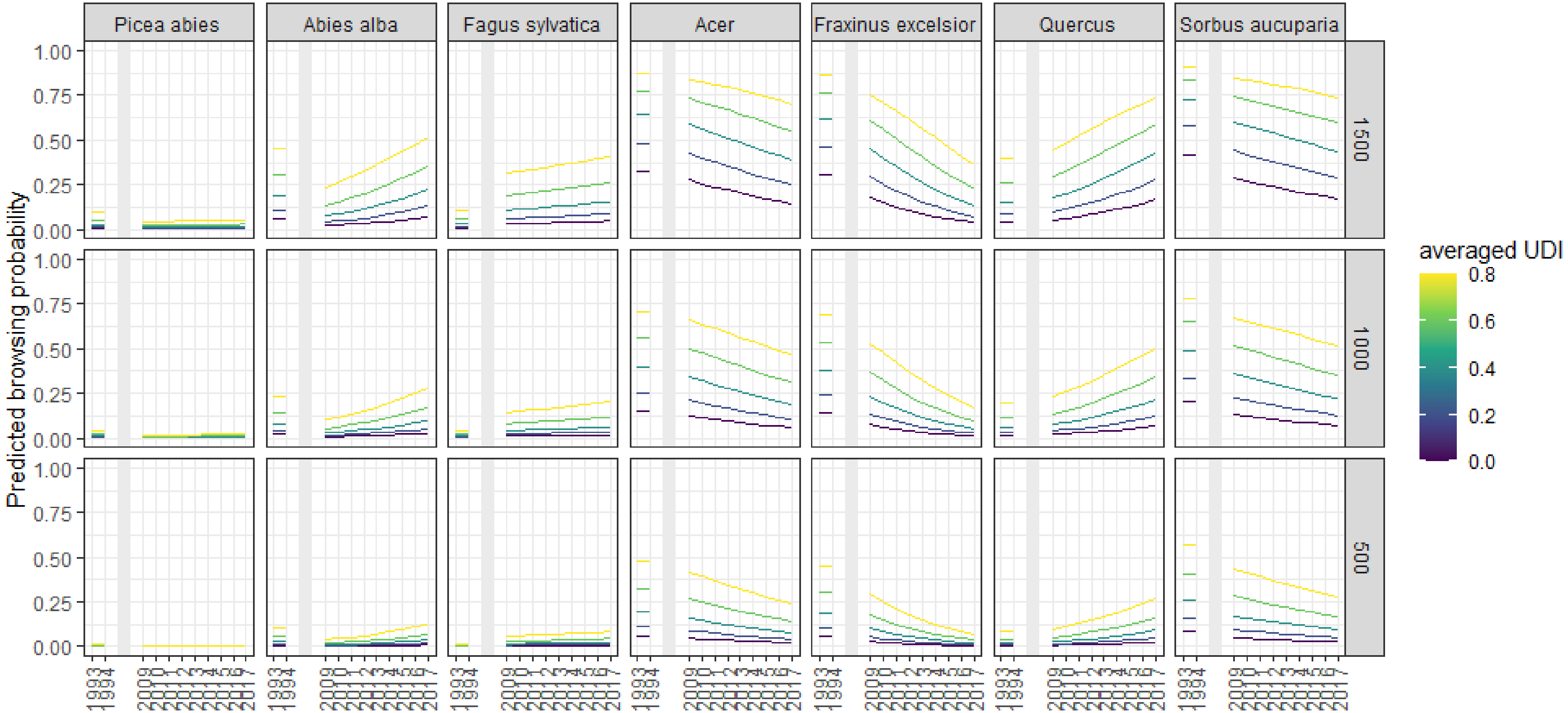


Figure 45: Predicted browsing probability over time, separated by tree species, altitude (bottom panels 500 m a.s.l., middle panels 100 m a.s.l., top panels 1500 m a.s.l.) and average ungulate density (UDI, represented by different colours) based on the Altitude–averagedUDI model.

3.2.2.3 Difference in browsing percentage between regions

The best model (lowest AIC) was obtained by including the production region, in addition to time NFI2–NFI4, year within NFI4, tree species, altitude and UDI (Region–Altitude–UDI model). The estimated odds ratios were thus computed for the three production regions (Figure 46). For calculating the estimates for the odds ratio, the median of the UDI and the median of the altitude were used. Since the model did not include an interaction term between species and production region, the effect of species was irrelevant in the contrasts (i.e. it cancelled out). All possible two-way contrasts within the production region level (Plateau–Pre-Alps/Alps; Jura–Pre-Alps/Alps; Jura–Plateau) were then analysed. This was done separately for the years 1993–1994 (NFI2), 2009 (start NFI4) and 2017 (end NFI4). **This analysis resulted in a significant difference between the Plateau and the Jura in the year 2009**. That is, the browsing percentage in the Plateau was higher than in the Jura (Figure 46). The opposite trend was found for 1993–1994 and 2017, i.e. more browsing tended to occur in the Jura than in the Plateau. This confirms the results presented in section 3.2.2.1.

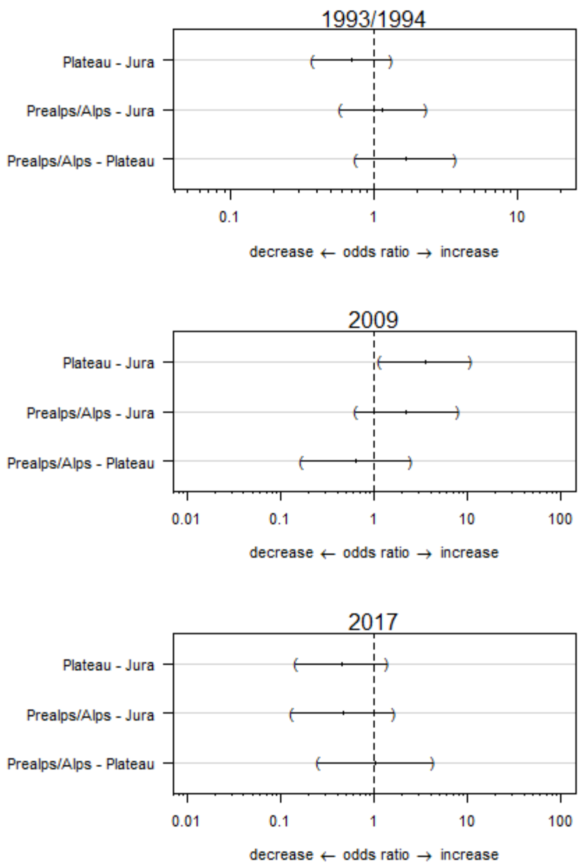


Figure 46: Differences in browsing between production regions for NFI2 (1993–1994) and for NFI4 in 2009 and 2017, all based on the Region–Altitude–UDI model. The dots show the odds ratios for browsing, and the intervals are simultaneous 95% confidence intervals, corrected using the Benjamini-Hochberg procedure for false discovery rate. An odds ratio >1 for Plateau – Jura corresponds to an increase in browsing from the Jura to Plateau.

3.2.2.4 Tree selection preferences

All statistical analyses until now were performed using only tree species that were frequent (i.e. >100 seedlings assessed for browsing during each NFI). In the analyses described here, ungulate preferences or “Appétence” was included (Table 8). The model with ungulate preference was significantly better than the model with “Appétence” (AIC Appétence model = 5628, AIC Preference model = 5514). **The higher the ungulate preference value, the higher the browsing probability** (1.40±0.07, estimate ± standard error; Figure 47). The interaction terms between time and ungulate preference were also both important, and a trend towards a smaller effect of preference was apparent at the end of NFI4 (Figure 47).

The forest developmental stage per NFI was also integrated into the Preference model. The stages were integrated as defined in NFI, or only separating young growth/thicket, timber (pole to medium timber), old timber and mixed forest. In no case did the developmental stage have a significant effect on the browsing probability.

A model including canopy shading indicated that shading at 40 cm or 129 cm above ground had no significant effect on browsing during the NFI4 period. Finally, a model excluding all plots with >90% shading at 129 cm resulted in the same relationships as the model including all plots.

3.2.2.5 Random deviations per plot

By plotting the plot-level random intercepts of different models, it was possible to visualise areas in which unmeasured processes caused more (or less) browsing than our models predicted. This was done for the Region-Altitude-UDI model (Table 7), which was found to be the best model based on the seven main tree species (see section 3.2.2.3), and for the Preference model (Table 8), which was based on all species with an ungulate preference classification (see above). Red patches in Figure 48 indicate a remaining higher browsing percentage of the seedlings within the corresponding NFI plots. Thus, these are not the “hotspots” of browsing but rather hotspots of deviation from the model estimates.

Using UDI and altitude, most of the browsing in the Alps hunting zone could be explained. In contrast, there were still several patches in the Jura and a strip in the Plain that has high unpredicted browsing. These plots do not stand out based on their forest developmental stages (Figure 9). There are some areas south of Lac de Joux that are mixed forest, but there was no general trend towards more browsing in mixed forests (i.e. developmental stage dropped out of the Preference model). The strip in the Plain corresponds partly to the black dots in Figure 10, i.e. plots with a very high percentage of shading. Nevertheless, there are many more places with high levels of shading (Figure 10), yet no common relationship between shading and the positive random deviations (red patches in Figure 48) was found (i.e. shading also had no significant effect in the model, see above).

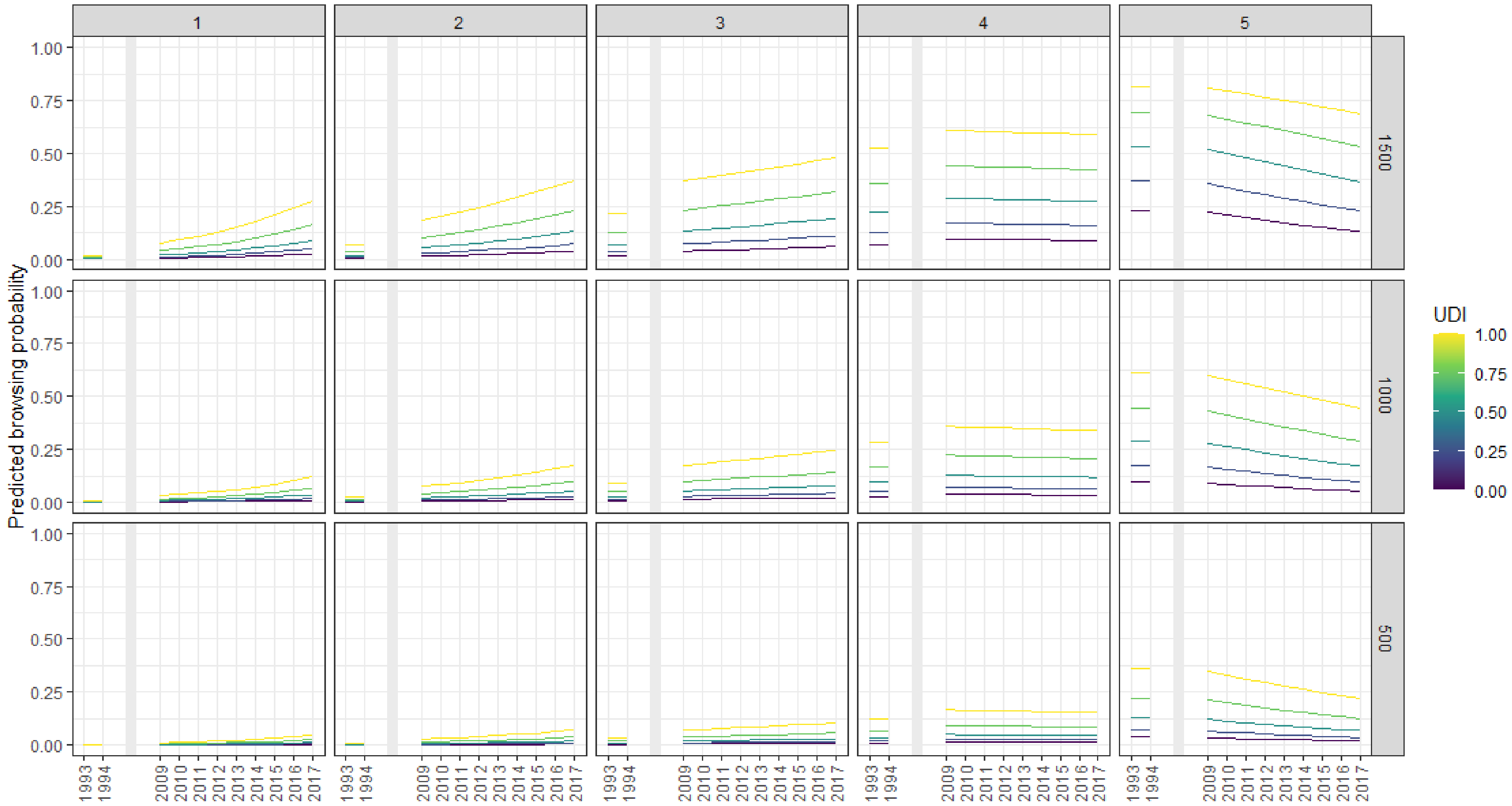


Figure 47: Predicted browsing probability over time, separated by tree species preference (arranged in columns with 1 = not selected to 5 = highly selected tree species), altitude (bottom panels 500 m a.s.l., middle panels 100 m a.s.l., top panels 1500 m a.s.l.) and UDI (represented by different colours) based on the Preference model.

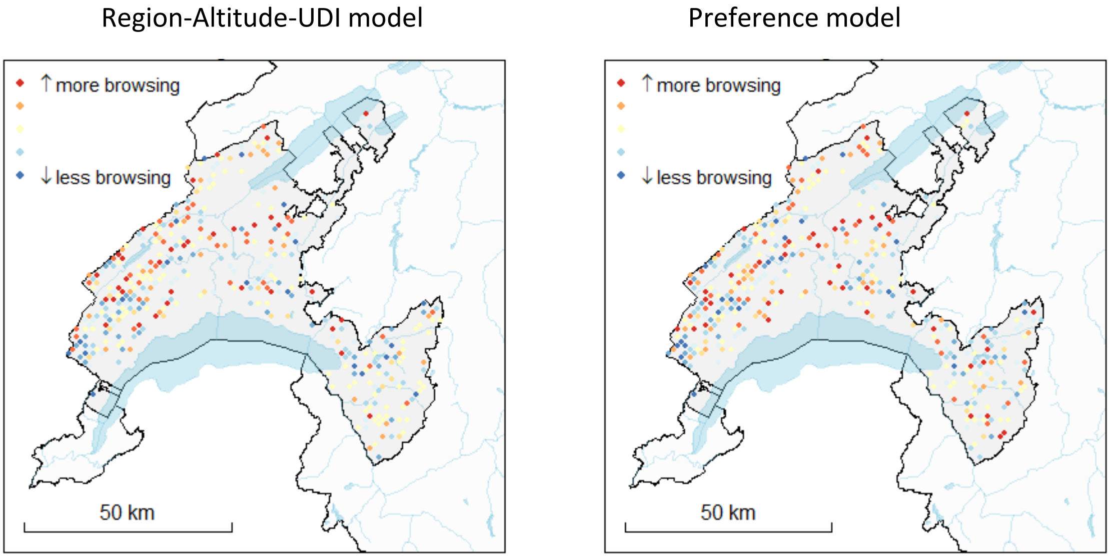


Figure 48: Plot-level random effects of the Region–Altitude–UDI model based on the seven main tree species (left; see Table 7) and of the Preference model based on all species with an ungulate preference classification (right; Table 8). Red patches indicate overall higher browsing frequencies, while blue patches indicate lower browsing frequencies than predicted with the models.

4. Discussion

4.1 Fraying/bark stripping

In the NFI plots of the canton of Vaud, there was practically no bark stripping of trees with a DBH ≥12 cm. That does not mean that there was no bark stripping. The phenomenon is known to be very patchy [1]. In other European sites bark-stripping rates were higher at high red deer density [39]. In an analysis of the NFI4b data (2009–2013) for the canton of Grisons, 0.7±0.2% of the trees ≥12 cm DBH were debarked [13]. Even there, however, bark stripping was not found in all subregions [13]. The chance of hitting a bark stripping patch with a √2 km grid, typical of the NFI, is simply very low.

Bark stripping and fraying were not separated in the assessment of the seedlings and saplings in the NFI. Since the highest percentages appeared in DBH class 0–3.9 cm, it was likely to have been fraying. Theoretically, the nearest sapling (DBH class 0–3.9 cm) within one circular subplot with a search radius of 2.5 m (method in NFI4) is less likely to be damaged than the saplings within two circular subplots with a radius of 2.12 m (method in NFI2). Since the actual number of assessed frayed/bark-stripped trees was sometimes the same in NFI2 and NFI4, this may indicate that fraying/bark stripping became more frequent over time.

It would be desirable to re-integrate fraying/bark stripping into the sampling of seedlings and saplings in the full NFI subplot-circles. Until this is the case, the dataset from the Swiss NFI is not fully suitable for assessing the temporal development of fraying and bark stripping over decades in the canton of Vaud.

4.2 Browsing

Differences in browsing between NFI2 and NFI4

NFI4 was conducted over nine years. During this period, large differences in browsing may have occurred. Such temporal differences in NFI4 could have masked a difference between the two NFIs. Therefore, two different approaches had been applied to estimate the differences in browsing between NFI2 and NFI4. Differences between the two approaches were expected in the case of trends during the NFI4 period (see next section).

First, a descriptive analysis of the browsing intensities calculated over the whole NFI2 (1993–1994 in the canton of Vaud) and NFI4 (2009–2017) periods was made. Considering the whole canton of Vaud, browsing on oak increased between the two NFIs (Figure 31), while it remained the same for all other species (Figure 25 to Figure 30). In the Plain (hunting zone) or Plateau (production region), the browsing intensity increased over time for silver fir and oak. Nevertheless, silver fir still (see Figure 1 and [18]) seems to be browsed less in the canton of Vaud than in many other regions in Switzerland [12, 15]. Overall, oak and rowan berry were browsed the most, with a browsing intensity in NFI4 of around 35%, followed by ash and maple, then silver fir, and finally spruce and beech (about 1-3.3%).

Second, a comparison was made between the predicted browsing probabilities in NFI2 and the predicted probabilities in 2009, at the beginning of the NFI4 period. This statistical analysis indicated a significant increase in browsing on beech and maple in the Plateau production region (Figure 38). There were additionally trends towards increased frequencies of browsing on oak, rowan berry, spruce and silver fir in the Plateau, for beech in the Jura and Alps/Pre-Alps and oak in the Jura (Figure 38). When the hunting zones were considered, significant increases were found for beech in the Jura and Alps and for oak overall (Figure 41), and trends of increase were found for beech in the Plain and for maple and ash in the Alps and Jura (Figure 41). In comparison with the results from the production regions, these findings suggest that browsing on beech and oak has probably truly increased throughout the canton of Vaud. In contrast, the frequency of browsing on maple particularly increased in the plots in the Plateau production region but in the Jura hunting zone (Figure 7), i.e. around the sectors 105 (MONT-TENDRE) and 145 (CHATEL). In general, the estimated odds ratios were all >0.2 and were due to differences in the methods between the browsing assessments in NFI2 and NFI4 (section 2.2.2). A significant decrease in browsing between NFI2 and the beginning of NFI4 was therefore unlikely for all tree species.

In both NFIs the large seedlings (height class 40–129 cm) had significantly higher browsing probabilities than the small seedlings (height class 10–39 cm; Figure 43). Browsing by ungulates has previously been observed to mostly occur at an intermediate height between the ground and the full reach of red deer in other regions in Switzerland [12] and in other countries [40, 41]. This is probably caused by the higher visibility of the large seedlings, as they stand out from the herbaceous vegetation.

From NFI2 to NFI4, there was an increase in the density of seedlings for many of the main tree species, i.e. spruce and oak in the Plain, silver fir and rowan berry in the Jura and Alps and in total, beech in the Plain and Jura and in total, and maple in all hunting zones and thus also in whole canton of Vaud (Figure 25 to Figure 31). The extent to which these changes were related to the changes in the forest developmental stage was not investigated in this study. However, the stages old timber and mixed forest increased in the NFI plots from NFI2 to NFI4 and the young and medium timber decreased, which could easily have influenced seedling densities (Table 5).

Temporal development of browsing between 2009 and 2017

Within the NFI4 period from 2009 to 2017, a significant decrease in browsing probability was observed for maple and ash in the Plateau production region (Figure 38). For the hunting zones, a significant decrease in browsing probability was observed for ash and maple in the Alps and for ash in the Jura (Figure 41). For the Alps hunting zone (Alps/Pre-Alps production region), decreasing trends in the predicted browsing probabilities were apparent for browsing on ash (Figure 39, Figure 42). In contrast, in the Jura production region no such trend emerged. Thus – like for maple between NFI2 and NFI4 – it must have been the ash trees in the NFI4 plots around the sectors 105 (MONT-TENDRE) and 145 (CHATEL), which are in the Plateau production region but in the Jura hunting zone (Figure 7), that experienced a decrease in browsing over the years. With respect to maple, decreasing trends in the predicted browsing probabilities were visible in the Alps/Pre-Alps production region (Figure 39), as well as in the Alps hunting zone (Figure 42). The decrease was not significant in either spatial unit, probably due to the relatively small numbers of maple in these NFI plots. The fact that maple decreased during the NFI4 period could explain why the results from the two approaches for estimating the differences in browsing between NFI2 and NFI4 differed for maple in the Plateau. Browsing on maple in the Plateau was lower during NFI2 (1993–1994) than in 2009 but probably higher than in 2017 (Figure 39).

A significant increase in browsing during the NFI4 period was not observed for any region/hunting zone. For silver fir and beech in the Jura production region and the Plain hunting zone, high estimated odds ratios were calculated (Figure 38). Therefore, it will be interesting to analyse the browsing data from NFI4 together with that from NFI5 to see if these trends continue.

There were very large differences in the predicted browsing probabilities between the tree species during NFI4. Spruce was overall the least browsed, while for silver fir and beech browsing was low but tended to increase over time. For the deciduous species ash, maple, oak and rowan berry, browsing was higher at the beginning of the NFI4 period, in particular in the Plateau production region and in the Alps and Jura hunting zones.

Notably, almost no large seedling of oak was found in NFI4. As every third “small” oak was browsed, browsing could be one reason for the few large oak seedlings. Generally, no seedling smaller than 10 cm is measured in NFI. However, there are certain places with high browsing percentages where seedlings – in particular silver fir –never reach the 10 cm threshold because they are killed as a result of browsing. Such effects cannot be excluded for the canton of Vaud and might explain why certain species were absent from some NFI plots. However, as ungulate browsing on silver fir was rather low, it is unlikely to be a common phenomenon whole over the canton of Vaud, but possibly a local impact.

Influence of ungulate numbers

Our analysis shows browsing to be more frequent if ungulate densities (approximated with the number of roe deer, red deer and chamois culled by hunting or found dead for other reasons) are higher. Likewise, the incidence of leader browsing has previously been found to be positively associated with the ungulate density index (UDI) in indicator areas in the eastern part of Switzerland [12], with an index of deer density at the site scale in England [42], or with deer presence at the plot scale in canton of Grisons and in Scotland [40, 43]. In addition, Hothorn et al. [44] showed that the risk of deer–vehicle collisions is positively correlated with browsing intensity and with harvest numbers of ungulates in southern Germany.

The number of roe deer, red deer and chamois culled by hunting (hunting data) and game keepers or found dead for other reasons (perish data) is of course not a good estimate of real ungulate densities.

The number of animals hunters are authorised to shoot each year is dependent on many variables, including management strategies, problems with tree regeneration, separation of wildlife sanctuaries or resting zones, and the number of ungulates. However, the larger the actual number of ungulates, the greater the acceptance of hunters to kill animals, and the greater the hunting success within a certain time. Thus, some relationship can – despite the above-mentioned problems – be expected. A significant positive relationship was found in all our models, irrespective of the exact variable used to estimate ungulate density.

In addition, though red deer is still less common than roe deer or chamois in the canton of Vaud, red deer had a large impact on the browsing probability. The effect of red deer is probably not quite five times higher than for roe deer, as. assumed when calculating the UDI following [28]. As hunting data rather than real density data was used in our study, however, it was not possible to estimate the actual proportional effect of the single animal species. The actual proportion is probably dependent not only on the body weight and feeding preferences of the different animal species, but also on interspecies competition between the ungulates. It might very well be that more browsing is observed where more reed deer are present, but that this higher browsing percentage is actually caused by roe deer and chamois, due to changes in their spatio-temporal behaviour to avoid or co-exist with red deer. Thus, higher densities of all three ungulate species have a clear positive effect on the probability of browsing. UDI turned out to be an important estimator in our models and thus can apparently capture the above-mentioned combined effects

Importantly, the calculated UDI values – based on the hunting and perish data provided by Canton Vaud – were very low compared with those reported in other studies. For example, the UDI in indicator areas in the eastern part of Switzerland (mainly the cantons of St Gallen and Thurgau) was estimated to be between 1.5 and 4 [12], while the UDI has been reported to be between 3.2 and 65 in Italy [28]. This may be related to differences in wildlife management and thus (at present) lower hunting targets in the canton of Vaud. However, apart from the rather low browsing intensities on silver fir in the canton of Vaud compared with in other parts of Switzerland, browsing on preferred tree species, such as rowan berry and oak, was high. Today, ungulates thus primarily have an impact on the most selected species in the canton of Vaud. That is, they have an impact on the species composition rather than on the total amount of tree regeneration [32]. As important tree species that can cope better with the changing climate (than spruce or beech) are most affected by this selective browsing (e.g. oak [8]), these forests may still be in browsing influence stage 3, following the classification of Fehr et al. [32]. In contrast to some studies with high ungulate densities, where a hunting increase did not reduce browsing on the preferred species [45], measures to reduce browsing in the canton of Vaud can – based on the current low UDI values – be expected to have an immediate impact.

Influence of altitude

Altitude per se cannot have a direct effect on browsing but can serve as a proxy for different environment conditions and processes that change with altitude. For example, higher altitude is associated with lower growth rates of seedlings and saplings, fewer growth flushes per year (no epicormic shoots, also called “Saint John's shoots”), a lagged reaction after winter browsing [46], and less of a reaction by seedlings during the vegetation period to damage in spring or early summer. Therefore, browsing is more clearly visible and for longer at higher altitudes, and is thus also more often assessed in the NFI. However, at higher altitudes browsing has larger impacts on individual seedlings, as fewer buds are present on the remaining shoots to react after damage [47]. Thus, in the forest–ungulate discussion great emphasis should still be placed on forests at higher altitudes.

Hotspots of browsing in the canton of Vaud

Places with large ungulate numbers (high estimated UDI) and at higher altitudes were found to be the main "hotspots" for browsing in the canton of Vaud. Apart from these "explainable" hotspots, several additional areas with a browsing percentage higher than predicted by the models can be seen in Figure 48. These apply to the seven main species but also to all others if the ungulate preference is taken into account. There was no indication that a certain forest developmental stage or high canopy shading could explain these "unexpected" hotspots. To our knowledge, the data from NFI2 and NFI4 is not suitable for determining why these areas had more observed than predicted browsing.

Nevertheless, according to the NFI4 data, 87% of all forest plots in the canton of Vaud had 60–100% canopy shading at 130 cm above ground (Figure 10). Every sixth plot was practically 100% shaded (black points in Figure 10). This is a much higher percentage than observed in the canton of St Gallen, where browsing impact estimations were made excluding all plots with >90% shading [27]. In a study based on indicator areas in Thurgau and St Gallen, shading was one of the main factors explaining seedling densities [48], and the seedlings tended to be more frequently browsed in stands with >80% canopy shading [12]. Generally, the less light that reaches the forest floor, the less tree regeneration that occurs and the less ground vegetation that can serve as an alternative food source for ungulates. Some of the unpredicted hotspots in the Plain in Vaud might be due to high shading.

In this study, the density of wild boar was not integrated into the statistical models. It is well known that regeneration of oak and beech is negatively correlated with the rooting frequency of wild boar [49]. Apart from their great effect on seed predation, wild boar also cause the death of oak seedlings [50]. What is less known, however, is that wild boars also eat silver fir seedlings; for example, in a study in Germany (Baden-Württemberg and Bayern) around 15% of the browsing on silver fir seedlings was attributed to wild boars by means of DNA analysis [51]. Some of the unpredicted hotspots of browsing in our study therefore could easily have been caused by wild boars. We recommend that future research include efforts to determine which animals are responsible for browsing so that wildlife management measures in forests can target the right animals.

5. Conclusion

In the Swiss canton of Vaud, the tree species most affected by browsing are those that are known to be particularly selected by ungulates. Other slightly less preferred tree species (e.g., silver fir) have a low browsing intensity in Vaud than in other regions in Switzerland. Overall, the greater the number of killed animals (hunting and perish data), the higher the browsing percentage. The higher the altitude, the higher the browsing percentage or the longer the browsing was visible and therefore measured/assessed in the NFI surveys. Thus, hotspots of browsing are above all places at high altitudes with large numbers of ungulates. This does not mean that there was little browsing in the Plateau production region in Vaud. Indeed, browsing increased the most between NFI2 and the beginning of NFI4 in the Plateau, and on oak. The ungulate density index values in the Plateau increased between the NFIs, mainly due to an increase in roe deer kills (hunting and perish data) in the Plateau. This elucidates the positive relationship between the temporal development of the frequency of browsing and the approximated ungulate density. For maple and ash in the Plateau region, browsing tended to decrease during the NFI4 period. This suggests that the higher culling effort during NFI4 probably initiated to reduce browsing. However, an increasing trend was observed for beech and silver fir. It will be interesting to analyse the browsing data from NFI4 together with that from NFI5 to see if these trends continue. Overall, ungulates primary have an impact on tree species that can cope with the changing climate and thus reduce the silvicultural potential in these forests.

6. References

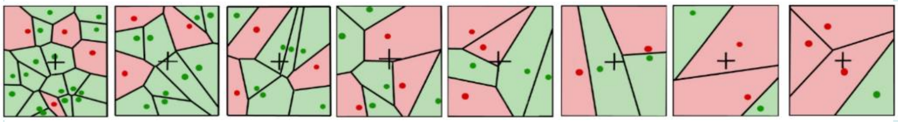
1. Kupferschmid, A.D. and P. Brang, *Notions de base pratiques: interactions entre le gibier et la forêt*, in *Forêt et gibier - Notions de base pratiques. Bases scientifiques et méthodologiques de la gestion intégrée du chevreuil, du chamois, du cerf élaphe et de leur habitat*. 2010, Office fédéral de l'environnement (OFEV): Bern. p. 9-40.
2. Abegg, M., B. Allgaier Leuch, and A.D. Kupferschmid, *Pathogènes, ravageurs et sécheresses oppriment la forêt.* Forêt, 2021. **74**(10): p. 13-15.
3. Kupferschmid, A.D., U. Wasem, and H. Bugmann, *Light availability and ungulate browsing determine growth, height and mortality of Abies alba saplings.* For. Ecol. Manage., 2014. **318**: p. 359-369.
4. Kupferschmid, A.D., *Compensation capacity of Central European tree species in response to leader shoot browsing*, in *Ungulates: evolution, diversity and ecology*, A. Menendez and N. Sands, Editors. 2017, Nova Science Publishers: Hauppauge, New York, USA. p. 1-63.
5. Krueger, L.M., et al., *Evaluating relationships among tee growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest.* Can. J. For. Res., 2009. **39**: p. 2460-2469.
6. Schulze, E.D., et al., *Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in Central and Southeastern Europe.* Ann. For. Res, 2014. **52**(20).
7. Didion, M., et al., *Ungulate herbivory modifies the effects of climate change on mountain forests.* Clim. Chang., 2011. **109**(3): p. 647-669.
8. Kupferschmid, A.D., M. Abegg, and P. Brang, *Wildeinfluss auf die Eiche in der Schweiz.* Bündner Wald, 2020. **73**(Juni 2020): p. 34-37.
9. Apollonio, M., R. Andersen, and R. Putman, *European ungulates and their management in the 21th century*. 2010, Cambridge, UK: Cambridge University Press. 604.
10. Breitenmoser, U., *Large predators in the alps: the fall and rise of man's competitors.* Biol. Conserv., 1998. **83**(3): p. 278-289.
11. DGE-BIODIV canton de vaud, *Rapport annuel sur la faune 2019 avec statistiques de la chasse et des dommages causés par la faune*. 2020, Direction générale de l'environnement, Division biodiversité et paysage.
12. Kupferschmid, A.D., et al., *Ungulate species and abundance as well as environmental factors determine the probability of terminal shoot browsing on temperate forest trees.* Forests, 2020. **11**(7): p. 764.
13. Huber, M. and A.D. Kupferschmid, *Wildeinflussmonitoring mittels LFI. GR im interregionalen Vergleich.* Bündnerwald, 2016. **3**: p. 24-30.
14. Abegg, M., et al., *Inventaire forestier national suisse IFN. Tableaux et cartes des résultats des relevés IFN 1983–2017 (IFN1, IFN2, IFN3, IFN4) disponibles sur internet*, in *Available from World Wide Web* <http://www.lfi.ch/resultate/>. 2020, Institut fédéral de recherches WSL: Birmensdorf.
15. Kupferschmid, A.D., et al., *Einfluss wildlebender Huftiere auf die Waldverjüngung: ein Überblick für die Schweiz.* Schweiz. Z. Forstwes., 2015. **166**(6): p. 420-431.
16. Abegg, M., B. Allgaier Leuch, and A.D. Kupferschmid, *La «dent du gibier» se fait toujours plus mordante.* Forêt, 2021. **74**(9): p. 21-23.
17. Gill, R.M.A., *A review of damage by mammals in north temperate forests: 1. Deer.* Forestry, 1992. **65**(2): p. 145-169.
18. Zinggeler, J., *Y a-t-il trop peu de jeunes arbres dans la forèt suisse?* Fôret, 1998. **11**: p. 9-11.
19. Stierlin, H.-R., et al., *Schweizerisches Landesforstinventar. Anleitung für die Feldaufnahmen der Erhebung 1993–1995*. 1994, Birmensdorf: Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft.
20. Keller, M., ed. *Schweizerisches Landesforstinventar, Feldaufnahmeanleitung 2013*. 2013, Eidg. Forschungsanstalt WSL: Birmensdorf. 214.

21. Bachofen, H. and A. Zingg, *Schweizerisches Landesforstinventar. Anleitung für die Erstaufnahme 1982-1986*. Vol. Ber. Nr. 304. 1988, Birmensdorf: Eidg. Anst. forstl. Versuchswes.
22. Keller, M., ed. *Schweizerisches Landesforstinventar, Anleitung für die Feldaufnahmen der Erhebung 2004-2007*. 2005, Eidg. Forschungsanstalt WSL: Birmensdorf. 393.
23. Schwyzer, A. and A. Lanz. *Verjüngungserhebung im schweizerischen Landesforstinventar*. in *Internationale Biometrische Gesellschaft - Deutsche Region AG Ökologie und Umwelt. 22 Tagung*. 2010. Göttingen, 20. und 21. September 2010: Die Grüne Reihe
24. Eiberle, K. and H. Nigg, *Grundlagen zur Beurteilung des Wildverbisses im Gebirgswald.* Schweiz. Z. Forstwes., 1987. **138**: p. 747-785.
25. Schwyzer, A. and J. Zinggeler, *Eine neue Methode zur Quantifizierung des Wildverbisses.* Schweiz. Z. Forstwes., 2000. **151**(4): p. 107-116.
26. Rüegg, D., *Verjüngungskontrolle: Methoden Stichproben in Indikatorflächen*. 2008: Dani Rüegg, Kaltbrunn.
27. Kupferschmid, A.D. and P.A. Gmür, *Einschätzung des Verbisseinflusses in zwei Wildräumen des Kantons St. Gallen.* Schweiz. Z. Forstwes., 2020. **171**(2): p. 79–90.
28. Motta, R., *Impact of wild ungulates on forest regeneration and tree composition of mountain forests in Western Italian Alps.* For. Ecol. Manage., 1996. **88**: p. 93-98.
29. Rüegg, D. and H. Nigg, *Mehrstufige Verjüngungskontrollen und Grenzwerte für die Verbissintensität.* Schweiz. Z. Forstwes., 2003. **154**(8): p. 314-321.
30. Stauffer, H.B., *Contemporary bayesian and frequentist statistical research methods for natural resource scientists*. 2008, Hoboken, New Jersey: John Wiley & Sons. Inc.
31. Fehr, M., et al., *Gutachtliche Beurteilung des Wildeinflusses auf die Waldverjüngung.* Schweiz. Z. Forstwes., 2019. **170**(3): p. 135–141.
32. Fehr, M., et al. *Évaluation d'expert de l'influence du gibier sur la régénération forestière*. 2021. DOI: dx.doi.org/10.5281/zenodo.4659564.
33. Benjamini, Y. and Y. Hochberg, *Controlling the false discovery rate: A practical and powerful approach to multiple testing.* . Journal of the Royal Statistical Society: Series B (Methodological), 1995. **57**: p. 289–300.
34. R Core Team, *R: A language and environment for statistical computing*. 2020, Vienna, Austria: R Foundation for Statistical Computing, http://www.R-project.org.
35. Dowle, M. and A. Srinivasan, *data.table: Extension of 'data.frame'. R package version 1.14.0.* 2021, URL: https://CRAN.R-project.org/package=data.table.
36. Brooks, M.E., et al., *glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling.* The R Journal:, 2017. **article published in 2017, volume 9:2**: p. URL https://journal.r-project.org/archive/2017/RJ-2017-066/index.html.
37. Hothorn, T., F. Bretz, and P. Westfall, *Simultaneous inference in general parametric models.* Biometrical Journal, 2008. **50**: p. 346–363.
38. Pebesma, E., *Simple Features for R: Standardized Support for Spatial Vector Data.* The R Journal, 2018. **10 439–446.**: p. URL https://doi.org/10.32614/RJ-2018-009.
39. Verheyden, H., et al., *Variations in bark-stripping by red deer Cervus elaphus across Europe.* Mammal. Rev., 2006. **36**(3): p. 217-234.
40. Welch, D., et al., *Leader browsing by red and roe deer on young Sitka spruce trees in Western Scotland (UK): I. Damage rates and the influence of habitat factors.* Forestry, 1991. **64**(1): p. 61-82.
41. Schweiger, J. and H. Sterba, *A model describing natural regeneration recruitment of Norway spruce (Picea abies (L.) Karst.) in Austria.* For. Ecol. Manage., 1997. **97**(2): p. 107-118.
42. Ward, A.I., et al., *Conifer leader browsing by roe deer in English upland forests: effects of deer density and understorey vegetation.* For. Ecol. Manage., 2008. **256**: p. 1333-1338.
43. Voser, P., *Einflüsse hoher Rothirschbestände auf die Vegetation im Unterengadin und im Münstertal, Kanton Graubünden*. Band 16, Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark. 1987, Druck Lüdin AG Liestal: Herausgegeben von der

Kommission der Schweizerischen Naturforschenden Gesellschaft zur wissenschaftlichen Erforschung des Nationalparks. 78
44. Hothorn, T., R. Brandl, and J. Müller, *Large-scale model-based assessment of deer-vehicle collision risk.* PLoS ONE, 2012. **7**(2): p. e29510.
45. Kamler, J., et al., *Reduction of herbivore density as a tool for reduction of herbivore browsing on palatable tree species.* Eur. J. For. Res., 2010. **129**(2): p. 155-162.
46. Kupferschmid, A.D. and C. Heiri, *Recovery of Abies alba and Picea abies saplings to browsing and frost damage depends on seed source.* Ecology and Evolution, 2019. **2019**(9): p. 3335–3354.
47. Kupferschmid, A.D., U. Wasem, and H. Bugmann, *Ungulate browsing leads to height and diameter growth reduction on Abies alba saplings planted along light gradients.* Eur. J. For. Res., 2015. **134**(1): p. 75-87.
48. Kupferschmid, A.D., et al., *Quantifying the relative influence of terminal shoot browsing by ungulates on tree regeneration.* For. Ecol. Manage, 2019. **446**: p. 331–344.
49. Bruinderink, G.W.T.A.G. and E. Hazebroek, *Wild boar (Sus scrofa scrofa L.) rooting and forest regeneration on podzolic soils in the Netherlands.* For. Ecol. Manage., 1996. **88**(1-2): p. 71-80.
50. Gomez, J.M. and J.A. Hódar, *Wild boars (Sus scrofa) affect the recruitment rate and spatial distribution of holm oak (Quercus ilex).* For. Ecol. Manage., 2008. **256**: p. 1384–1389.
51. Schneider, M., *Verbissnachweis mittels kriminaltechnologischer Methoden*, in *Institut für Wildbiologie und Jagdwirtschaft (IWJ), Department für Integrative Biologie und Biodiversitätsforschung*. 2017, Universität für Bodenkultur: Wien. p. 46.

7. Appendix

7.1 Information used to calculate the ratio of mean vs mean of ratio



									Total
Number of trees	20	12	10	8	6	4	4	4	68
Number of browsed trees	4	3	3	3	3	2	2	3	23
Browsed trees as % of all trees	4/20= 20%	25%	30%	37.5%	50%	50%	50%	¾= 75%	RoM=34% MoR=42%

Ratio of mean (RoM): default for NFI and VEKO: number of browsed trees divided by total number.

Mean of ratio (MoR): Average of browsing percentage per sample plot, i.e. number of browsed trees divided by total number per sample plot, averaged across plots.

With the stem count proportion used for RoM, sample areas with a higher stem count are weighted more heavily, since each tree is weighted equally. In the case of the stem count fraction used for MoR, each sample area is weighted equally. A mathematical overweighting of dense regeneration is in clear contrast to what actually happens in the forest. Most plants from dense growth will inevitably disappear over time because they do not have enough space. As a result of natural selection, where there are x small trees today, there will be only a few trees in the tree layer in the future.

7.2 Fraying on all tree species

Table 16 (this and next page): Number of seedlings or saplings in NFI2 in height class 10–39 cm and in height class 40–129 cm and DBH class 0–3.9 cm together that were not frayed or bark stripped (NO), were frayed or bark stripped (F/B), or had a dried treetop and thus no information about fraying was available(D). The total number of saplings and seedlings (T) and the percentage of frayed and bark-stripped seedlings and saplings (P=FB/(FB+NO)) are given, separately for each tree and shrub species.

NFI2 fraying/bark stripping	Height class 10–39 cm					Height class 40–129 cm and DBH class 0–11.9 cm				
	NO	*F/B*	*D*	*T*	*P [%]*	*NO*	*F/B*	*D*	*T*	*P [%]*
Shrub species										
Alnus viridis	0	0	0	0	NA	31	0	0	31	0.0
Amelanchier ovalis	2	0	0	2	0.0	0	0	0	0	NA
Berberis vulgaris	1	0	0	1	0.0	1	0	0	1	0.0
Buxus sempervirens	0	0	0	0	NA	46	0	0	46	0.0
Cornus mas	8	0	0	8	0.0	8	0	0	8	0.0
Cornus sanguinea	1	0	0	1	0.0	214	0	9	223	0.0
Corylus avellana	32	0	0	32	0.0	223	1	5	229	0.4
Crataegus sp.	15	0	0	15	0.0	122	1	8	131	0.8
Euonymus sp.	35	0	0	35	0.0	13	0	1	14	0.0
Ilex aquifolium	13	0	0	13	0.0	67	0	1	68	0.0
Juniperus communis	31	0	1	32	0.0	12	1	0	13	7.7
Laburnum anagyroides	1	0	0	1	0.0	23	0	1	24	0.0
Ligustrum vulgare	0	0	0	0	NA	323	0	2	325	0.0
Lonicera sp.	183	0	4	187	0.0	370	0	15	385	0.0
Pinus mugo	61	0	2	63	0.0	7	0	1	8	0.0
Prunus mahaleb	0	0	0	0	NA	1	0	0	1	0.0
Prunus padus	37	0	0	37	0.0	66	0	1	67	0.0
Prunus spinosa	6	0	0	6	0.0	107	1	4	112	0.9
Rhamnus cathartica	0	0	0	0	NA	1	0	1	2	0.0
Rhamnus frangula	7	0	0	7	0.0	11	1	0	12	8.3
Sambucus nigra	0	0	1	1	NA	53	4	5	62	7.0
Sambucus racemosa	10	0	0	10	0.0	79	2	15	96	2.5
Viburnum lantana	3	0	1	4	0.0	34	1	0	35	2.9
Viburnum opulus	60	0	0	60	0.0	60	0	2	62	0.0
Coniferous tree species										
Abies alba	181	0	1	182	0.0	496	7	6	509	1.4
Larix decidua, Larix kaempferi	0	0	0	0	NA	12	0	0	12	0.0
Picea abies	201	1	3	205	0.5	971	8	23	1002	0.8
Pinus mugo arborea	1	0	0	1	0.0	4	0	0	4	0.0
Pinus sylvestris	7	0	0	7	0.0	44	0	0	44	0.0
Pseudotsuga	8	0	0	8	0.0	6	2	0	8	25.0
Taxus baccata	0	0	0	0	NA	4	0	0	4	0.0

NFI2 fraying/bark stripping	Height class 10–39 cm					Height class 40–129 cm and DBH class 0–11.9 cm				
	NO	*F/B*	*D*	*T*	*P [%]*	*NO*	*F/B*	*D*	*T*	*P [%]*
Deciduous tree species										
Acer campestre	11	0	1	12	0.0	41	0	0	41	0.0
Acer opalus	4	0	0	4	0.0	45	0	1	46	0.0
Acer platanoides	37	0	0	37	0.0	23	0	0	23	0.0
Acer pseudoplatanus	388	0	8	396	0.0	582	13	27	622	2.2
Aesculus hippocastanum	0	0	0	0	NA	0	0	0	0	NA
Alnus glutinosa	0	0	0	0	NA	7	0	0	7	0.0
Alnus incana	20	0	5	25	0.0	115	0	5	120	0.0
Betula pendula	0	0	0	0	NA	2	0	0	2	0.0
Carpinus betulus	12	0	2	14	0.0	37	0	1	38	0.0
Castanea sativa	1	0	0	1	0.0	7	0	0	7	0.0
Fagus sylvatica	1227	0	5	1232	0.0	3038	3	46	3087	0.1
Fraxinus excelsior	611	0	9	620	0.0	996	12	47	1055	1.2
Juglans regia	1	0	0	1	0.0	0	0	0	0	NA
Malus sylvestris	0	0	0	0	NA	1	0	0	1	0.0
Populus alba, Populus x canescens	0	0	0	0	NA	7	1	1	9	12.5
Populus nigra s.l.	0	0	0	0	NA	1	0	0	1	0.0
Populus sp..	0	0	0	0	NA	1	0	0	1	0.0
Populus tremula	2	0	1	3	0.0	8	1	0	9	11.1
Prunus avium	0	0	0	0	NA	50	0	2	52	0.0
Pyrus communis	0	0	0	0	NA	1	0	0	1	0.0
Quercus petraea	82	0	0	82	0.0	32	0	0	32	0.0
Quercus robur	11	0	2	13	0.0	34	0	1	35	0.0
Robinia pseudoacacia	0	0	0	0	NA	7	0	2	9	0.0
Salix sp.	4	0	0	4	0.0	131	4	6	141	3.0
Sorbus aria	26	0	0	26	0.0	124	0	1	125	0.0
Sorbus aucuparia	72	0	1	73	0.0	292	4	8	304	1.4
Sorbus domestica	1	0	0	1	0.0	2	0	0	2	0.0
Sorbus torminalis	0	0	0	0	NA	9	0	0	9	0.0
Tilia cordata	2	0	0	2	0.0	15	0	1	16	0.0
Tilia platyphyllos	0	0	0	0	NA	17	0	0	17	0.0
Ulmus glabra	3	0	1	4	0.0	28	0	2	30	0.0
Ulmus minor	3	0	0	3	0.0	69	0	1	70	0.0
other deciduous trees	0	0	0	0	NA	33	0	0	33	0.0

Table 17: Number of seedlings in NFI4 in height class 10–39 cm and in height class 40–129 cm that were not frayed or bark stripped (NO) or were frayed or bark stripped (F/B) the total number of seedlings (T) and the percentage of frayed and bark-stripped seedlings (P=FB/(FB+NO)) are given, separately for each tree and shrub species.

NFI4 fraying/bark stripping	Height class 10–39 cm				Height class 40–129 cm			
	NO	*F/B*	*T*	*P [%]*	*NO*	*F/B*	*T*	*P [%]*
Shrub species								
Alnus viridis	4	0	4	0.0	9	0	9	0.0
Corylus avellana	14	0	14	0.0	23	0	23	0.0
Ilex aquifolium	5	0	5	0.0	11	0	11	0.0
Juniperus communis ssp communis	0	0	0	NA	1	0	1	0.0
Laburnum anagyroides	1	0	1	0.0	1	0	1	0.0
Prunus padus	3	0	3	0.0	3	0	3	0.0
Coniferous tree species								
Abies alba	40	0	40	0.0	23	0	23	0.0
Larix decidua	0	0	0	NA	0	0	0	NA
Picea abies	45	0	45	0.0	68	1	69	1.4
Pinus mugo arborea	1	0	1	0.0	1	0	1	0.0
Pinus sylvestris	1	0	1	0.0	0	0	0	NA
Pseudotsuga menziesii	0	0	0	NA	0	1	1	100.0
Taxus baccata	0	0	0	NA	0	0	0	NA
Deciduous tree species								
Acer campestre	1	0	1	0.0	4	0	4	0.0
Acer opalus	2	0	2	0.0	0	0	0	NA
Acer platanoides	2	0	2	0.0	0	0	0	NA
Acer pseudoplatanus	42	0	42	0.0	36	0	36	0.0
Ailanthus altissima	1	0	1	0.0	1	0	1	0.0
Alnus glutinosa	0	0	0	NA	2	0	2	0.0
Alnus incana	1	0	1	0.0	2	0	2	0.0
Betula pendula	0	0	0	NA	0	0	0	NA
Carpinus betulus	1	0	1	0.0	4	0	4	0.0
Castanea sativa	3	0	3	0.0	1	0	1	0.0
Fagus sylvatica	99	0	99	0.0	126	0	126	0.0
Fraxinus excelsior	60	0	60	0.0	37	0	37	0.0
Juglans regia	0	0	0	NA	0	0	0	NA
Populus tremula	0	0	0	NA	2	0	2	0.0
Populus x canescens	0	0	0	NA	1	0	1	0.0
Prunus avium	2	0	2	0.0	7	0	7	0.0
Pyrus communis, Pyrus pyraster	0	0	0	NA	0	0	0	NA
Quercus petraea	13	0	13	0.0	3	0	3	0.0
Quercus pubescens	0	0	0	NA	0	0	0	NA
Quercus robur	1	0	1	0.0	0	0	0	NA
Quercus rubra	0	0	0	NA	0	0	0	NA
Robinia pseudoacacia	0	0	0	NA	0	0	0	NA
Salix caprea	4	0	4	0.0	11	0	11	0.0
Salix sp.	1	0	1	0.0	1	0	1	0.0
Sorbus aria	5	0	5	0.0	9	0	9	0.0
Sorbus aucuparia	59	0	59	0.0	32	0	32	0.0
Sorbus torminalis	1	0	1	0.0	0	0	0	NA
Tilia cordata	0	0	0	NA	1	0	1	0.0
Tilia platyphyllos	0	0	0	NA	0	0	0	NA
Ulmus glabra	0	0	0	NA	1	0	1	0.0
Ulmus minor	0	0	0	NA	0	0	0	NA

Table 18: Number of saplings in NFI4 in DBH class 0–3.9 cm and in DBH class 4–11.9 cm that were not frayed or bark stripped (NO) or were frayed or bark stripped (F/B). The total number of saplings (T) and the percentage of frayed and bark-stripped saplings (P=FB/(FB+NO)) are given, separately for each tree and shrub species.

NFI4 fraying/bark stripping	**DBH class 0–3.9 cm**				**DBH class 4–11.9 cm**			
	NO	*F/B*	*T*	*P [%]*	*NO*	*F/B*	*T*	*P [%]*
Shrub species								
Alnus viridis	8	0	8	0.0	6	0	6	0
Corylus avellana	36	3	39	7.7	15	0	15	0
Ilex aquifolium	5	0	5	0.0	7	0	7	0
Juniperus communis ssp communis	1	0	1	0.0	1	0	1	0
Laburnum anagyroides	3	0	3	0.0	2	0	2	0
Prunus padus	1	0	1	0.0	1	0	1	0
Coniferous tree species								
Abies alba	31	2	33	6.1	53	0	53	0
Larix decidua	1	0	1	0.0	1	0	1	0
Picea abies	47	1	48	2.1	81	1	82	1.2
Pinus mugo arborea	1	0	1	0.0	1	0	1	0
Pinus sylvestris	0	0	0	NA	0	0	0	NA
Pseudotsuga menziesii	0	0	0	NA	1	0	1	0
Taxus baccata	0	0	0	NA	3	0	3	0
Deciduous tree species								
Acer campestre	1	0	1	0.0	1	0	1	0
Acer opalus	4	0	4	0.0	2	0	2	0
Acer platanoides	2	0	2	0.0	1	0	1	0
Acer pseudoplatanus	28	1	29	3.4	20	1	21	4.8
Ailanthus altissima	1	0	1	0.0	1	0	1	0
Alnus glutinosa	2	0	2	0.0	2	0	2	0
Alnus incana	4	0	4	0.0	1	0	1	0
Betula pendula	1	0	1	0.0	1	0	1	0
Carpinus betulus	3	0	3	0.0	2	0	2	0
Castanea sativa	1	0	1	0.0	0	0	0	NA
Fagus sylvatica	112	0	112	0.0	70	1	71	1.4
Fraxinus excelsior	19	1	20	5.0	19	0	19	0
Juglans regia	3	0	3	0.0	0	0	0	NA
Populus tremula	1	0	1	0.0	0	0	0	NA
Populus x canescens	1	0	1	0.0	0	0	0	NA
Prunus avium	4	1	5	20.0	3	1	4	25
Pyrus communis, Pyrus pyraster	1	0	1	0.0	0	0	0	NA
Quercus petraea	0	0	0	NA	0	0	0	NA
Quercus pubescens	0	0	0	NA	1	0	1	0
Quercus robur	1	0	1	0.0	2	0	2	0
Quercus rubra	0	0	0	NA	0	1	1	100
Robinia pseudoacacia	0	0	0	NA	1	0	1	0
Salix caprea	12	1	13	7.7	12	0	12	0
Salix sp.	1	0	1	0.0	1	0	1	0
Sorbus aria	10	0	10	0.0	11	0	11	0
Sorbus aucuparia	29	2	31	6.5	9	0	9	0
Sorbus torminalis	1	0	1	0.0	1	0	1	0
Tilia cordata	2	0	2	0.0	3	0	3	0
Tilia platyphyllos	1	0	1	0.0	1	0	1	0
Ulmus glabra	0	0	0	NA	2	0	2	0
Ulmus minor	0	0	0	NA	1	0	1	0

7.3 Descriptive analysis of browsing

7.3.1 Browsing on all tree species

Table 19 (this and next page): Number of seedlings in NFI2 in height class 10–39 cm and in height class 40–129 cm that were not browsed (NO), were browsed (B), or had no information about browsing (NA) The total number of seedlings (T) and the percentage of browsed seedlings (P=B/T) are given, separately for each tree and shrub species.

NFI2 browsing	Height class 10–39 cm					Height class 40–129 cm				
	NO	*B*	*NA*	*T*	*P [%]*	*NO*	*B*	*NA*	*T*	*P [%]*
Shrub species										
Alnus viridis	2	0	0	2	0.0	5	2	0	7	28.6
Amelanchier ovalis	1	0	0	1	0.0	0	0	0	0	NA
Berberis vulgaris	0	0	0	0	NA	1	0	0	1	0.0
Buxus sempervirens	8	0	0	8	0.0	27	0	0	27	0.0
Cornus mas	0	1	0	1	100.0	1	2	0	3	66.7
Cornus sanguinea	30	2	0	32	6.3	109	21	6	136	16.2
Corylus avellana	12	3	0	15	20.0	89	3	2	94	3.3
Crataegus sp.	34	1	0	35	2.9	67	4	7	78	5.6
Euonymus sp.	11	2	0	13	15.4	4	3	1	8	42.9
Ilex aquifolium	31	0	1	32	0.0	44	0	1	45	0.0
Juniperus communis ssp communis	1	0	0	1	0.0	9	0	1	10	0.0
Laburnum anagyroides	0	0	0	0	NA	3	0	0	3	0.0
Ligustrum vulgare	178	5	4	187	2.7	293	9	2	304	3.0
Lonicera sp.	56	5	2	63	8.2	268	13	12	293	4.6
Pinus mugo arborea	1	0	0	1	0.0	4	0	0	4	0.0
Pinus mugo prostrata	0	0	0	0	NA	7	0	0	7	0.0
Prunus mahaleb	0	0	0	0	NA	0	0	0	0	NA
Prunus padus	37	0	0	37	0.0	56	0	0	56	0.0
Prunus spinosa	2	4	0	6	66.7	67	15	4	86	18.3
Pyrus communis, Pyrus pyraster	0	0	0	0	NA	0	0	0	0	NA
Rhamnus cathartica	0	0	0	0	NA	1	0	0	1	0.0
Rhamnus frangula	6	1	0	7	14.3	6	2	1	9	25.0
Sambucus nigra	0	0	1	1	NA	24	2	2	28	7.7
Sambucus racemosa	10	0	0	10	0.0	30	5	10	45	14.3
Viburnum lantana	3	0	1	4	0.0	12	6	0	18	33.3
Viburnum opulus	60	0	0	60	0.0	45	2	2	49	4.3
Coniferous tree species										
Abies alba	173	8	1	182	4.4	284	18	8	310	6.0
Larix decidua	0	0	0	0	NA	0	0	0	0	NA
Larix decidua, Larix kaempferi	0	0	0	0	NA	1	0	0	1	0.0
Picea abies	198	3	4	205	1.5	575	8	26	609	1.4
Pinus sylvestris	7	0	0	7	0.0	37	0	0	37	0.0
Pseudotsuga menziesii	8	0	0	8	0.0	3	0	1	4	0.0
Taxus baccata	0	0	0	0	NA	0	0	0	0	NA

NFI2 browsing	Height class 10–39 cm					Height class 40–129 cm				
	NO	*B*	*NA*	*T*	*P [%]*	*NO*	*B*	*NA*	*T*	*P [%]*
Deciduous tree species										
Acer campestre	9	2	1	12	18.2	21	4	0	25	16.0
Acer opalus	4	0	0	4	0.0	17	4	1	22	19.0
Acer platanoides	36	1	0	37	2.7	17	3	0	20	15.0
Acer pseudoplatanus	311	77	8	396	19.8	220	155	19	394	41.3
Aesculus hippocastanum	0	0	0	0	NA	0	0	0	0	NA
Ailanthus altissima	0	0	0	0	NA	0	0	0	0	NA
Alnus glutinosa	0	0	0	0	NA	1	0	0	1	0.0
Alnus incana	19	1	5	25	5.0	57	0	4	61	0.0
Betula pendula	0	0	0	0	NA	2	0	0	2	0.0
Carpinus betulus	12	0	2	14	0.0	13	0	1	14	0.0
Castanea sativa	1	0	0	1	0.0	3	0	0	3	0.0
Fagus sylvatica	1214	13	5	1232	1.1	1908	26	36	1970	1.3
Fraxinus excelsior	517	94	9	620	15.4	466	160	27	653	25.6
Juglans regia	1	0	0	1	0.0	0	0	0	0	NA
Liriodendron tulipifera	0	0	0	0	NA	0	0	0	0	NA
Malus sylvestris	0	0	0	0	NA	0	0	0	0	NA
Populus alba, Populus x canescens	0	0	0	0	NA	5	0	1	6	0.0
Populus nigra s.l.	0	0	0	0	NA	0	0	0	0	NA
Populus sp.	0	0	0	0	NA	1	0	0	1	0.0
Populus tremula	0	2	1	3	100.0	2	4	1	7	66.7
Populus x canescens	0	0	0	0	NA	0	0	0	0	NA
Prunus avium	0	0	0	0	NA	24	10	2	36	29.4
Quercus petraea	81	1	0	82	1.2	14	1	0	15	6.7
Quercus pubescens	0	0	0	0	NA	0	0	0	0	NA
Quercus robur	11	0	2	13	0.0	6	0	1	7	0.0
Quercus rubra	0	0	0	0	NA	0	0	0	0	NA
Robinia pseudoacacia	0	0	0	0	NA	1	0	1	2	0.0
Salix caprea	0	0	0	0	NA	0	0	0	0	NA
Salix sp.	4	0	0	4	0.0	56	2	4	62	3.4
Sorbus aria	16	10	0	26	38.5	34	29	0	63	46.0
Sorbus aucuparia	42	30	1	73	41.7	96	80	4	180	45.5
Sorbus domestica	1	0	0	1	0.0	2	0	0	2	0.0
Sorbus torminalis	0	0	0	0	NA	1	2	0	3	66.7
Tilia cordata	2	0	0	2	0.0	5	1	1	7	16.7
Tilia platyphyllos	0	0	0	0	NA	1	0	0	1	0.0
Ulmus glabra	1	2	1	4	66.7	11	1	2	14	8.3
Ulmus minor	3	0	0	3	0.0	21	0	0	21	0.0
other deciduous trees	0	0	0	0	NA	3	0	0	3	0.0

Table 20 (this and next page): Number of seedlings in NFI4 in height class 10–39 cm and in height class 40–129 cm that were not browsed (NO), were browsed (B), or had no information about browsing (NA). The total number of seedlings (T) and the percentage of browsed seedlings (P=B/T) are given, separately for each tree and shrub species.

NFI4 browsing	**Height class 10–39 cm**					**Height class 40–129 cm**				
	NO	*B*	*NA*	*T*	*P [%]*	*NO*	*F/B*	*D*	*T*	*P [%]*
Shrub species										
Alnus viridis	6	0	0	6	0.0	0	0	0	0	NA
Amelanchier ovalis	0	0	0	0	NA	5	0	1	6	0.0
Berberis vulgaris	0	0	0	0	NA	0	0	0	0	NA
Buxus sempervirens	0	0	0	0	NA	0	0	0	0	NA
Cornus mas	0	0	0	0	NA	0	0	0	0	NA
Cornus sanguinea	0	0	0	0	NA	0	0	0	0	NA
Corylus avellana	12	3	0	15	20.0	0	0	0	0	NA
Crataegus sp.	0	0	0	0	NA	18	2	2	22	10.0
Euonymus sp.	0	0	0	0	NA	0	0	0	0	NA
Ilex aquifolium	11	6	4	21	35.3	0	0	0	0	NA
Juniperus communis ssp communis	0	0	0	0	NA	33	3	13	49	8.3
Laburnum anagyroides	0	1	0	1	100.0	1	0	0	1	0.0
Ligustrum vulgare	0	0	0	0	NA	3	2	0	5	40.0
Lonicera sp.	0	0	0	0	NA	0	0	0	0	NA
Pinus mugo prostrata	0	0	0	0	NA	0	0	0	0	NA
Prunus mahaleb	0	0	0	0	NA	0	0	0	0	NA
Prunus padus	15	3	1	19	16.7	11	2	0	13	15.4
Prunus spinosa	0	0	0	0	NA	0	0	0	0	NA
Rhamnus cathartica	0	0	0	0	NA	0	0	0	0	NA
Rhamnus frangula	0	0	0	0	NA	0	0	0	0	NA
Sambucus nigra	0	0	0	0	NA	0	0	0	0	NA
Sambucus racemosa	0	0	0	0	NA	0	0	0	0	NA
Viburnum lantana	0	0	0	0	NA	0	0	0	0	NA
Viburnum opulus	0	0	0	0	NA	0	0	0	0	NA
other shrubs	0	0	0	0	NA	0	0	0	0	NA
Coniferous tree species										
Abies alba	111	8	1	120	6.7	89	5	3	97	5.3
Larix decidua	0	0	0	0	NA	1	0	0	1	0.0
Larix decidua, Larix kaempferi	0	0	0	0	NA	0	0	0	0	NA
Picea abies	190	2	3	195	1.0	228	2	2	232	0.9
Pinus mugo arborea	3	0	0	3	0.0	2	0	0	2	0.0
Pinus sylvestris	1	0	0	1	0.0	0	0	0	0	NA
Pseudotsuga menziesii	0	0	0	0	NA	3	0	0	3	0.0
Taxus baccata	0	0	0	0	NA	0	0	0	0	NA

NFI4 browsing	Height class 10–39 cm					Height class 40–129 cm				
	NO	*B*	*NA*	*T*	*P [%]*	*NO*	*F/B*	*D*	*T*	*P [%]*
Deciduous tree species										
Acer campestre	8	5	1	14	38.5	5	4	0	9	44.4
Acer opalus	1	1	0	2	50.0	0	0	0	0	NA
Acer platanoides	26	1	0	27	3.7	0	0	0	0	NA
Acer pseudoplatanus	490	28	9	527	5.4	75	73	14	162	49.3
Aesculus hippocastanum	0	0	0	0	NA	0	0	0	0	NA
Ailanthus altissima	1	0	0	1	0.0	4	0	1	5	0.0
Alnus glutinosa	0	0	0	0	NA	0	0	0	0	NA
Alnus incana	1	0	1	2	0.0	4	0	0	4	0.0
Betula pendula	0	0	0	0	NA	0	0	0	0	NA
Carpinus betulus	8	0	0	8	0.0	18	2	1	21	10.0
Castanea sativa	11	3	0	14	21.4	1	1	0	2	50.0
Fagus sylvatica	1060	36	30	1126	3.3	736	48	72	856	6.1
Fraxinus excelsior	248	30	10	288	10.8	127	16	22	165	11.2
Juglans regia	1	0	0	1	0.0	0	0	0	0	NA
Liriodendron tulipifera	0	0	0	0	NA	0	0	0	0	NA
Malus sylvestris	0	0	0	0	NA	0	0	0	0	NA
Populus alba, Populus x canescens	0	0	0	0	NA	0	0	0	0	NA
Populus nigra s.l.	0	0	0	0	NA	0	0	0	0	NA
Populus sp.	0	0	0	0	NA	0	0	0	0	NA
Populus tremula	0	0	9	9	NA	1	0	0	1	0.0
Populus x canescens	0	0	0	0	NA	2	0	0	2	0.0
Prunus avium	8	0	1	9	0.0	6	2	1	9	25.0
Pyrus communis, Pyrus pyraster	0	0	0	0	NA	0	0	0	0	NA
Quercus petraea	117	66	6	189	36.1	10	2	0	12	16.7
Quercus pubescens	1	0	0	1	0.0	0	0	0	0	NA
Quercus robur	7	2	1	10	22.2	2	0	0	2	0.0
Quercus rubra	0	0	0	0	NA	0	0	0	0	NA
Robinia pseudoacacia	0	0	0	0	NA	0	0	0	0	NA
Salix caprea	0	0	0	0	NA	14	5	1	20	26.3
Salix sp.	0	0	0	0	NA	0	1	0	1	100.0
Sorbus aria	3	3	1	7	50.0	11	3	1	15	21.4
Sorbus aucuparia	80	40	2	122	33.3	82	43	4	129	34.4
Sorbus domestica	0	0	0	0	NA	0	0	0	0	NA
Sorbus torminalis	4	0	0	4	0.0	0	0	0	0	NA
Tilia cordata	1	0	0	1	0.0	1	1	0	2	50.0
Tilia platyphyllos	0	0	0	0	NA	1	0	0	1	0.0
Ulmus glabra	0	0	0	0	NA	1	1	0	2	50.0
Ulmus minor	0	0	0	0	NA	0	0	0	0	NA
other deciduous trees	0	0	0	0	NA	0	0	0	0	NA

7.3.2 Browsing intensity within production regions

Table 21: Mean of ratio (MoR), standard deviation and ratio of mean (RoM) in NFI2 and NFI4 of the seven main tree species, separated by production region. Values in italics and a smaller font size are based on a total of <20 actually assessed seedlings (i.e. not extrapolated). Values in bold are based on >200 actually assessed seedlings, and those in bold italics are based on 100–200 actually assessed seedlings.

Production region	NFI2			NFI4		
	MoR [%]	SE	RoM [%]	MoR [%]	SE	RoM [%]
Alps and Pre-Alps						
Abies alba	26.6	10.4	25.2	11.7	6.6	10.5
Picea abies	***5.0***	***3.0***	***2.3***	2.3	2.3	0.9
Acer spp.	36.0	8.5	47.5	29.6	7.7	26.8
Fagus sylvatica	***17.5***	***8.5***	***5.0***	***4.8***	***4.5***	***1.2***
Fraxinus excelsior	**40.7**	**8.0**	**28.4**	21.0	7.8	19.4
Sorbus aucuparia	33.4	8.5	45.9	36.1	8.5	40.7
Quercus spp.	NA	NA	NA	0.0	NA	0.0
Plateau						
Abies alba	**1.0**	**0.6**	**1.4**	12.9	6.6	8.0
Picea abies	**0.6**	**0.6**	**0.7**	**1.5**	**1.5**	**0.7**
Acer spp.	**31.9**	**5.7**	**14.9**	**22.0**	**7.1**	**5.4**
Fagus sylvatica	**0.0**	**0.0**	**0.1**	**6.0**	**2.4**	**4.6**
Fraxinus excelsior	**19.7**	**4.0**	**15.5**	**6.0**	**2.9**	**10.0**
Sorbus aucuparia	29.1	13.8	11.3	39.0	14.1	35.0
Quercus spp.	0.0	0.0	0.0	17.6	12.1	10.2
Jura						
Abies alba	**10.9**	**3.6**	**6.0**	***9.1***	***4.4***	***4.1***
Picea abies	**1.3**	**0.8**	**1.9**	**2.4**	**2.3**	**1.5**
Acer spp.	**31.2**	**4.6**	**24.9**	**29.1**	**6.0**	**13.2**
Fagus sylvatica	**4.3**	**1.5**	**1.5**	**6.6**	**1.9**	**3.9**
Fraxinus excelsior	**21.2**	**6.7**	**16.0**	***16.4***	***6.7***	***6.7***
Sorbus aucuparia	***42.9***	***6.3***	***53.8***	***32.1***	***6.3***	***30.1***
Quercus spp.	7.9	7.7	2.0	***19.2***	***11.8***	***35.8***