

MENDELOVA UNIVERZITA V BRNĚ

Lesnická a dřevařská fakulta

Ústav lesnické botaniky, dendrologie a geobiocenologie

**Natural regeneration of silver fir (*Abies alba* Mill.)  
in the National Nature Reserve Salajka**

DIPLOMOVÁ PRÁCE

Brno 2017

Jan Holík

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**Autor:** Jan Holík

**Název diplomové práce:** Přirozená obnova jedle bělokoré (*Abies alba* Mill.) v NPR Salajka

**Title of diploma thesis:** Natural regeneration of silver fir (*Abies alba* Mill.) in the National Nature Reserve Salajka

## **ABSTRAKT**

Tato studie se zabývala vývojem přirozené obnovy dřevin v temperátním jedlo-bukovém přirozeném lese ponechaném samovolnému vývoji od 30. let 20. století. Výzkumná plocha se nacházela v přísně chráněné Národní přírodní rezervaci Salajka v Západních Karpatech. Předmětem výzkumu byl okus zvěří, vznik a mortalita přirozené obnovy, které představují jedny z hlavních prvků koexistence druhů. Bylo použito dvou výběrových statistických metod, trvalé sítě 98 inventarizačních ploch rozmístěných pravidelně po celé rezervaci a transektu s 54 transektovými plochami. Buk si postupně získával absolutní převahu v přirozené obnově. Okus limitoval růst jedle, klenu a smrku, jedinci zřídka překonávali výšku 0,5 m. U jedle byl potvrzen efekt “koncentrovaného zdroje”, jelikož okus byl intenzivnější za přítomnosti vysokého počtu konspicivních jedinců. Vznik nových jedinců a mortalita jedle a buku se lišila, což poukazuje na jejich specifické životní strategie. Výsledky zdůrazňují význam pravidelného, ale méně rozsáhlého vzniku nových jedinců jedle a masivního, ale relativně méně častého vzniku nových jedinců buku. Mortalita přirozené obnovy převažovala nad vznik nových jedinců u obou druhů, ale na rozdíl od buku byl tento poměr u jedle téměř vyrovnaný. Výška jedinců přirozené obnovy jako jediná dobře predikovala jejich mortalitu. Okus zvěří, vznik a mortalita přirozené obnovy tvoří důležitou část regeneračních procesů lesa a jejich role by měla být uznána jak v lesnictví, tak v ochraně přírody.

**Klíčová slova:** vývojová dynamika, jedle bělokorá (*Abies alba* Mill.), buk lesní (*Fagus sylvatica* L.), přirozená obnova, různověký jedlo-bukový les, zakládání, mortalita

## **ABSTRACT**

This study addressed the development of natural regeneration of tree species over the period 2009–2016 in a temperate fir-beech old-growth forest left to a spontaneous development since 1930s. The research site was located in the strictly protected National Nature Reserve Salajka, lying in the Western Carpathians mountain range. Ungulate game browsing, establishment and mortality of natural regeneration as the main drivers of species coexistence were studied, using two alternative sampling methods, permanent network of 98 inventory plots regularly positioned across the whole forest reserve and transect with 54 transect plots. Beech was found to secure gradually absolute dominance over other tree species in natural regeneration. The growth of fir, maple and spruce was hindered by browsing since the individuals rarely exceeded the height of 0.5 m. Further, the resource concentration effect was found in fir as browsing was more intense under high conspecific densities. Establishment and mortality of fir and beech differed, suggesting the species-specific life-history strategies. The results demonstrated the importance of regular and inextensive establishment of fir and huge but relatively less frequent establishment of beech. Mortality outweighed establishment in both species, though fir ratio tended to be almost balanced. The height of natural regeneration was revealed to be the only good predictor of mortality. Browsing, establishment and mortality of natural regeneration comprise an important part of forest regeneration processes and their role should be acknowledged by both forest and nature conservation management.

**Keywords:** developmental dynamics, silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), natural regeneration, uneven-aged fir-beech forest, establishment, mortality

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# 1. Introduction

Natural regeneration of tree species in mixed temperate fir-beech forests has been of particular interest in many European countries recently (e.g. Ammer 1996; Diaci et al. 2010; Klopčič et al. 2010; Saniga et al. 2011). The main reason behind it has often been the decline of silver fir (*Abies alba* Mill.) and the expansion of European beech (*Fagus sylvatica* L.). There are studies that hypothesized the decline of silver fir (fir) to be a result of complex and region-specific causes (Vrška et al. 2009; Diaci et al. 2011), however, leading often to a similar outcome. Whereas factors such as air pollution likely do not play that much role at present as in the past (Elling et al. 2009), some are still highly relevant such as browsing (Klopčič et al. 2010). From a different standpoint, the periods of the decline of fir were also suggested to be a significant part of fir dynamics (Volařík, Hédli 2013). Moreover, competitiveness of European beech (beech) and fir differ (Szwagrzyk et al. 2012) and might be shifted by climate change, thus possibly giving beech an advantage over other species under certain conditions (Kramer et al. 2010). The fact is that the decline of fir is particularly notable on the level of natural regeneration and early life stages, since they are often totally absent. Many studies ascribed it to the effect of ungulate game browsing (Diaci et al. 2011; Klopčič, Boncina 2012), which might be potentially responsible for the alternation of tree species in forest community (Heuze et al. 2005). In addition, deer population size has risen all around Europe, except for the south-eastern part of the continent (Burbaite, Csányi 2010), where more stable proportion of fir seedlings and saplings was reported (Diaci et al. 2011). Further, the total absence of fir natural regeneration as well as low seed production of fir have been observed only rarely (Szewczyk, Szwagrzyk 2010; Paluch 2011), though little is known about the establishment and mortality of fir and beech natural regeneration in the long-term, since such studies are mostly the exception.

This study addresses the dynamics of tree natural regeneration in a mixed temperate fir-beech old-growth forest over the period 2009–2016. Specifically, the aims of this study were to 1) describe the development of natural regeneration over time, 2) assess the impact of browsing on natural regeneration in connection to biotic and habitat factors, 3) assess the role of establishment and mortality of fir and beech as an integral part of species life-history strategy and 4) formulate recommendations for nature conservation and forestry.

## 2. Review

Natural regeneration of tree species comprises an elementary part of forest regeneration processes, ensuring the dynamic continuity of forest ecosystems. In old-growth unmanaged forests, it lays a basis of the future forest structure, predetermining the species composition, age, height and diameter structure that is characterized both in spatial and temporal terms. The research and monitoring activities in such forests are supposed to gather fresh evidence of natural forest dynamics that is not directly impacted by man and convey it for instance to forest management or nature conservation.

Mixed fir-beech forests are testimony of how dynamic forest ecosystems in a temperate zone of Europe can be and how well-founded the research in these forests is. Fir and beech are both shade-tolerant species (Nagel et al. 2010) that share a similar ecological niche (Liepelt et al. 2009), thereby forming forest communities under the influence of the same disturbance regime (Firm et al. 2009, Šamonil et al. 2009). In the long history of beech and fir coexistence, they have been accompanied by human activities from the very beginning of their return from the southern European refugia after the last glaciation ended (Liepelt et al. 2009). Despite the available sources of information on the past role of both species in forest ecosystems (pollen, charcoal or forestry data), enabling partially the reconstruction of the former species composition and forest structure (Kozáková et al. 2011), little was known about the actual aspects of natural fir-beech dynamics until the regular long-term monitoring of old-growth forests had been launched in Central Europe (Vrška et al. 2009; Diaci et al. 2011).

Two opposite trends have become a thoroughly studied area of research in fir-beech forests, the decline of fir and expansion of beech. The decline of fir has been reported since at least 19<sup>th</sup> century. It is characterized as decrease in the proportion of fir, density of fir, absence of young life stages and it is sometimes connected to the ageing of fir generations since there is a notable discrepancy between the proportion of mature and young (sapling, pole-size trees) fir individuals (Vrška et al. 2009). Fir was found to decline due to a set of complex and often region-specific causes such as air pollution in the second half of the 20<sup>th</sup> century (Elling et al. 2009; Bošela et al. 2014), sensitivity to climate change (Gazol et al. 2015), low genetic adaptability (Bergmann et al. 1990), past land use and forest and wildlife management practices (Vrška et al. 2009, Diaci et al. 2011), ungulate game browsing (Heuze et al. 2005, Klopčic et al. 2010), low species competitiveness (Woziwoda, Kopeć 2015), expansion of beech (Kramer et al.

2010) and others. Fir was also found to form pure forest stands originated from the colonisation of abandoned agricultural land (Rozman et al. 2013), when beech dispersal is probably limited at this early stage of succession and expands later. Thus the decline might be an essential part of fir dynamics (Volařík, Hédli 2013). Conversely, the expansion of beech has been reported elsewhere in Europe (Szwagrzyk, Szewczyk 2008; Diaci et al. 2010; Saniga et al. 2011) and is not connected only to sites with fir (Poljanec et al. 2010). The causes are not well understood, though it might be partially triggered by climate change (Kramer et al. 2010).

From the current potential causes of fir decline, ungulate game browsing seems to hinder the growth of natural regeneration of fir to a considerable degree (Ammer 1996; Heuze et al. 2005; Klopčič et al. 2010). Moreover, red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) population size has dramatically increased all around Europe and generated the unresolved deer-forest conflict<sup>1</sup> (Čermák, Mrkva 2007; Burbaite, Csányi 2010). However, the deer-forest conflict has its roots in the past and present land use, landscape and wildlife management and a key remedy is hardly to be seen at the scale of local forest management unit or small region but more likely at the scale of whole landscape (Jarnemo et al. 2014). Conservation areas protecting old-growth forests may promote the sanctuary effect (Grignolio et al. 2014), luring animals for instance by favourable settling stimulus, i.e. favourable habitat in terms of thermal and hiding cover, edge effect and level of disturbance (Barret, Schmitz 2013). This situation may give rise to heavy browsing inside the reserve, regardless of deer density (Reimoser, Gossow 1996; Jarnemo et al. 2014) which is non-linearly related to seedling growth and mortality (Trembley et al. 2007). Given that this might be even amplified in the less extensive conservation areas (Grignolio et al. 2014), the impact of deer browsing can lead to the alternation of species dominance and thereby forest structure, promoting indirectly less attractive and less palatable species (Heuze et al. 2005). Tree species have developed various resistance mechanisms to mitigate the impact of herbivory such as secondary metabolites reducing the digestibility of browse (Pellisier 2013; Ohse et al. 2016). Moreover, broadleaves are supposed to suffer from browsing less since they store nutrients in stems and roots, whereas conifers in foliage (Gill 1992). The reaction of individuals to browsing results from the complex interplay of factors. Browsing on tree species can be more pronounced in winter due to the shortage of alternative food supply (Häsler, Senn 2012) and it can seriously reduce the

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<sup>1</sup> Also referred to as human-wildlife conflict in broad terms.

growth reaction of seedlings compared to browsing in vegetation period (Kupferschmid, Bugmann 2013). Conversely, deep snow cover may play a part in lower availability of browse in winter (Visscher et al. 2006). Further, higher light availability in a gap stimulates the positive growth reaction after browsing and can serve as the escape strategy of seedlings (Kupferschmid et al. 2013), however, tolerance strategy is usually better under shaded and generally adverse conditions (Vandenberghe et al. 2008). It is also common that vigorously growing, bigger and older individuals are repeatedly browsed, though they are usually more tolerant to browsing (Kupferschmid et al. 2013). Either stimulated or reduced browsing impact may depend on local plant density, known as the resource concentration and dilution effect (Hambäck et al. 2014) as browsing on tree species is often influenced by nearby biotic neighbours such as herbal plants, shrubs or conspecific and heterospecific tree seedlings, providing natural protection or alternative forage (Reimoser, Gossow 1996; Heuze et al. 2005, Jarnemo et al. 2014).

Natural regeneration of tree species is spread across the forest floor without regard to light availability in a temperate fir-beech forest (Nagel et al. 2010). Shade-tolerant tree species such as fir and beech can typically withstand under very low light levels in the form of advance regeneration, i.e. seedling or sapling bank (Szwagrzyk et al. 2001) that is reorganized after gap formation and determines the gap filling process, thereby driving the species coexistence of fir and beech (Nagel et al. 2010). Species capable of survival in adverse conditions have a distinct advantage over others, however, might be limited in terms of seed production that either does not occur frequently or is constrained by spatial seed dispersal (Szewczyk, Szwagrzyk 2010; Paluch 2011). Another constraint consists in the variation of edaphic factors, driving the properties of seedbed, germination of seeds and in consequence seedling survival (Paluch 2005; Nopp-Mayr et al. 2012; Szwagrzyk et al. 2015). This edaphic variation is determined by a wide and complex range of biotic and abiotic interactions such as pit and mound microsites resulting from the tree uprooting disturbances (Šebková et al. 2012), the effect of conspecific or heterospecific mature trees (Paluch 2005) or light levels at the forest floor (Szwagrzyk et al. 2001). Further, mortality of seeds, germinants and young seedlings is generally high (Mazur 1989; Nopp-Mayr et al. 2012; Szwagrzyk et al. 2001). Browsing can play a role in seedling survival, depending on species resistance (Harmer 2001; Vandenberghe et al. 2008) and low light levels that may increase survival after browsing (Vandenberghe et al. 2008). Importantly, species



coexistence is driven by certain mechanisms. The ‘Janzen-Connell’ effect implies that high conspecific density of seedlings promotes increased activity of host-specific predators, herbivores and pathogens, thereby reducing the survival of seedlings and giving a chance to less abundant and rare species (Janzen 1970; Connell 1971). This density-dependent mechanism seems to determine seedling survival both in a temperate (Bai et al. 2012; Yan et al. 2015) and tropical forest (Comita, Hubbell 2009) and may vary, depending on the life-history strategies of species such as shade tolerance, dispersal of species (Comita, Hubbell 2009; Bai et al. 2012), successional stage of ecosystem and life stage of individuals (Yan et al. 2015).

### 3. Materials and methods

#### 3.1. Study area

The study was carried out in the National Nature Reserve (NNR) Salajka located in the Nature Forest Area 40 – the Moravsko-Slezské Beskydy Mountains and the Protected Landscape Area Beskydy. The NNR Salajka represents a remnant of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) natural forest on the north-western edge of the Carpathians. It is situated in the eastern part of the Czech Republic on the border with Slovakia. Currently, the total reserve area covers 21,9 ha. (Adam et al. 2003).



Fig. 1. The National Nature Reserve Salajka in the Moravsko-Slezské Beskydy Mountains (the Western Carpathians)

Average annual precipitation ranges from 1050 to 1370 mm and mean annual temperature from 5 to 6°C (Tolasz et al. 2007). Within the year 190 days are with temperature higher than 5°C, 133 days with temperature higher than 10°C. On average, there are 140 days with a snow cover. The Moravsko-Slezské Beskydy Mountains fall within a component part of the sizeable flysh belt of the Western Carpathians. Skeletic

Cambisols and Haplic Cambisols are the prevailing soils stretching mostly over slopes with steep north-eastern and gentler south-eastern aspect at an altitude of 715–820 m a.s.l (Adam et al. 2003). Phytocenoses are classified as the associations *Dentario enneaphylli-Fagetum* and *Dentario glandulosae-Fagetum* (Šamonil, Vrška 2007). The NNR Salajka is home to two species of large herbivores: red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.). The average population density of red and roe deer was 2.4 and 1.4 per 1 km<sup>2</sup> respectively, based on game census from 2006 carried out in two nearby forest reserves by Suchomel et al. (2010).

Since the 15th century walachian colonization began putting pressure on the forest ecosystems in the The Moravsko-Slezské Beskydy Mountains. Nevertheless, first reference made about local forest exploitation comes from 1794. Patch felling of individual trees, especially conifer ones, was customary at that time as well as grazing of livestock. Until the 1930s, various forms of the clearcutting and shelterwood presented a common practice as well as underplanting in spruce stands. Interestingly, top-quality mature trees of silver fir were transported to the Netherlands and used for shipbuilding (Adam et al. 2003). In spite of these irregular human interventions forest old-growth traits were still well-preserved. Although the reserve was officially designated in 1956 it has been under strict forest protection already since 1937 (Vrška 1998).

First research attempts date back to 1959 when M. Vyskot established a pair of permanent inventory plots (Vyskot 1968). However, the most comprehensive forest research was carried out by Průša (Průša 1977, 1985). His contribution towards better understanding of forest ecosystem deeply affected the way of how modern old-growth forest research is addressed in the Czech Republic (e.g. Vrška 1998; Šamonil, Vrška 2007; Janík et al. 2016).

The proportion of fir has been decreasing in the long term in the NNR Salajka. On the basis of the forest management plan data from 1837, past proportion of fir accounted for 62 % but it dropped to 20 % in 2007. On the contrary, beech proportion increased twofold since 1837 amounting to 70 %. Norway spruce (*Picea abies* (L.) H. Karst) and sycamore maple (*Acer pseudoplatanus* L.) can be regarded as admixed tree species in the NNR Salajka (Přívětivý 2013). The reserve area is state-owned under the management of Nature Conservation Agency of the Czech Republic. The surrounding forest stands are owned by the Ostravsko-Opavská Diocese ([www.cuzk.cz](http://www.cuzk.cz)).

### 3.2. Regular network of permanent inventory plots

The area of the NNR Salajka was overlaid with regular square network in 2009. Each square contained the centers of inventory plots (IP). In total 196 circular IPs were set up using systematic sampling design (Appendix 1.). There were two IPs for one plot center (giving 98 plot centers in total), the small IP with a radius of 0.80 m and area 2m<sup>2</sup> and the large IP with a radius of 3.34 m and area 35 m<sup>2</sup>. Plot centres laid 44.25 m apart

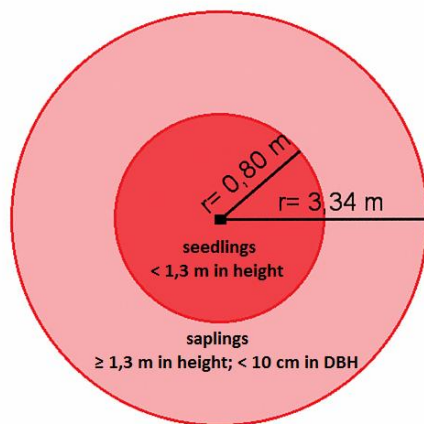


Fig. 2. Scheme of inventory plot.

and they were identified by an iron stake driven into the ground. All the trees up to 10 cm in diameter at breast height (DBH) were considered as natural regeneration. Small IPs were used for an inventory of all natural regeneration up to 1.3 m in height (seedlings). Newly emerged one-year old individuals were also regarded as seedlings. On large IPs, all natural regeneration higher than 1.3 m and up to 10 cm in DBH (saplings) was documented (Fig. 2.).

Seedlings were grouped into three height classes on a small IP as follows: <0.15 m, 0.15–0.49 m and >0.5 m. Similarly, saplings were split into three diameter classes on a large IP in this manner: <3 cm, 3–7 cm and 7–10 cm. Natural regeneration of all tree species was recorded but only the results for fir, beech, maple and spruce are presented since other tree species were documented only sporadically. In addition, all individuals were assessed in terms of current browsing, i.e. browsing coming from the past winter and actual growing season. Individuals with browsed terminal shoots or heavily browsed lateral shoots (more than 20 % of shoots browsed) were considered as browsed, thus respecting the methodology of Čermák et al. (2009). Browsing rate stands for a percentage of browsed individuals in this study.

Data collection was carried out every year in the late summer or early autumn in the period of 2009–2016. In total, there was a dataset including seven years of measurements (data were not collected in 2011). Results for the period 2009–2012 were evaluated by Přivětivý (2013). Subsequently, Holík (2014) took over the work and re-

evaluated the results covering also the year 2013. Browsing impact on natural regeneration had begun to be assessed since 2014.

### **3.3. Transect**

In the north-northeast part of the NNR Salajka, a transect 110 m by 8 m was established with an ESE-WNW orientation along its long side. Its position was selected on account of mature fir presence in the immediate vicinity (Appendix 1.). The main gist behind this design was to focus on that part of the NNR Salajka where fir has potentially similar chance to recruit alongside beech so that natural regeneration dynamics of both species could be relevantly argued over time.

Natural regeneration of all species up to 10 cm in DBH was mapped on the whole transect using the Field-Map technology in 2013. In the oncoming years, natural regeneration was measured exclusively on TPs as a result of selected sampling approach (described below). Newly emerged one-year old individuals were also recorded. Tree species was identified in all the individuals and comparing to IP methodology height of individuals was measured to the nearest centimetre. Then individuals were sorted into the same height and diameter classes likewise on IPs. In addition, one-year old seedlings (“establishment”) and older seedlings (“seedlings”) were differentiated. To provide more detailed information browsing evaluation was broken down into three categories: terminal shoot, lateral shoot (more than 20 % of shoots damaged) and both terminal and shoot browsing. The data collection was conducted every year in the late summer. The data were collected yearly from 2013 to 2016.

Having established transect in 2013, a stratified sampling approach was consequently adopted. All fir natural regeneration (1089 individuals) was grouped together no matter whether it was classified as establishment (152 individuals) or a seedling (937 individuals). Furthermore, transect was segmented into regular square grid network with a square side equal to 1 m. In each segment the density of fir individuals was calculated. Based on the criteria of fir density and fir height (h), fir density classes A, B, C or D were determined for all segments (Tab. 1).

All selected segments were assigned random numbers thus serving as a sampling basis. In the respective fir density class and height interval each random number series was put in ascending order. Only records with the six lowest values were taken in from each fir density class and height interval resulting altogether in 72 segments. The decision to take the six lowest values was arbitrary.

One fir individual was picked out in each segment and was surrounded by circular buffer zone with a radius of 0.5 m. No buffer zone overlaid one another. Central fir selection criteria went as follows: 1) the nearest fir to the segment centre was selected, 2) in case of buffer zone collision the nearest fir without buffer zone collision (no-collision fir) was selected, 3) no-collision fir was selected in the respective segment at first, 4) if no-collision fir was not available in the respective segment, the nearest no-collision fir was selected from adjacent segments. In case of conflict segment priority was set according to random number values assigned in the previous process. The segment with a lower value had a priority and its selection was definite. When higher-value segment was selected, the process was restarted respecting the above-mentioned criteria. Since fir density class A was always the empty set (Tab. 1) final number of segments and thus final number of central fir individuals was 54 (Appendix 2.).

*Tab. 1 Fir density classes separated according to height intervals whereby the classification of transect segments was conducted, thus serving as a sampling basis. The frequency of each cell was equal to 6.*

	$2 \leq h < 10 \text{ cm}$	$10 \leq h < 20 \text{ cm}$	$20 \leq h \leq 200 \text{ cm}$
A	0	0	0
B	1	1–3	1
C	2–3	4–5	2
D	4–5	6–11	3–4

Buffer zones with central fir individuals defined 54 circular transect plots (“TP”) on which the data collection was carried out in the late summer or early autumn over the period 2014–2016, thus resulting in a dataset covering four years of measurements (including the first total transect measurement in 2013). In 2014 all individuals were tagged with numbered iron labels to make their repeated identification feasible. Establishment emerging in the next years was also additionally tagged. For similar purpose, maps of all TPs were drawn in 2014 and were updated each oncoming year to reflect the current situation. If TP could not be identified in the field (either it was impossible to find or central fir from 2013 did not exist in 2014), the closest possible fir with similar height was searched out and a new substitute TP was set up. However, in

case of central fir mortality during the next years a new TP was not re-established and the initial TP was respected.

In 2014, 2015 and 2016 photosynthetically active radiation (PAR) was measured on all TPs using a pair of LaiPen LP 100, i.e. one reference above-canopy device and one below-canopy device. PAR is quantified as  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  which is a measure of the photosynthetic photon flux density. The canopy PAR transmittance (light availability) was computed when related to automatic reference measurements above the canopy in dual sensor mode (PSI 2015). Below-canopy measurements were taken above TPs at a height of 1.3 m under relatively uniform overcast sky conditions in the late summer of each respective year.

### **3.4. Data analysis**

All data were analysed in IBM SPSS Statistics 24. Plots and tables were drawn in Microsoft Office Excel 2007 and STATISTICA 12. A series of generalised linear mixed-effect models (GLMMs) with Poisson distribution (log-link function) was performed (Bolker et al. 2009) and top-down approach was followed (West et al. 2015) to assess the effect of predictors on the density of browsed individuals (target count variable). Predictors (fixed effects) used in the models finally included height of individuals, density of conspecific individuals, density of heterospecific individuals, total density, height variation and light availability on browsing rate of natural regeneration. Interactions of fixed effects were tested but finally excluded from the model since it deteriorated the model quality and no interaction was statistically significant. Height of individuals denoted the height class of individuals. There was only a small number of individuals in the 3. height class, so individuals of the 2. and 3. height class were pooled. Height of individuals as a continuous variable was also tested and provided similar results as the height class variable. Since the height distribution was right-skewed and had to be log-transformed, the height class variable was finally included. Density of conspecific individuals, heterospecific individuals and total density were log-transformed to meet the assumption of normality. To avoid errors transforming the cases with zeros, number one was added to all the cases. Height variation stood for the coefficient of variation of the height variable. Final fixed-effect models were then extended with random factor (transect plot). GLMM analysis was run separately for fir and beech data subsets. Models were compared using Akaike Information Criterion (AIC) (Burnham, Anderson 2002). To interpret the models, rate ratios were used which



stood for the exponentiated Poisson regression coefficients (Fig. 8 and 9.). Values above one indicated a positive effect of a factor, conversely, values below one implied a negative effect of a factor.

Mortality of natural regeneration was predicted also by employing GLMM analysis with binomial distribution (log-link function) following the same procedure as in the previous case. Only subset of fir and beech individuals present in 2013 was taken in for analysis (382 individuals alive). The target variable was binomial demonstrating whether individuals were alive (1) or dead (0) in 2016 (289 individuals alive). The effect of species, browsing, height class, total density, density of conspecific, heterospecific neighbours, density of browsed conspecific, heterospecific neighbours, light availability and height variation were tested (fixed effects). Density of conspecific, heterospecific neighbours, density of browsed conspecific and heterospecific neighbours were log-transformed. Density of browsed heterospecific individuals was excluded from the analysis because it could not meet the assumption of normality even after logarithmic transformation. Light availability and height variation were also excluded since they deteriorated the model quality as well as all considered interactions of predictors. GLMM analysis was run for separate subsets of height classes with the pooled 2. and 3. height class and subsets of fir and beech individuals. However, none of these models produced significant effect of predictors so the analysis was performed for complete set of the data.

To assess the dynamics of natural regeneration over time and thus to test for differences in means of total and species-specific mortality, establishment, browsing and densities over years separately on transect and inventory plots, the bias-corrected and accelerated bootstrap technique was employed (Efron 1987). If the analysed sample size was too small, nonparametric Kolmogorov-Smirnov test was used instead.



## 4. Results

### 4.1. The dynamics of natural regeneration over time

#### 4.1.1. Inventory plots – seedlings (< 1.3 m in height)

To assess the development of natural regeneration the inventory data from 2009 and 2016 were compared. Fir was the most abundant species in 2009 (47.5 %), followed by beech (21 %), maple (27 %) and spruce (4.5 %). In 2016, fir proportion dropped to 38.9 %, so did beech (16.7 %) and maple proportion (6.4 %) because spruce proportion went massively up and as the only species significantly (37.9 %,  $p=0.046$ ). However, the only absolute decrease in density took place in maple (0.48-fold) and fir density increased 1.65-fold, beech 1.25-fold and spruce 16.85-fold. Total density of all seedlings increased twofold comparing to 2009 ( $p=0.001$ ) (Tab. 2.).

Tab. 2. Species densities and proportions in 2009 and 2016 on IPs. % denotes the proportion of species in the respective height class except the species category All where it stands for relative density ratios among the height classes (in the grey line).

Year	Species	Density per ha							
		< 0,15 m	%	0,15–0,49 m	%	0,5–1,3 m	%	All	%
2009	Fir	9699	53,7	431	17,0	0	0	10130	47,5
	Beech	2209	12,2	1509	59,6	754	100	4472	21,0
	Spruce	700	3,9	269	10,6	0	0	970	4,5
	Maple	5442	30,1	323	12,8	0	0	5765	27,0
	All	18050	84,6	2532	11,9	754	3,5	21337	100
2016	Fir	16129	43,2	574	11,0	52	10,0	16756	38,9
	Beech	3028	8,1	3758	72,0	418	80,1	7203	16,7
	Spruce	16025	42,9	261	5,0	52	10,0	16338	37,9
	Maple	2140	5,7	626	12,0	0	0	2767	6,4
	All	37322	86,7	5219	12,1	522	1,2	43064	100

As for total density, the 1. height class (< 0.15 m) accounted for about 85 % both in 2009 and 2016, however, in absolute terms it increased twofold comparing to 2009 ( $p=0.003$ ). The increase of density occurred also in the 2. height class (0.15–0.49 m), though it was not significant. Relative density ratios remained almost the same among height classes, i. e. 1. height class 85 %, 2. height class 12 % and 3. height class 3 % (Tab. 2.).

In the 1. height class fir was still the most abundant species (43.2 %) closely followed by spruce (42.9 %) which density increased 22.89-fold. Beech was getting more and more dominant in the 2. height class (72 %) and 3. height class (80.1 %). Fir, spruce and maple were basically missing in the 3. height class. Interestingly, the density

of beech in the 3. height class was comparable to the density of fir in the 2. height class. Though obvious shifts took place on the level of species and height classes, none of them were statistically significant (Tab. 2.).

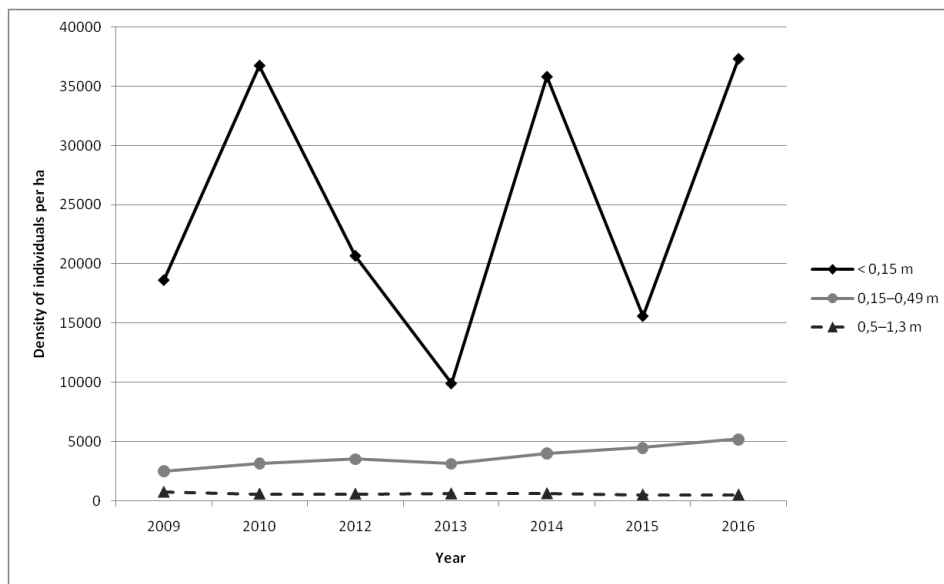


Fig. 3. Dynamics of densities in all the height classes over the period 2009–2016

The density of the 1. height class was very dynamic bouncing up and down over time. Sudden falls and rises of density seem to have occurred over a span of 1 or 2 years (Fig. 3). Interestingly, all species reflected the years of density falls and rises in a similar way, however, the extent was pronounced in the most abundant fir and beech (Fig. 4.). The 2. and 3. height class demonstrated more steady and balanced dynamics with slow density growth of the 2. height class (Fig. 5).

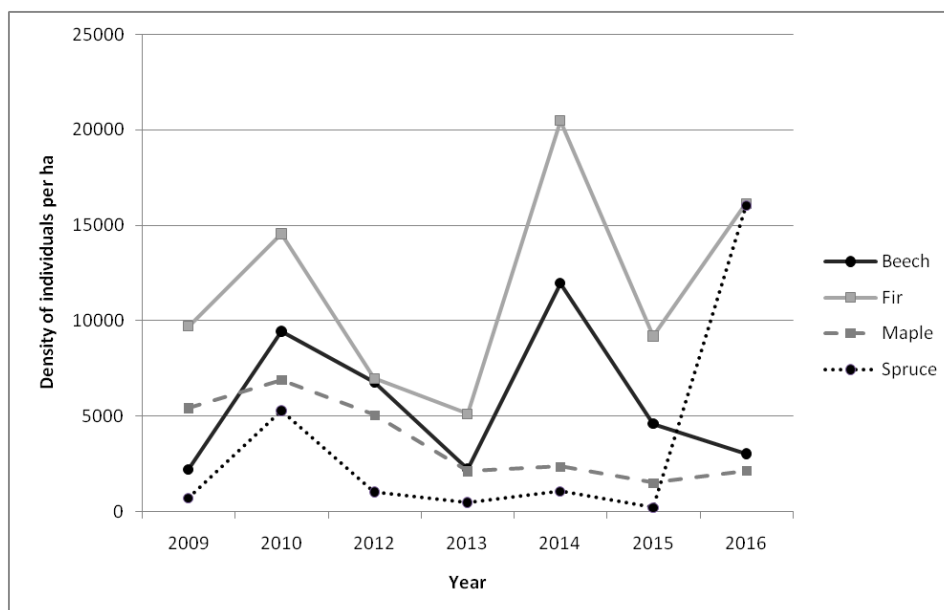


Fig. 4. Dynamics of seedlings in the 1. height class

#### 4.1.2. Inventory plots– saplings ( $\geq 1.3$ m in height, $< 10$ cm in diameter)

Saplings were dominated by beech in both 2009 and 2016 (almost 100 %). The density of beech saplings was somewhat stable over time, accounting for more than 500 individuals per hectare in total with less than 200 individuals per hectare in each diameter class. Relative density ratios seemed to be quite stable over time, i.e. 1:1:1 among the diameter classes. Moreover, slight density shifts were documented. It appears that certain proportion of individuals left the 2. diameter class, thereby increasing density of the 3. diameter class. However, neither the transition of seedlings to saplings nor the transition of saplings to the higher diameter classes could not be detected, since the method cannot provide such detailed information.

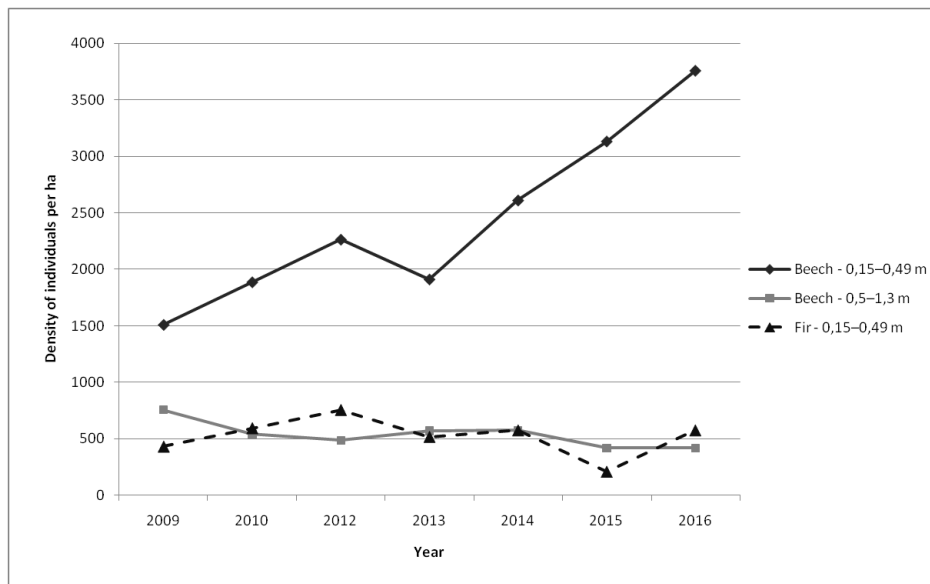


Fig. 5. Dynamics of fir seedlings in the 2. height class and beech seedlings in the 2. and 3. height class. Fir seedlings in the 3. height class are not displayed since very low density was recorded.

#### 4.1.3. Transect plots- seedlings ( $< 1.3$ m in height)

The development of natural regeneration on transect was described only for seedlings since there was just a small number of individuals above 1.3 m in height. To assess the development of seedlings the data from 2013 (the first year of transect measurement) and 2016 were contrasted. Fir was the most abundant species in 2013 (65.3 %), followed by beech (28.7 %), spruce (4.7 %) and maple (1.3 %). In 2016, fir proportion dropped to 59.8 % and beech proportion to 27.8 %, although in absolute terms increased 1.14- and 1.21-fold respectively. Conversely, spruce and maple proportion went up to 9.3 % (2.45-fold) and 3.2 % (3.01-fold) respectively. Total density of all seedlings also increased. However, none of the changes were significant

(spruce and maple densities were not tested because there was just a small number of individuals).

As for total density, the 1. height class (< 0.15 m) accounted for about 47.5 % in 2009 and rose to 56 % in 2016 ( $p=0.003$ ). Increase of density occurred also in the 2. height class (0.15–0.49 m), however, it relatively decreased from 45.2 to 37 %. The 3. height class did not relatively changed, only a slight absolute increase was documented. Relative density ratios remained more or less the same among the height classes, i. e. the 1. height class 50 %, 2. height class 40 % and 3. height class 10 %. Moreover, total density of all the species did not changed significantly from 2013 to 2016.

*Tab. 3. Species densities and proportions in 2013 and 2016 on inventory plots. % denotes the proportion of species in the respective height class except the species category All where it stands for relative density ratios among the height classes (in the grey line). Densities originally related to 1 m<sup>2</sup> were recalculated to be on the same scale (1 hectare) as inventory densities.*

Year	Species	Density per ha							
		< 0,15 m	%	0,15–0,49 m	%	0,5–1,3 m	%	All	%
2013	Fir	36441	91,2	17781	46,8	659	10,7	54881	65,3
	Beech	1317	3,3	17342	45,7	5488	89,3	24148	28,7
	Spruce	1537	3,8	2415	6,4	0	0	3951	4,7
	Maple	659	1,6	439	1,2	0	0	1098	1,3
	All	39953	47,5	37978	45,2	6147	7,3	84078	100
2016	Fir	48100	82,3	13440	34,8	943	12,9	62483	59,8
	Beech	2829	4,8	20277	52,4	5895	80,7	29001	27,8
	Spruce	6130	10,5	3301	8,5	236	3,2	9667	9,3
	Maple	1415	2,4	1650	4,3	236	3,2	3301	3,2
	All	58475	56,0	38669	37,0	7309	7,0	104453	100

In the 1. height class fir was still the most abundant species (91.2 %) with documented increase ( $p=0.009$ ) followed by spruce (10.5 %) which density increased 4-fold. Beech became dominant in the 2. height class (52.4 %) and prevailed also in the 3. height class (80.7 %). There was decrease in the density of fir in the 2. height class from 46.8 to 34.8 %, though not significant. Proportion of fir accounted for 12.9 % in the 3. height class. Similarly to inventory, spruce and maple densities were not tested because there was just a small number of individuals.

Overall, the results from transect revealed marked differences when compared to inventory findings. Species composition on transect and inventory plots is contrasted in Fig. 6.

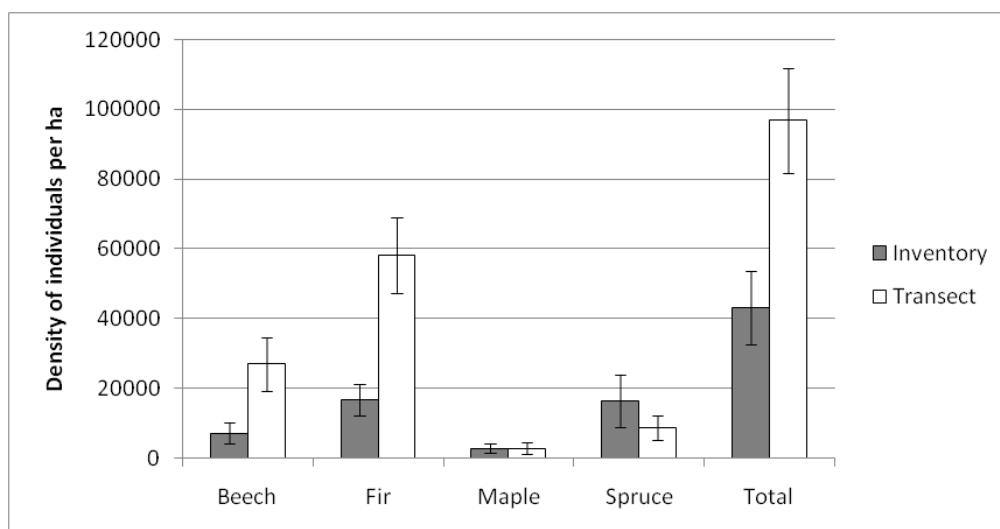


Fig. 6. Species composition in 2016. Inventory and transect results contrasted.

## 4.2. Browsing of natural regeneration

### 4.2.1. Inventory plots

Following findings are related only to seedlings since in this study saplings were not considered relevant when evaluating the effect of browsing on natural regeneration.

Proportion of all browsed individuals decreased over the years from 18.6 % in 2014 to 10.7 % in 2016 probably as a result of immense increase of fir and spruce individuals in the 1. height class, nevertheless, proportion of total browsed individuals approximately coincided over the years (about 4000 individuals every year). Considering only overall browsing rate, the most browsed species differed over time. In 2014, it was beech (33.8 %), in 2015 spruce (54.5 %) and in 2016 maple (33.9 %) (Tab.4.).

It can be concluded that less individuals in the height class higher the browsing rate. Interestingly browsing rates were consistent over the years in the 1. and 2. height class, i.e. about 5 and 50 % respectively. Browsing rate was generally high in the 3. height class with a rapid fall in 2016 (Tab.4.).

The most browsed species in the 1.height class was maple in all the years followed by fir which browsing rate ranged from 5 to 7 % over years. In contrast, browsing rate in the 2. height class was dramatically higher in all the years, exceeding 70 % in fir and spruce. Browsing rate of maple was also very high (always more than 50 %), though not that balanced over the years as in other species. Browsing rate of beech ranged from 30–40 %. Beech and fir were heavily browsed in the 3. height class over the years. For instance, in 2015 all the individuals were browsed (Tab.4.).

Tab. 4. Inventory density of unbrowsed and browsed individuals. % denotes the proportion of browsed individuals in the respective species category except All species category where it stands for relative browsing ratios among the height classes (in the grey line).

Year	Species	Density per ha											
		< 0,15 m	Browsed	%	0,15–0,49 m	Browsed	%	0,5–1,3 m	Browsed	%	All	Browsed	%
2014	Fir	20462	1148	5,6	574	470	81,9	0	0	0	10130	1618	16,0
	Beech	11954	104	0,9	2610	835	32,0	754	574	76,1	4472	1513	33,8
	Spruce	1044	52	5,0	209	157	75,1	52	0	0	970	209	21,5
	Maple	2349	209	8,9	626	418	66,8	0	0	0	5765	627	10,9
	All	35809	1513	4,2	4019	1880	46,8	806	574	71,2	21337	3967	18,6
2015	Fir	9187	470	5,1	209	157	75,1	104	104	100	9500	731	7,7
	Beech	4594	104	2,3	3132	1148	36,7	418	418	100	8143	1670	20,5
	Spruce	209	0	0,0	365	313	85,8	0	0	0	574	313	54,5
	Maple	1514	261	17,2	731	626	85,6	0	0	0	2245	887	39,5
	All	15504	835	5,4	4437	2244	50,6	522	522	100	20462	3601	17,6
2016	Fir	16129	1148	7,1	574	418	72,8	52	52	100	16756	1618	9,7
	Beech	3028	157	5,2	3758	1409	37,5	418	157	37,6	7203	1723	23,9
	Spruce	16025	104	0,6	261	209	80,1	52	0	0,0	16338	313	1,9
	Maple	2140	574	26,8	626	365	58,3	0	0	0,0	2767	939	33,9
	All	37322	1983	5,3	5219	2401	46,0	522	209	40,0	43064	4593	10,7

#### 4.2.2. Transect plots

Following findings are related only to seedlings since in this study saplings were not considered relevant when evaluating the effect of browsing on natural regeneration.

There were marked differences between the results from IPs and transect likewise between total densities of individuals. Transect total density of individuals ranged from about 80 to 100 thousands whereas inventory total density of individuals were 2-5 times smaller depending on the year compared (Fig. 6.). Similarly, marked differences were documented also in terms of browsing rate. Transect density of browsed individuals (about 30–60 thousand individuals per ha) was approximately 7,5–15 times higher than inventory density of browsed individuals (Tab 4 and 5.).

Proportion of all browsed individuals significantly increased over the years from 35.8 % in 2013 to 59.8 % in 2016 ( $p=0.001$ ). Taking into account only the overall browsing rate, the most browsed species differed over the years. In 2013 it is fir (45.6 %), in 2014 beech (66.2 %), in 2015 spruce (76 %) and in 2016 maple (64.3 %). These results are consistent with inventory findings. Except 2013, browsing rate exceeded 50 % in fir and beech, 45 % in spruce and 35 % in maple. Browsing rate of fir grew over the years with a significant difference between 2013 and 2016 ( $p=0.041$ ) and so did browsing rate of beech ( $p=0.001$ ). However, in case of beech there was not such a growing tendency of browsing rate over time. Notwithstanding species-specific differences, browsing rate of fir, spruce and maple rose over years.

Tab. 5. Transect density of unbrowsed and browsed individuals. % denotes the proportion of browsed individuals in the respective species category except All species category where it stands for relative browsing ratios among the height classes (in the grey line).

Year	Species	Density per ha											
		<0,15 m	Browsed	%	0,15–0,49 m	Browsed	%	0,5–1,3 m	Browsed	%	All	Browsed	%
2013	Fir	36441	12513	34,3	17781	12293	69,1	659	220	33,4	54881	25026	45,6
	Beech	1317	0	0,0	17342	2415	13,9	5488	878	16,0	24148	3293	13,6
	Spruce	1537	220	14,3	2415	1317	54,5	0	0	0,0	3951	1537	38,9
	Maple	659	0	0,0	439	220	50,1	0	0	0,0	1098	220	20,0
	All	39953	12732	31,9	37978	16245	42,8	6147	1098	17,9	84078	30075	35,8
2014	Fir	47417	22172	46,8	14708	12952	88,1	659	220	33,4	62784	35343	56,3
	Beech	4390	1098	25,0	20416	15367	75,3	5049	3293	65,2	29855	19757	66,2
	Spruce	2634	878	33,3	3073	2195	71,4	220	0	0,0	5927	3073	51,8
	Maple	2195	0	0,0	1756	1537	87,5	0	0	0,0	3951	1537	38,9
	All	56637	24148	42,6	39953	32050	80,2	5927	3512	59,3	102517	59710	58,2
2015	Fir	38417	18660	48,6	17342	14269	82,3	659	220	33,4	56418	33148	58,8
	Beech	3293	439	13,3	20416	15367	75,3	4390	3732	85,0	28099	19538	69,5
	Spruce	1098	659	60,0	4171	3293	78,9	220	220	100,0	5488	4171	76,0
	Maple	1537	0	0,0	1976	1976	100,0	220	220	100,0	3732	2195	58,8
	All	44344	19757	44,6	43905	34904	79,5	5488	4390	80,0	93737	59052	63,0
2016	Fir	48100	25936	53,9	13440	12968	96,5	943	707	75,0	62483	39612	63,4
	Beech	2829	236	8,3	20277	11789	58,1	5895	4244	72,0	29001	16269	56,1
	Spruce	6130	1179	19,2	3301	3065	92,9	236	236	100,0	9667	4480	46,3
	Maple	1415	236	16,7	1650	1650	100,0	236	236	100,0	3301	2122	64,3
	All	58475	27587	47,2	38669	29473	76,2	7309	5423	74,2	104453	62483	59,8

Interestingly, browsing rates were very consistent over the years in the 1. and 2. height class except 2013, i.e. about 45 % and 80 % respectively. Except 2013, browsing rate was high in the 3. height class, exceeding 60 %.

The most browsed species in the 1. height class was fir and spruce during the whole period. Focusing on fir, browsing rate was steadily and significantly increasing from 34.3 % in 2013 to 53.9 % in 2016 ( $p=0.001$ ). Similar trend was obvious also in the 2. and 3. height class, however not significant. Browsing rate of beech also significantly grew in the 2. and 3. height class ( $p=0.001$ ) as well as in the 1. height class (not tested, no browsed individuals in 2013). Browsing rate was high in maple and spruce in the 2. height class ranging from 70 to 90 % in spruce and 85 to 100 % in maple in the last three years. Spruce and maple were less abundant in the 1. height class and usually also less browsed.

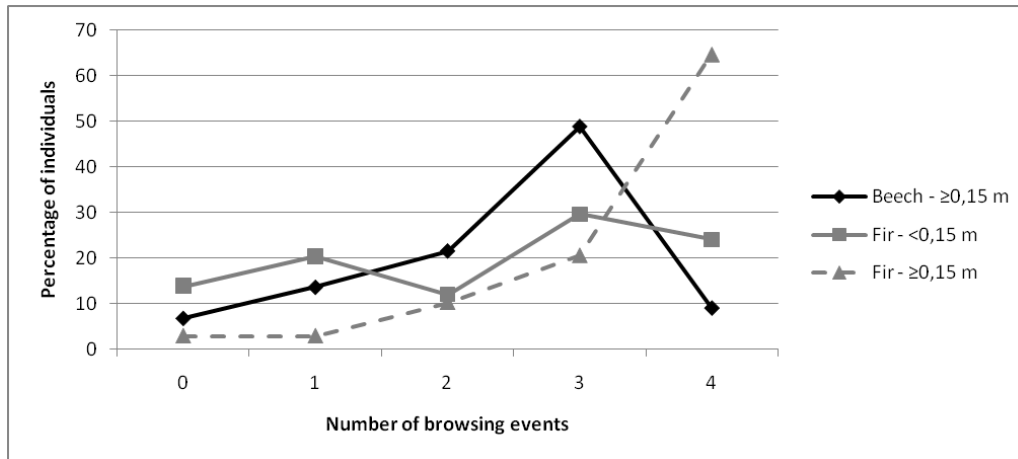


Fig. 7. The percentage of fir and beech individuals with 0–4 browsing events. Only individuals alive for the whole study period were selected (265 individuals) and sorted into height classes. 2. and 3. height class were pooled. There were no beech individuals below 0.15 m in height alive for the whole study period.

In addition, it was found that total number of years in which individuals were documented was significantly correlated with how many time individuals were browsed ( $r^2=0.722$ ;  $p < 0.001$ ). Basically, if the individuals stayed alive for more years browsing was very often repeated. Furthermore, when considering beech and fir individuals for the whole four-year study period, beech was significantly associated with three ( $p < 0.001$ ) and fir with four browsing events ( $p < 0.001$ ). More than 65 % of fir and 58 % of beech individuals demonstrated three browsing events at least and only about 20 % of both fir and beech demonstrated either one or no browsing event at all (Fig. 7.). Differences on the level of height classes were not that pronounced (Fig. 7.) and only a weak positive correlation was shown ( $r^2=0.234$ ,  $p < 0.0001$ ).

Tab. 6. Results of the GLMM analysis for the density of browsed fir and beech individuals. Pooled 2. and 3. height class ( $\geq 0.15$  m) was used as a factor level for comparison. 54 transect plots were considered as a random effect. SE denotes the standard error. Significant effects are coloured grey. Akaike Information Criterion was 358.400 and 215.148 for the fir and beech model respectively.

Fixed effect	Fir			Beech		
	Coefficient	SE	p	Coefficient	SE	p
Intercept	-0,88	0,28	0,002	-1,535	0,5950	0,011
Height class ( $\geq 0,15$ m)	0,39	0,15	0,009	0,703	0,3268	0,034
Conspecific	0,36	0,16	0,025	0,224	0,3161	0,480
Heterospecific	0,02	0,09	0,825	0,166	0,1385	0,235
Total	0,75	0,15	0,000	0,947	0,2316	0,000
Light	0,02	1,88	0,993	-0,522	2,6568	0,845
Height variation	0,00	0,00	0,519	3,286E-05	0,0030	0,991



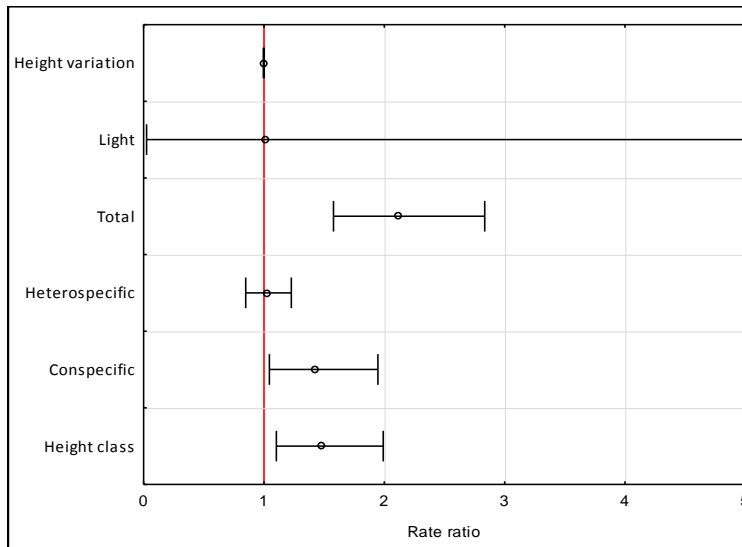


Fig. 8. Results of the GLMM analysis for the density of browsed fir individuals. Rate ratio denotes the exponentiated Poisson regression coefficients. Bars crossing the red line are significant.

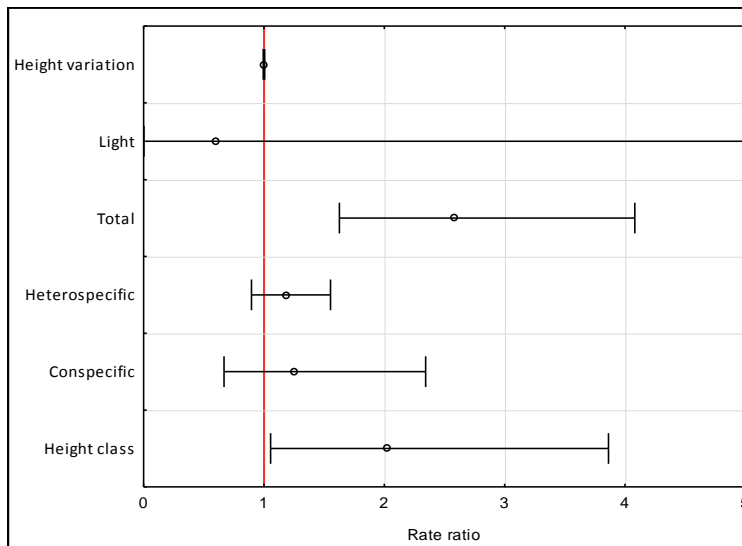


Fig. 9. Results of the GLMM analysis for the density of browsed beech individuals. Rate ratio denotes the exponentiated Poisson regression coefficients. Bars crossing the red line are significant.

Tab. 6. shows the summary of the GLMM analysis for the density of browsed fir and beech individuals. From all the fixed effects, height class, density of conspecific individuals and total number of individuals were significant. The results indicated that there was a positive effect of height class, density of conspecific individuals and total density of individuals on the density of browsed fir individuals. In case of beech height class and total density of individuals were found to have a positive effect on the density of browsed individuals. Fig. 8 and 9. show the magnitude of the effects contributing to the models.

Browsing of both terminal and lateral shoots was the most common, amounting to 73 % on average. Browsing of lateral and terminal shoots separately was not that common since it accounted for 14 and 13 % on average, respectively. No significant differences were found on the species level.

### 4.3. Mortality of natural regeneration

Mortality of individuals varied over time and species. The last documented height was generally higher in beech (the mean 22.2 cm) than in fir individuals (the mean 8.8 cm) ( $p < 0.001$ ). The differences are more clearly shown in Tab. 7. Absolute majority of mortality took place in the 1. height class (almost 80 %). However, it was 86.3 % of total mortality of fir and only 48 % of total mortality of beech. Moreover, in the 2. height class fir and beech mortality accounted for 12.8 and 48 % respectively. The 3. height class consisted only of few individuals. Thus beech mortality was more evenly distributed along the height classes than fir mortality.

*Tab. 7. Fir and beech mortality along the height classes. % stands for a percentage of total number of fir and beech individuals in the respective height class.*

Height class	Species	Total	%
< 0,15 m	Fir	101	86,3
	Beech	12	48,0
	All	113	79,6
0,15–0,49 m	Fir	15	12,8
	Beech	11	44,0
	All	26	18,3
0,5–1,3 m	Fir	1	0,9
	Beech	2	8,0
	All	3	2,1
All	Fir	117	100
	Beech	25	100
	All	142	100

There were also differences in mortality over the years, i.e. individuals of different heights were culled over time. Mortality in 2013 differed significantly from the one in 2014 ( $p = 0.001$ ) and 2015 ( $p = 0.005$ ) in terms of height of individuals meaning mortality of higher individuals in 2013. The mean difference of mortality density distributions was not significant over years ( $p = 0.066$ ), i.e. the numbers of culled individuals were consistent over the years. Tab. 1 shows that they ranged from 40 to 50 individuals per year. Fir mortality was also consistent over years accounting for about 15 % of total number of individuals every year. Beech mortality dropped from 8 % in 2013 and 2014 to 4 % in 2015. Total seedling mortality did not fall

below 10 % (Tab. 8). Considering only the initial sample of individuals from 2013, 75.7 % of all the individuals survived until 2016, 70.8 % and 84.4 % of fir and beech respectively (Tab. 2). Mortality of beech initial sample decreased from 8 % in 2013 to 2.1 % in 2015. Mortality of fir initial sample was variable over the years ranging from 16 % in 2013 to 10.6 % in 2015.

*Tab. 8. Mortality of fir and beech individuals in the period 2013–2016. % denotes annual mortality. Mortality could not be documented in 2016. Actual recorded numbers are shown.*

Species	2013			2014			2015			2016		
	Alive	Died	%	Alive	Died	%	Alive	Died	%	Alive	Died	%
Fir	250	40	16	286	39	14	257	38	15	265	-	-
Beech	110	9	8	136	11	8	128	5	4	123	-	-
All	360	49	14	422	50	12	385	43	11	388	-	-

From all the fixed effects (Tab. 9.) had only height class a significant positive effect on mortality of individuals (Fig. 10.). Neighbourhood of the focal individual (density of conspecific and heterospecific neighbours), species and browsing influenced the quality of the model but were not significant. To ascertain the cause of mortality in the different life stages (height classes in this study) and different species, a set of GLMMs analysis was run, though none of the models revealed significant effect. The results of these models are not shown.

*Tab. 9 Results of the GLMM analysis for mortality of fir and beech individuals. In categorical variables Species, Browsing and Height class, beech, browsed and pooled 2. and 3. height class ( $\geq 0.15$  m) were used as factor levels for comparison. 54 transect plots were considered as a random effect. SE denotes the standard error. Significant effects are coloured grey. Akaike Information Criterion was 1618.605.*

Fixed effect	Coefficient	SE	p
Intercept	0,21	0,66	0,748
Species (beech)	0,10	0,55	0,850
Browsing (browsed)	-0,48	0,39	0,213
Height class ( $\geq 0,15$ m)	-1,10	0,38	0,004
Conspecific	-0,58	0,44	0,192
Browsed consp	0,35	0,41	0,394
Heterospecific	-0,05	0,35	0,888
Total	-5,63	3,22	0,081

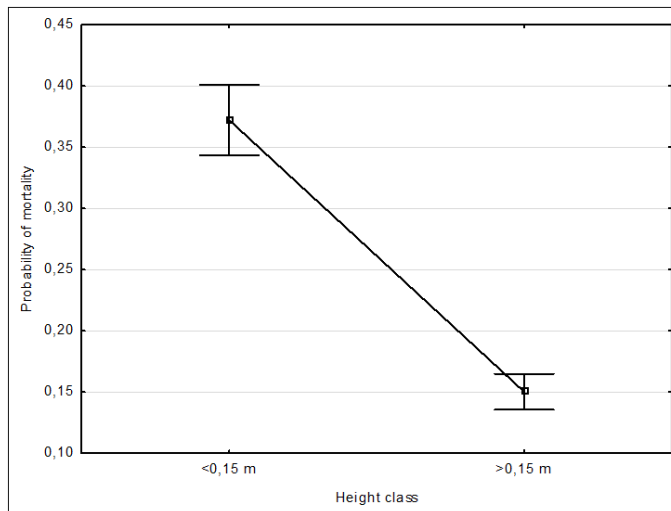


Fig. 10. Predicted probability of mortality of fir and beech individuals for the 1. height class (< 0.15 m) and the pooled 2. and 3. height class ( $\geq 0.15$  m).

#### 4.4. Demography of natural regeneration

The relative contribution of each process studied (browsing, establishment and mortality) was year- and species-specific (Fig. 11.). Except 2013, browsed individuals accounted for more than 50 % of total density of individuals (54 % on average). Establishment was the most variable part of demographical processes over the years and accounted for 10 % of total density of individuals on average. It differed significantly between 2013 and 2016 ( $p=0,025$ ). Mortality was more balanced reaching its maximum in 2013 (13 %) and accounted for 11 % on average. Total density of individuals fluctuated over time depending on a variation of establishment and mortality.

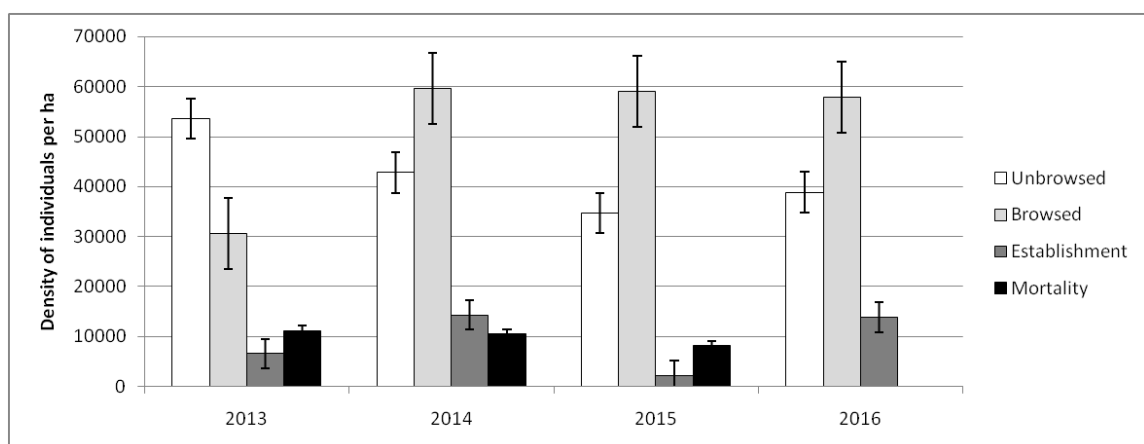


Fig. 11. Total number of unbrowsed and browsed individuals, establishment and mortality per hectare. Species are not contrasted. Mortality could not be documented in 2016.

On the species level the importance of browsing is still preserved both in fir and beech (mostly 50 % of total individuals browsed). Interestingly, differences begun to be more pronounced in the relative importance of establishment. Establishment was still highly variable on a species level but fir establishment was more balanced and accounted yearly for more than 10 % of total density of individuals whereas beech establishment peaked at 9 % in 2014 but did not exceed 5 % in the other years. There was no beech establishment in 2013. Furthermore, mortality of beech was twice as small as of fir, i.e. 6 and 12 % respectively (Tab. 10.).

*Tab. 10. Overview of fir and beech total density of individuals, browsed number of individuals, establishment and mortality per hectare in the period 2013–2016. Mortality could not be documented in 2016.*

Species	Year	Total	Browsed	%	Establishment	%	Mortality	%
Fir	2013	54881	25465	46	6586	12	8781	16
	2014	62784	35343	56	10537	17	8561	14
	2015	56418	33148	59	1537	3	8342	15
	2016	58174	36880	63	10098	17	-	-
Mean		58064	32709	56	7189	12	8561	15
Beech	2013	24148	3293	14	0	0	1976	8
	2014	29855	19757	66	2634	9	2415	8
	2015	28099	19538	70	439	2	1098	4
	2016	27001	14928	55	1098	4	-	-
Mean		27276	14379	51	1043	4	1829	7

## 5. Discussion

### 5.1. The development of natural regeneration

There were not any major changes in the species composition of natural regeneration as well as in the species composition along the height classes in the NNR Salajka over the period 2009–2016. It was found that fir individuals comprised the majority of seedlings up to 0,15 m in height. However, seedlings up to 0,5 m in height were made up of both fir and beech, though beech was more abundant. Seedlings the height of 0,5 m were almost exclusively dominated by beech and so were saplings. Over the 7 years of this study, both fir and beech seems to have preserved their role in natural regeneration, since the density distribution of both was stable along the height classes. Though, there was an increase of beech individuals in the 2. and 3. height class and a slight increase of fir individuals in the 3. height class on TPs. Similar situation concerning species dominance and height structure of natural regeneration has been observed elsewhere (e.g. Szwagrzyk, Szewczyk 2008; Diaci et al. 2010; Saniga et al. 2011), suggesting that the expansion of beech is also taking place in the NNR Salajka. Despite the natural regeneration of fir appears outcompeted by beech at present, it might be only a temporally limited process since the density of small fir individuals is high. Thereby, outgrowing beech could release a new niche favourable for other species to capture and fir could take an advantage of established seedling bank. Although seedling bank was found to play an important part in the forest dynamics (Nagel et al. 2010), it is hard to predict the species composition of mature trees on the basis of the species composition of individuals in the initial life stages without long-term observations, especially after rich seed masting and consequent massive wave of emerging germinants (Szwagrzyk et al. 2001). But when a new gap is formed the chances of filling the gap are higher for species with already established seedling or sapling bank (Nagel et al. 2010).

Based on the results, seedlings up to 0,15 m were the most variable part of natural regeneration in terms of frequent temporal fluctuations in density, regardless of species. Major falls in the densities of individuals were documented in 2013 and 2015. Although the density of individuals was low also in 2009, it is not considered as decrease in density since there is no context of previous measurements. Nevertheless, the year 2013 and 2015 had the extreme weather conditions in common, since the

density of seedlings dropped to 50 and 45 % of the previous years' densities in 2013 and 2015 respectively. However, the decrease was not that dramatic on TPs as on IPs probably because of different sampling approaches. Whereas TPs encompass predominantly nutrient-rich fir-beech forest type<sup>2</sup>, IPs cover five other forest types (Adam et al. 2003), suggesting also the influence of wider variety of edaphic factors, thereby the influence of different conditions for regeneration and mortality processes (Paluch 2005), however, rich fir-beech forest type is the most common in the NNR Salajka (Adam et al. 2003). In 2013, precipitation made up only 25 and 59 % of the long-term normal and temperature also deviated by positive 2.4 and 1.9° C in July and August respectively. In 2015, the situation was similar, though lasting from June to August with precipitation of less than 50 % of the long-term normal and temperature higher by 3,6 and 5° C in July and August respectively (CHMU, Historical data)<sup>3</sup>. However, there was a dramatic decrease in the density of individuals already in 2012, thus the effect of extreme weather conditions might have been intensified even more in 2013. Moreover, Sack (2004) experimentally verified that drought stress can drive species survival to a considerable degree. In accordance with the findings of Mazur (1989) and Szwagrzyk et al. (2001), seedlings densities were confirmed to be strongly fluctuating over time. Notwithstanding temporal variability at a fine scale, sites with high densities of beech individuals were found relatively temporarily constant (Szewczyk, Szwagrzyk 2010).

From a different perspective, there were years (2010, 2014 and 2016) of marked rises in the densities of individuals up to 0,15 m in height. These results from IPs and TPs coincide, although they are more pronounced from IPs (note: measurements started in 2013 on TPs). The establishment on TPs was highest in 2014 both in fir (about 10000 individuals per ha) and beech (only about 2600 individuals per ha), but all the years in the period 2013–2016 demonstrated new seedlings emerging (except 2013 in beech). While fir showed more abundant establishment occurring basically every year, beech establishment seemed to be relatively frequent but remained quite low in numbers. As shown by Szewczyk, Szwagrzyk (2010), new establishment of beech was very rare in the period 1994–2006 and emerged mainly in a single event, following

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<sup>2</sup> Forest type is utilised in the Czech Republic as a forest typology unit differentiating among various forest sites. There are six forest types in the NNR Salajka: slope fir-beech with firn undergrowth (2,63 ha), rich fir-beech with woodruff undergrowth (9,63 ha), rich fir-beech with maple admixture (0,91 ha), enriched fir-beech with butterbur undergrowth (3 ha), ravine fir-beech (1,96 ha) and waterlogged fir-beech forest type (0,6 ha).

<sup>3</sup> The meteorological historical cumulative data for the Moravsko-Slezský kraj region were used. The date access available online ([www.chmi.cz](http://www.chmi.cz)).

probably a mast year. They also found a significant discrepancy between huge seed production of beech trees during a mast year and consequent low mean germination rate (2,83 %). Thus the beech advantage of irregular but massive seed masting over the other tree species could not be manifested (Szwagrzyk et al. 2015). Conversely, fir produced less seeds but more evenly over the years. As a consequence the number of germinating individuals was also low and relatively constant over time (Szwagrzyk et al. 2015). In this study similar findings were revealed only in case of fir suggesting relatively low-medium frequent establishment and thus regular seed production of mature trees. These results are in accord with Paluch (2011). He found that the dominant mature fir individuals happen to produce seeds very frequently regardless of other fir individuals capable of fructification. Furthermore, during the years of low seed production a prevalent proportion of seeds was classified as damaged (either truly damaged or empty), thus indirectly suggesting potentially frequent, though possibly limited establishment of fir (Paluch 2011). In contrast, Nopp-Mayer et al. (2012) made a case for the importance of beech and fir sporadic masting shortly after mast years due to higher seed survival as a result of moderate seed predation in intermast periods. Interestingly, they also found higher seed predation and thus lower seed survival in an old-growth forest than in a managed forest probably as a consequence of higher complexity of predator guilds related to old-growth forests. Furthermore, this study shows that there was very low but relatively frequent establishment of beech over a span of three years with a peak in 2014.

As far as maple and spruce are concerned, the fate of both species in the NNR Salajka is hard to predict on the basis of available data. Nevertheless, the fact is that proportion of maple went up on TPs in the 1. and 2. height class and seems to have secured its position as an admixed species. An argument for the expansion of maple would be unfounded in the NNR Salajka and a comparison to the sites where the actual maple expansion was reported is limited due to different site conditions (Dobrowolska, Veblen 2008) or probably site-specific underlying causes (Janík et al. 2016). Similarly, there was a massive boom in the density of spruce individuals in the 1. height class to such an extent that had never been documented over the period 2009–2016 in the NNR Salajka. The role of a new wave of spruce establishment one year following seed masting cannot be overestimated, since one-year old seedlings experience considerable mortality (e.g. Mazur 1989; Szwagrzyk et al. 2001).



The results demonstrated some differences from IPs and TPs even though they never ran contrary and coincided for most of time. The main difference was in the magnitude of provided information. For instance, the species composition varied on TPs and IPs (Fig. 7.) as well as the densities of individuals and the changes of the densities over time (Tab. 2 and 3.). As briefly mentioned above, the rationale behind the adopted inventory and transect sampling approaches were not the same. Whereas IPs were placed regularly around the whole protected area regardless of natural regeneration occurrence, TPs were determined by stratification of fir individuals to fir density classes and height intervals (Tab. 1). Thus, the occurrence of natural regeneration on TPs was virtually guaranteed by this sampling approach, which was also confirmed in 2014 after the identification of almost all the plots (in few cases IPs must have been replaced since they could not be identified). Moreover, TPs do not encompass such a gradient of various forest sites as IPs and as a consequence potential variability of ecological processes involved is expected to be more limited. The elementary assumption of the TPs selection was that the continuity of fir natural regeneration along fir density classes and height intervals would assure also the variation of ongoing ecological processes (e.g. various context-dependent browsing and mortality, light availability). The spatial constraint of transect also contributed to the differences between the inventory and transect results, however, the most important transect criterion for a representative sample of fir natural regeneration was fulfilled. To summarise both methods, the permanent inventory plots were supposed to provide a general overview of the natural regeneration development in the NNR Salajka and transect aimed to draw more attention to the processes on the level of cohorts and individuals of species. Even though the scaling of results is very limited using both sampling approaches, it enables to draw analogies at least.

## **5.2. Browsing of natural regeneration**

Browsing of natural regeneration significantly increased from 35,8 % in 2016 to 59,8 % in 2013, corresponding also to two-fold increase in absolute terms (from 30 thousand to 60 thousand of individuals per ha). However, this was registered only on TPs. Since the browsing impact in 2013 was evenly lower across the species, there must have been another factor involved beside the ungulate game preferences. Historical climatic data showed that the winter 2012/2013 was characterized by above-normal precipitation and temperature that was very close to the normal (CHMU,

Historical data). Even though snow cover was not recorded, the results suggest that the snow cover in 2012/2013 was deep enough to prevent some natural regeneration from browsing. The similar findings were observed by Homolka, Heroldová (2003), concluding that deer overwintered at lower elevations during the winter with a deep snow cover, thus preventing natural regeneration at higher elevations from browsing. This assumption accords also with the findings of Visscher et al. (2006) who documented the decline in browse availability as snow depth increased in connection to forest type. They found that mixed and deciduous forest communities (possibly comparable to the NNR Salajka) provided relatively more available browse than conifer forest communities regardless of snow depth. From a different perspective, Häsler, Seen (2012) observed the highest ungulate consumption of fir in winter, ascribing it to the site-specific variation in diet composition. Thus silver fir was considered to be a shortage food species in a spruce-fir-beech forest because both red and roe deer reduced its consumption towards summer when other sources of food became available. Given that the browsing of fir is generally predominant in winter, more negative effect on height growth can be expected comparing to the effect of browsing during the vegetation period (Kupferschmid, Bugmann 2013).

Despite the differences between TPs and IPs browsing was found to be height-dependent as reported by many other authors (e.g. Ammer 1996; Klopčič et al. 2010). Browsing of natural regeneration rose over the years, though only fir browsing increased across all the height classes. Beech browsing increased in the 2. and 3. height class. However, it is difficult to assess the browsing impact on species because browsing was heavy in all the species (Tab. 2) and it varied over the years. It can be inferred that fir and beech were heavily browsed in the 2. and 3. height class approximately to a similar extent, although fir was more browsed in the 2. height class and more beech individuals were spared browsing. The inventory results follow the same pattern as the transect results, however, the magnitude of browsing is different. Beech and fir were the most browsed species in terms of total numbers, though browsing of beech was marginal in the 1. height class and also the 2. height class was relatively less browsed in case of fir. Notwithstanding these differences, beech is the only species that increased in density and remained dominant above the height of 0,15 m during the study period. Thus to answer the question about the influence of browsing on fir and beech and about the temporal and in case of this study also sampling-dependent variation, others aspects need to be taken into account. Skarpe, Hester (2008)

pointed out that plants have evolved various resistance strategies (tolerance, avoidance) to mitigate an adverse impact of herbivory. Apart from morphological resistance and nutrient storage allocation, which is crucial especially when considering different strategies of broadleaves and conifers (stem and root storage in broadleaves and foliage storage in conifers), browsing can induce chemical changes in the form of secondary metabolites (phenols, terpenes), which can reduce digestibility of browse in ungulates (Gill 1992). Even though fir have evolved chemical strategies (low-digestible tannins) how to cope with browsing, Pellisier (2013) did not find efficient repulsive response of fir to browsing, indicating that fir is not able to escape from ungulates consumption through chemical strategies. Ohse et al. (2016) simulated the roe deer browsing and found that saliva can lead to changes in phenolic acids in leaves of beech and in hydrosable tannins and flavonols in maple leaves, thereby confirming the species-specific response to ungulate herbivory. However, these chemical defences cannot work only by themselves since beech was found resistant to browsing even though its growth was significantly affected (Harmer 2001). Vandenberghe et al. (2008) observed that even though more biomass was removed by browsing in fir and spruce than beech and maple, compensatory growth after browsing was not higher in broadleaves. Nevertheless, they simulated browsing as a one-clipping event, thus the results might be far from non-controlled natural conditions. For instance, repeated browsing was a common practice according to the results of this study. More than 75 % of fir and beech individuals were browsed at least twice during the 4 years of study and were still alive at the end of the study. Thus fir seems to incline more towards browsing tolerance strategies, since even individuals browsed every year accounted for almost one third of the initial density in 2013. Fir resistance was confirmed also by Vandenberghe et al. (2008) and Pellisier (2012), however, repeated browsing was not considered in their studies. According to the results of this study, the number of browsing events was positively correlated ( $r^2=0.722$ ;  $p < 0.001$ ) with the number of years for which individuals were documented (not necessarily standing for the number of years alive). Basically, the older the individual the more often it appeared to be browsed. Moreover, only weak positive correlation was shown between the number of browsing events and the height of individuals ( $r^2=0.234$ ;  $p < 0.001$ ). Kupferschmid et al. (2013) proved that the occurrence of browsing events was positively correlated with age, height and diameter of individuals. The correlation was probably stronger in their study because the lateral shoot browsing was omitted. In this

study, the lateral and terminal shoot browsing accounted for 14 and 13 % on average and it was not finally considered separately from browsing of both terminal and lateral shoots. In addition, Kupferschmid et al. (2013) noticed that well-growing fir individuals were often more browsed than suppressed ones. Repeatedly browsed individuals had higher concentrations of manganese and roe deer identified them probably by certain morphological traits. In general, the needles of browsed terminal shoots of fir were larger and more selected by roe deer (Häsler, Senn 2012).

Furthermore, spruce and maple were heavily browsed over the years. Above the height of 0.15 m, maple was the most browsed species on TPs suggesting that maple is one of the most palatable species in the NNR Salajka as confirmed also by Ammer (1996). In addition, maple is an admixed species in the NNR Salajka and its heavy browsing coincide with the assumption that rare species are browsed more than the dominant ones (Čermák et al. 2009). Despite this handicap, maple was found very browsing-tolerant when growing under shaded conditions (Vandenberghe et al. 2008) and also more browsing-tolerant than fir (Ammer 1996). Nevertheless, the alternative findings from the clipping experiment were also shown by Harmer (2001) who demonstrated the lowest tolerance of maple to browsing from all the species tested (pedunculate oak, common ash and beech) regardless of shaded or full-light conditions. However, these studies used different methods and life stages of maple. Whereas Harmer (2001) used seedlings of maple with the height of 30–40 cm, Vandenberghe et al. (2008) tested very small individuals below 15 cm in height. Thus, their findings might not be exactly contradictory but more likely address different life stages of maple which can vary in life-history strategies. Comparing the growth of natural regeneration of maple, beech and fir in fenced and non-fenced areas, maple and fir were significantly hindered by browsing in terms of establishment to taller height classes, even though the densities of individuals did not differ in the study of Klopčič, Boncina (2012). Similarly to the results of this study, Klopčič, Boncina (2012) found that browsing limited the height growth and occurrence of maple and fir to 50 and 20 cm respectively, whereas beech did not exhibit any growth and occurrence differences between fenced and non-fenced areas, supporting higher browsing tolerance of beech. In this study, no maple higher than 50 cm was found on IPs and only few individuals were recorded on TPs. Although the development of natural regeneration could not be assessed within enclosures in this study, the dramatic fall in the density of individuals as described by Klopčič, Boncina (2012) between fenced and non-fenced areas, is obvious between

the 1. and 2. height class for all the species except beech. These differences are even more abysmal on IPs. Thus the absence of individuals in the taller height classes might indicate the browsing impact and browsing resistance of species, however, given the assumption that the site and stand conditions are favourable and no other growth limitations intervene. For instance, species could be outcompeted by another no matter how serious the browsing impact was and become absent in the taller height classes. Furthermore, spruce is considered an admixture in the NNR Salajka. Spruce position and role is unique among other species, since it has support from the outside of the reserve in terms of seed masting. To be specific, the forest stands surrounding the NNR Salajka are comprised mainly of mature spruce trees, thereby “polluting” the reserve with non-native seed of spruce. This became most pronounced in 2016 when the whole forest reserve was flooded by a wave of spruce establishment to an extent that had not been recorded during the seven years of study period. Any unambiguous predictions can hardly be made about the future perspective of this new spruce wave of establishment since many factors play a part, notably the factory of high mortality in the early life stages. The fact about spruce natural regeneration in the NNR Salajka is that it was heavily browsed with only few individuals exceeding 0.5 m in height. However, spruce has been found less preferred species (Ammer 1996; Heuze et al. 2005) suggesting its lower palatability and thereby it could be competitively at an advantage. Heuze et al. (2005) showed that the selectivity of fir seedlings by deer can lead to a gradual alternation of species in natural regeneration. Given the assumption of spruce occurrence, spruce was always favoured by fir browsing and similarly to the NNR Salajka, its expansion was facilitated even more when present in the nearby mature stands. Even though the survival of spruce saplings was significantly reduced by a simulated clipping treatment (Vandenberghe et al. 2008) it does not enable to make much conclusions about the development of natural regeneration. However, when exposed to browsing under the site conditions of mountain and subalpine spruce forest, spruce regeneration can become hindered by browsing because the different context of limiting factors is involved (Kupferschmid, Bugmann 2005).

As noted by Hambäck et al. (2014) higher plant density can lead either to increased or decreased herbivory impact (resource concentration and dilution effect). According to the results of a GLMM analysis, density-dependent concentration effect was found in natural regeneration of fir, meaning that higher fir density increased the number of browsed fir individuals. Moreover, the total density of individuals was also

found to have a positive effect on browsing of fir. On the contrary, the density of beech did not reveal to have any influence on browsing of fir. In case of beech only the total density of individuals had a positive effect on browsing. From an opposite perspective of ungulate game density-dependence, Klopčič et al. (2010) revealed that the browsing rate of fir was positively correlated with the density of red deer, however, no correlation was found between the density of fir seedlings and deer density. Additionally, the relationship between ungulate game density and browsing of balsam fir was found to be non-linear, depending on full-canopy and open-canopy conditions (Tremblay et al. 2007). However, Reimoser, Gossow (1996) observed the greatest browsing impact in the areas with the lowest game density, suggesting that forest structure is the primary driver of predisposition to browsing. In addition, Barrett, Schmitz (2013) concluded that forest thermal environment was a better predictor of browsing impact during the vegetation period (i.e. warmer sites were also more browsed) and deer density in winter. According to the results of this study, it seems that spatial scale of the decision-making process of deer is substantial in the understanding of browsing. It is suggested that deer is probably attracted by the distinct groups of natural regeneration and subsequently, it feeds preferably on browse plants such as fir and the concentration effect of other fir individuals present even amplifies the browsing impact. Furthermore, food supply concentration was found not to be related to deer density when comparing area with various silvicultural systems (Reimoser, Gossow 1996). However, Jarnemo et al. (2014) suggested that local deer usage of stands can give an account of browsing impact on a smaller stand scale. The supply of alternative forage (shrubs, herbs and other nearby forest stands) considerably reduced browsing impact in their study. Likewise, Heuze et al. (2005) noticed that browsing was not that pronounced when fir seedlings were growing close to *Vaccinium* species and surrounded by dense understorey, providing probably safe microsites for regeneration and/or alternative forage for deer. Moreover, browsing was increased in individuals growing amidst palatable herbaceous species, thus not supporting the assumption that alternative forage can reduce browsing impact. Contrary to the results of this study, browsing of fir was not related to the density of fir individuals as reported by Häsler, Senn (2012). Reimoser, Gossow (1996) came to conclusion that less fir individuals fully surrounded by other seedlings were browsed (unfortunately species were not differentiated), demonstrating the dilution effect and the protective role of groups of individuals against browsing. Furthermore, as suggested by the results of GLMM, light availability did not play a role in how much

both fir and beech individuals were browsed. It could be caused by the limited variation of light conditions typical for old-growth forests, however, Kupferschmid et al. (2013) also did not find any relationship between light conditions and browsing impact, testing it with a wide range of conditions from full to open canopy. What was found to be light-dependent was the response of natural regeneration after browsing (Vandeberghe et al. 2008; Kupferschmid et al. 2013). Finally, the results imply that the interplay between plant and herbivore ecology likely determines the development of natural regeneration. Even though the concentration effect was confirmed in fir, the scale, local ungulate game usage and other biotic and abiotic habitat factors must be a necessary part of the research on browsing to enable the comparisons with other browsing studies and improve the understanding of scale-dependence in browsing ecology (Weisberg, Bugmann 2003).

### **5.3. Mortality and establishment of natural regeneration**

Mortality of natural regeneration on TPs was year-specific in terms of height of individuals since 35 % of fir individuals above 0.15 m in height experienced mortality in 2013 and less than 8 % in 2014 and 2015. This might be explained by extreme summer meteorological situation with above-average temperature and less rainfalls in 2013 as discussed above. Thus, it is possible that these conditions became critical also for taller individuals. However, natural regeneration might be buffered against mortality by low light levels in an old-growth forest (Sack 2004). Mortality of beech was more balanced along the height classes since 48 and 44 % of individuals of beech died in the 1. and 2. height class respectively. Likely explanation could be lower establishment of beech. Moreover, a GLMM analysis revealed that the odds were 0.33 times lower that the individuals in the 2. height class would experience mortality comparing to those in the 1. height class. Yan et al. (2015) came to a similar conclusion when assessing the survival of seedlings below 20 cm in height, ascribing it to higher susceptibility of smaller seedlings to various biotic and habitat factors. On the contrary, Harmer (2001) did not observe any connections between mortality and height of individuals possibly because of limited height variation of sampled seedlings. Furthermore, the results of this study did not reveal that browsing would affect mortality of individuals. However, only the last documented browsing was used to predict mortality, since dead individuals could not be found and classified as browsed or not browsed. In consequence, this might potentially hide the real impact of browsing

on mortality and thus, substantially influence the results. As found by Harmer (2001), the survival of maple seedlings was significantly lower after browsing but beech survival was not changed. Vandenberghe et al. (2008) also documented lower survival of spruce and maple after browsing under shaded conditions, however, the beech and fir survival was almost unaffected. Harmer (2001) and Vandenberghe et al. (2008) simulated browsing as an artificial clipping event that enabled to analyse the effect of browsing on mortality of natural regeneration. These studies considered only the effect of one browsing event and Vandenberghe et al. (2008) worked even with transplanted seedlings, thus also not considering repeated browsing which was found to be common in this study. Kupferschmid et al. (2014) separated the effect of light conditions and browsing by comparing the fenced and unfenced sampling plots and found that browsing caused at least 88 % of the total mortality of fir saplings under closed canopy conditions. In addition, no effect of negative density dependence<sup>4</sup> (NDD) was found to affect mortality of natural regeneration by GLMM. The analyses carried out separately for fir and beech provided the same insignificant results. However, only the level of natural regeneration altogether was considered and NDD was not investigated among various life stages of trees. Yan et al. (2015) observed the marked effect of NDD in small seedlings caused by the occurrence of conspecific neighbours, resulting in the higher survival in the neighbourhood of heterospecific species. However, there was the effect of NDD in taller seedlings brought about by mature conspecific trees. Apart from the life-stage variation of NDD, Bai et al (2012) reported the importance of NDD in seedlings less than 4 years old. Mortality of older seedlings was more affected by habitat conditions. NDD was also found to be more pronounced in gravity-dispersed species compared to wind-dispersed species. Comita, Hubbell (2009) took into consideration different life-history strategies of species in the tropics and found that the negative effect of conspecific neighbours was stronger for light-demanding species compared to shade-tolerant species. Taken together, it seems that mortality of natural regeneration is affected by neighbourhood effects and browsing, however, frequency of browsing, age and size of individuals and habitat conditions (such as light) is probably what determines its overall magnitude. For this reason, long-term studies incorporating all these factors are necessary in the future research. Nevertheless, only the effect of size (height) of natural regeneration was revealed to impact the mortality

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<sup>4</sup> Negative density dependence is involved when nearby conspecifics impair performance. It can constrain locally abundant species and promote less successful or abundant species and facilitates species coexistence (Wright 2001).



of individuals in the NNR Salajka and spatial statistics is suggested to adopt to confront other possible effects on mortality since it might be more appropriate to reveal the underlying ecological processes of species coexistence (Brown et al. 2011).

Interestingly, the number of both fir and beech individuals culled each year was very similar, ranging from 40 to 50 individuals and the mortality of fir was balanced over the years accounting for 15 % on average. Mazur (1989) also reported quite stable mortality rate of fir over time depending on site and stand conditions. However, he calculated mortality separately for establishment (one-year old seedlings) and new growth (older seedlings up to 0.5 m in height), thus comparisons with this study are limited. As for beech, mortality amounted to 8 % in 2013 and 2014 with decrease to 4 % in 2015. Comparing fir and beech, the magnitude of mortality of both species was different, i.e. approximately four times more individuals of fir died every year. Moreover, the magnitude of establishment of both species was also different closely corresponding to the magnitude of mortality. It seems that the investment and allocation of sources vary in fir and beech. Beech was found to produce seeds sporadically but in explosive quantities with a higher percentage of germinating seeds than fir (Szewczyk, Szwagrzyk 2010; Szwagrzyk et al. 2015). The results of this study likely show a similar pattern, however, in spite of the mast year of beech in 2013, relatively small amount of establishment emerged on TPs in the following year, suggesting that either transect was not representative to reflect seed masting of beech (potentially due to the effect of seed dispersal limitation) or there was high predation of beech seeds that hindered the beech establishment. The former might be true since the inventory results recorded more pronounced increase in the density of individuals below 0.15 m in height. Another explanation could be a lack of mature beech individuals in the vicinity of transect, which is not the case as there are many around transect. Furthermore, fir was found to produce seeds more often and in less extensive quantities (Paluch 2011) with a lower percentage of germinating seeds than beech and more continuous establishment to seedlings forming a relatively stable seedling bank over time (Szewczyk, Szwagrzyk 2010). This study demonstrates the comparable results in terms of annual establishment and stable seedling bank. Additionally, the establishment of fir almost compensated for mortality in the four-year period of study, reaching up to 12 and 15 % on average (7189 and 8561 individuals per ha) respectively. In case of beech, establishment and mortality was less balanced, amounting to 4 and 7 % on average (1043 and 1829 individuals per ha) respectively. Taken together, fir was

characterized by regular though light-medium establishment only slightly outweighed by very even annual mortality. Conversely, beech exhibited, comparing to fir, low establishment not compensating for mortality over the years of study. However, it is likely that the massive beech establishment occurred in 2014 on IPs, though it was not that reflected on a small scale of transect. Thus, the results of this study suggest that fir and beech possess the species-specific life-history strategies at the seed-to-seedling life stage.

#### **5.4. Implications for nature conservation and forestry**

Based on the results of this study, there are several issues for nature conservation to address. Firstly, the NNR Salajka and other comparable forest reserves characterized by spontaneous development and passive management have witnessed the expansion of beech with simultaneous decline of fir along the early life stages. The decision to be made is whether to challenge fir artificially, excluding it from the deer-forest conflict by putting up enclosures or to adopt the wait-and-see strategy, observing if at least some proportion of fir is able to withstand under the current conditions and maintain the viable populations. Moreover, browsing cannot be accepted as the ultimate cause of decline in the fir natural regeneration, since there are other factors that might play a role, such as the shift of tree competitiveness as a result of climate change. Thus, it is suggested to establish the research observational network of a few smaller enclosures representatively covering the variation of forest conditions or the partial enclosure of the reserve and follow the natural dynamics of tree regeneration processes within, rather than fencing the whole area of the reserve that would entail a regular and long-term investment of time, people and money. Besides, conservative measures to protect the single individuals of fir should be maintained. Further, transformations of mostly spruce forest stands surrounding the NNR Salajka towards more appropriate species composition and structure are proposed because any actual protection buffer zone has not been established around the reserve since its designation in 1956, apart from the protection zone existing only *de jure*. One of the most obvious problems is the dispersal of especially spruce seeds from adjacent forest stands and the attractiveness of the reserve to ungulate game, luring animals by favourable settling stimulus. Moreover, the NNR Salajka covers only about 20 hectares and hunting outside the reserve cannot be separated from hunting inside it. The main problem is the sanctuary effect in the reserve. For this reason, deer hunting in the reserve should serve to raise the alertness

of animals, rather than to decrease locally its density which was found to have the counterproductive effects (Grignolio et al. 2014).

Furthermore, mortality of natural regeneration was most pronounced in individuals below 0.15 m in height, probably as a result of susceptibility to biotic and habitat factors. Consequently, an effort to protect even this early stage should be made, for instance following the regeneration fellings in the uniform system or the selection fellings in the selection system. The results of this study suggests that when utilising natural regeneration in silviculture, very frequent though less extensive establishment of fir can be expected even in intermast periods, whereas beech establishment emerges less frequently but potentially in huge quantities.

## 6. Conclusion

The long-term changes in natural regeneration of tree species were observed over the period 2009–2016 in a temperate old-growth fir-beech forest located in the Western Carpathians mountain range. Natural regeneration of very early life stages was found to substantially fluctuate over time, depending on establishment and consequent mortality rate. The density of individuals ranged from 10 to 38 thousand per hectare. The years with pronounced decrease in the density of individuals below the height of 0.15 m were characterized by extreme meteorological conditions (above-average temperature and rainfall deficiency in summer) that likely induced or at least amplified the impact of mortality on natural regeneration since all the species, regardless of their proportion and establishment, indicated the impact of mortality in a similar way.

Further, a continuous alternation of fir and beech was documented on the level of natural regeneration, probably as a result of ungulate game browsing impact that disturbs the species coexistence mechanisms and thus, indirectly promoting beech and suppressing fir. Beech was gradually securing an absolute dominance among individuals above the height of 0.5 m over the years. It seems that browsing limits the height of fir, maple and spruce to 0.5 m or even less as the density especially of fir individuals was highly unbalanced between the 1. and 2. height class. The argument that this could be a result of geographically restricted processes is not relevant since similar observations concerning the expansion of beech or the fir and beech alternation has been reported elsewhere in the Czech Republic as well as in other European countries. Moreover, the lack of fir individuals of early life stages cannot also account for this phenomenon because there was 5-16 times (depending on the sampling method) more individuals of fir than beech below 0.15 m in height. The relative importance of browsing was more pronounced generally in taller individuals, however, it could not solely give an account of the low densities of fir and maple individuals in the taller height classes. The detailed study on browsing and species-specific tolerance would be needed, however, the first results suggest that repeated browsing was common and might play a role. In addition, it was found that the number of browsed fir individuals was positively correlated with the density of conspecific individuals and the total density of individuals, supporting the effect of resource concentration. In contrast, the number of browsed beech individuals did not show such a relation. Light availability did not have any effect on the number of browsed individuals.

The temporal variation of mortality of natural regeneration was generally low, meaning that the total number of culled individuals was very similar each year, especially in case of fir. Moreover, mortality was more pronounced in individuals below 0.15 m in height and it is suggested that extreme meteorological conditions might have caused mortality even of taller individuals that are usually more resistant as supported by GLMM results, showing that mortality is largely a matter of size of individuals. No effect of negative density dependence was revealed on the level of natural regeneration and it is proposed that further research differentiating the life-history strategies of species, life stages of individuals and habitat conditions warrants attention to confirm the findings. Furthermore, species-specific life-history strategies of fir and beech were demonstrated in this study. Fir was characterized by regular though light-medium establishment only slightly outweighed by steady annual mortality, highlighting the importance of frequent but inextensive establishment in intermast periods. Conversely, beech exhibited, comparing to fir, low establishment not compensating for mortality over the years. However, it is likely that the massive beech establishment emerged in 2014 across the reserve (as suggested by the inventory results), though it was not reflected on a small scale of transect, e.g. due to seed dispersal limitation or predation. Thus, the importance of extensive but relatively less frequent establishment and seed masting in beech cannot be refuted.

In conclusion, the goal of this study was to investigate the role of browsing, establishment and mortality in natural regeneration of tree species, studying a temperate old-growth fir-beech forest in the Western Carpathians. These three processes are closely causally interconnected, though all of them operating on different spatial and temporal scales. Browsing was found to shape the species composition and height structure of natural regeneration, potentially shifting the whole structure of forest ecosystem in the long-term. The findings on establishment and mortality of natural regeneration demonstrated the species-specific life-history strategies of fir and beech. Both forestry and nature conservation should acknowledge these processes, following the rationale of adaptive management and ongoing global changes can offer a good set of reasons why to do so. More research is needed into the effect of the biotic and abiotic neighbourhood of seedlings on browsing and the role of negative density dependence in temperate fir-beech forests. This might help to disentangle the conditions in which tree species are more competitive and to assess the importance of other factors such as deer browsing that might alter the species coexistence to a considerable degree.

## Závěr

Byly zaznamenány dlouhodobé změny v přirozené obnově dřevin temperátního přirozeného jedlo-bukového lesa Západních Karpat za období 2009–2016. Přirozená obnova prvotních vývojových stádií byla výrazně časově proměnlivá v závislosti na vzniku nových jedinců a následné míře mortality. Počet jedinců se ve studovaném období pohyboval od 10 do 38 tisíc na hektar. Značný pokles počtu jedinců pod 0,15 m výšky byl spojen s roky extrémních meteorologických situací (nadprůměrné teploty a srážkový deficit v letním období), které pravděpodobně iniciovaly nebo přinejmenším zesílily dopad mortality na přirozenou obnovu. Všechny druhy dřevin bez ohledu na jejich zastoupení a vznik nových jedinců odrážely vliv mortality podobným způsobem.

Na úrovni přirozené obnovy bylo potvrzeno postupné nahrazování jedle bukem, nejspíše jako výsledek okusu zvěří, který narušuje mechanismy koexistence druhů, a tak nepřímo prosazuje buk a potlačuje jedli. Buk si během let postupně zajišťoval úplnou převahu nad 0,5 m výšky. Zdá se, že okus limituje výšku jedle, klenu a smrku na 0,5 m nebo i méně, jelikož poměr počtu jedinců mezi 1. a 2. výškovou třídou byl velmi nevyrovnaný. Mohlo by se jednat o geograficky omezený proces, ale obdobné pozorování expanze buku a nahrazování jedle bukem byly hlášeny jak z České republiky, tak i z dalších evropských zemí. Ani nedostatek jedinců prvotních vývojových stádií neposkytuje dostatečné vysvětlení, jelikož jedle byla 5–16 krát početnější mezi jedinci do 0,15 m výšky. Význam okusu byl relativně větší u vyšších jedinců, nicméně nemohl samostatně vysvětlit nízké počty jedinců jedle a klenu ve vyšších výškových třídách. K tomu by byla nutná detailní studie zaměřená na okus a druhou toleranci okusu. První výsledky ale naznačují, že opakovaný okus byl běžný a může hrát důležitou roli. Navíc bylo zjištěno, že počet poškozených jedinců byl pozitivně korelován počtem konspicivních jedinců a celkovým počtem jedinců, což poukazuje na efekt “koncetrovaného zdroje”. Počet jedinců buku ale žádný takový vztah neukázal. Míra světelného požitku také neměla žádný efekt na počet poškozených jedinců.

Časová proměnlivost mortality přirozené obnovy byla obecně nízká, tj. každý rok uhynul podobný počet jedinců, což platilo zejména u jedle. Mortalita byla značná u jedinců do 0,15 m výšky. Extrémní meteorologické podmínky mohly způsobit mortalitu i vyšších jedinců. Nicméně výsledky GLMM analýzy poukázaly na to, že mortalita jedinců je závislá na jejich výšce. Nebyla potvrzena negativní závislost na hustotě (negative density dependence) na úrovni přirozené obnovy, nicméně k ověření výsledků

by bylo nutné provést další výzkum, který by rozlišoval životní strategie druhů, vývojová stádia jedinců a podmínky prostředí. Výsledky dále naznačovaly na specifické životní strategie jedle a buku. Jedle byla typická pravidelným mírným až středně rozsáhlým vznikem nových jedinců, které jen lehce převažovala každoroční vyrovnaná mortalita. Z toho vyplývá, že pravidelný a méně rozsáhlý vznik nových jedinců a produkce semen mezi semennými roky, jsou důležité. Naopak buk byl typický vznikem nízkého počtu nových jedinců, který nekompensoval mortalitu. Nicméně je pravděpodobné, že masivní vznik nových jedinců buku se odehrál v roce 2014 po celé rezervaci, ale nebyl pozorován na úrovni transektu, např. kvůli omezenému šíření semen nebo jejich predaci. Takže důležitost mohutné a méně časté produkce semen a vzniku nových jedinců buku nemůže být zavržena.

Cílem této studie bylo zjistit význam okusu dřevin zvěří, vzniku a mortality přirozené obnovy dřevin na příkladu temperátního přirozeného jedlo-bukového lesa Západních Karpat. Tyto procesy jsou kauzálně velmi úzce propojené, ačkoliv operují na odlišných časových a prostorových úrovních. Okus dřevin zvěří utvářel druhové složení a výškovou strukturu přirozené obnovy. Vliv zvěře je tak z dlouhodobého hlediska potenciálně schopen měnit celou strukturu lesního ekosystému. Vznik a mortalita přirozené obnovy souvisely pravděpodobně se specifickými životními strategiemi druhů. Jak lesnictví, tak ochrana přírody by měly uznat význam těchto procesů a následovat myšlenky adaptivního managementu. Jako dobrý důvod mohou sloužit současné globální změny. Další úsilí by mělo směřovat na výzkum vlivu biotického a abiotického okolí jedinců přirozené obnovy na míru okusu a role negativní závislosti na hustotě (negative density dependence) v temperátních jedlo-bukových lesích. Tím by se mohlo ukázat, jestli a za jakých podmínek mohou mít druhy dřevin kompetiční výhodu nad ostatními a do jaké míry se uplatňuje samotná kompetice dřevin, když do ní mohou vstupovat a měnit ji faktory, kterými jsou například okus zvěří nebo klimatická změna.

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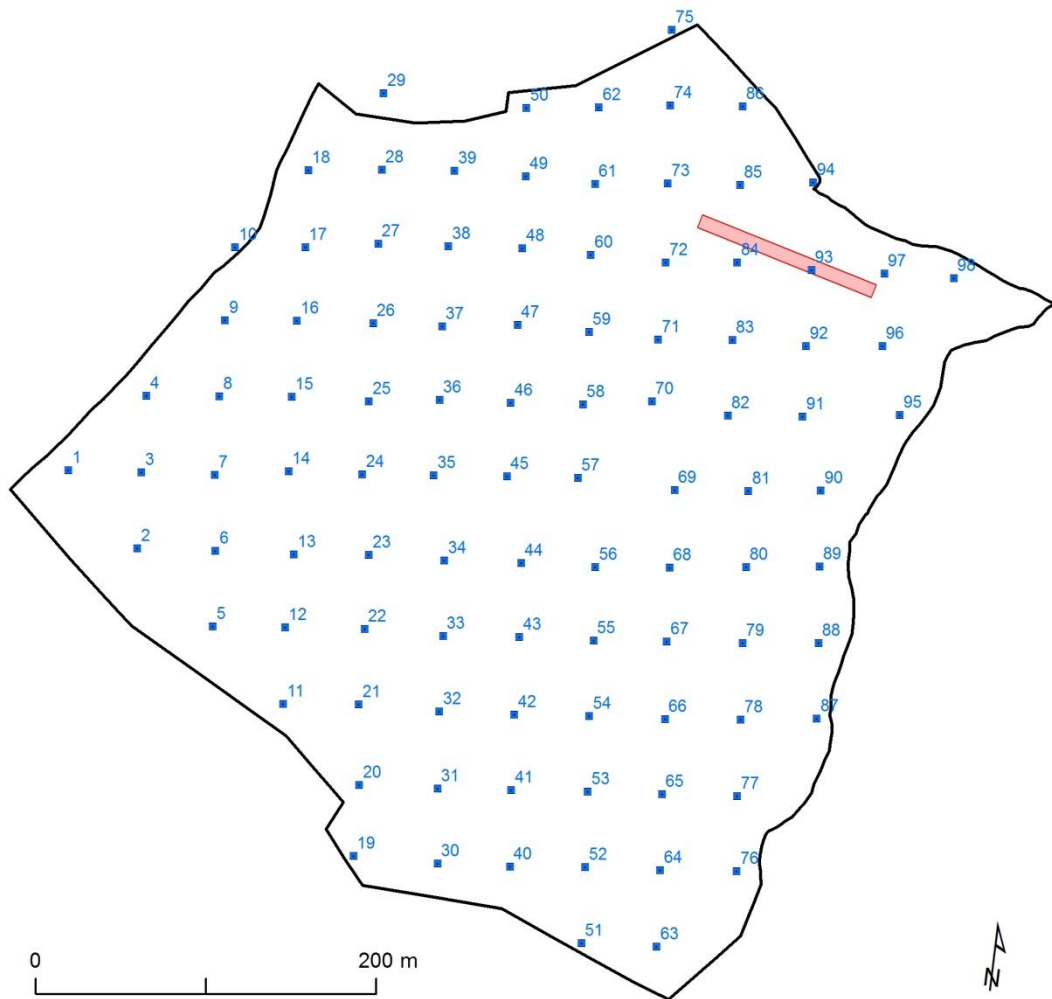
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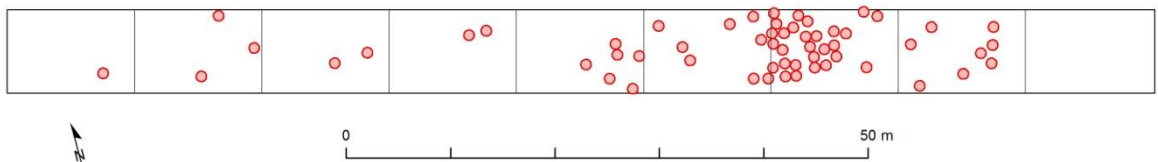
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# Appendices



Appendix 1. The outline of the NNR Salajka with a regular network of 98 inventory plots. Blue points denote the position of the centre of inventory plot. Transect is displayed in red colour.



Appendix 2. The outline of transect with 54 transect plots.