

# Joining of the historical research and future prediction as a support tool for the assessment of management strategy for European beech-dominated forests in protected areas

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## Abstract

European beech-dominated forests are crucial for maintaining biodiversity in forested mountain landscapes of the European temperate zone. This paper presents the results of research and assessment of management strategy for mountain beech-dominated forests in the Jeseníky Mountains (Czech Republic). Our approach is based on combining research on historical development of the forest ecosystem, assessment of its current state, and predictions of future dynamics using a forest growth simulation model. Using such a method makes it possible to understand the current state of the mountain beech-dominated forest ecosystem and predict its future development as a response to specific management strategies. The application of this method is therefore appropriate for assessing the suitability of selected management strategies in mountain protected areas. Our results show that a non-intervention management for mountain beech forest in the next 80 years complies with the Natura 2000 requirement to maintain the existing character of the forest habitat. Thus, the current management plan for the beech-dominated forests in the Jeseníky Mountains does not require significant corrections in the context of its conservation targets (i.e. maintaining biodiversity and current character of the forest ecosystem dominated by beech). The results of this study suggest that combining the knowledge on historical development with forest growth simulation can be used as a suitable support tool to assess management strategies for forest habitats in protected areas.

**Keywords**

Beech-dominated forest, biodiversity, forest history, forest management plan, growth simulation model, Natura 2000

**Introduction**

Because most of the forests in Europe have been influenced by human activity, primeval forests currently account for less than 1 % of the total area of European forests (Vanbergen et al. 2005). Biodiversity and dynamics in these forests should be paid more attention as concluded by ministerial conferences on forest conservation in Europe, which have also declared the need of arresting the loss of biological diversity and supporting sustainable management (Parviainen et al. 2007). Primeval forests – thanks to their long history – are ideal research subjects for studies on spatial structure related to biodiversity (Nagel et al. 2013) and for studies on methods of sustainable forest management, which are aimed at maintaining forest biodiversity (Holeksa et al. 2009).

Primeval European beech forests consist of a mosaic of sub-stands which can be typified to the developmental stage (phase) by the structure of the tree layer (Fischer 1997). Thus the key to understanding the natural dynamics of primeval European beech forests is the concept of the small development cycle (Standovár and Kenderes 2003). Natural cyclic regeneration of primeval European beech forests mainly includes the tree species of the terminal phases, especially the beech itself. Changes of tree composition within the cycle are the exception – in European beech forest light-demanding tree pioneer species seem to be restricted to rather small patches under natural conditions (Yamamoto 2000), in contrast to the big developmental cycle in boreal spruce forest, where the role of pioneer tree species in forest natural dynamics is very important in large areas (Angelstam and Kuuluvainen 2004).

European beech and fir-beech forests are the predominant types of natural potential vegetation from planar to montane vegetation zones of temperate Europe (Bohn et al. 2002). For these forest ecosystems, the theory of the small development cycle of temperate mixed forest was conceptualized (Schmidt-Vogt 1985). The three phases of this development cycle (growth, optimum and disintegration stage) were defined based on analyses of the forest stand structure, which is considered to be an important biodiversity indicator generally used to support forest management decision-making (Kenderes et al. 2008).

The theory of the small development cycle has a long history. In 1959 Leibundgut developed the former idea of Rubner (1925) about different structural characteristics of sub-stands of European beech forests by documenting the different physiognomy of beech forest patches and analysing the growth behaviour of the trees in detail. Numerous authors used this idea to analyse virgin deciduous forests in temperate zones of Europe with special attention to European beech forests. Remmert (1992) postulated the following sequence of events and tree species concerning the European beech forests:

- (1) A fraction of a beech forest stand becomes disturbed (e.g. by windfall).

- (2) The first phase of the tree layer regeneration is dominated by pioneer trees (e.g. *Betula* sp.) in open space of the disturbed patch, while the old beech trees along the border of the open disturbed area are going to die off owing to “sunburn” (the cambium of the exposed beech trunks dies).
- (3) Regeneration starts in the shadow of the pioneer trees and a new forest stand, again dominated by beech, builds up. Remmert finished the description of this cycle with the words: “Very often there is a short-cut in the cycle, and beech follows beech”.

It is interesting, that Remmert’s former idea about European beech maintaining dominance across the full forest development cycle has been confirmed in current studies (e.g. Glatthorn et al. 2017).

In 1995 Korpel published extensive results regarding the primeval European beech dominated forests in Slovakia (Appendix 1: fig. A1). The numerous examples presented in this study document the lack of pioneer-dominated phases in the regeneration cycle; beech, fir and spruce dominate all the regeneration phases. These results are supported by modelling of the tree species composition during the regeneration process. The most important parameters in competition amongst trees are height increment and shading capacity combined with shade tolerance. The European beech is a shade tree, and middle-aged and old growth beech have high rates of annual height increment. Models based on these parameters (e.g. Roloff 1992) predict a pure beech forest after 150 years of cycling. Thus it can be stated that cyclic regeneration of primeval European beech forests predominantly includes the tree species in the terminal phases and those that are shade tolerant, especially beech and fir. Under natural conditions for beech forest regeneration cycles (e.g. in protected areas without human activity) light-demanding pioneers seem to be restricted to small forest patches in short time episodes.

Currently the theory of the small development cycle is, in literature, also known as the concept of forest gap dynamics (Rugani et al. 2013). Investigation of gap characteristics and tree regeneration patterns is central for our understanding of beech forest dynamics (Vacek et al. 2017). Fine-scale gap-phase dynamics is a main characteristic feature of primeval beech-dominated forests in temperate Europe (Splechtna et al. 2005). Gaps are important in maintaining plant species diversity in beech forests (Degen et al. 2005). The size, shape, age and temporal changes of gaps in beech forests influence the regeneration patterns of tree species, due to different ecological traits of the particular tree species and the effects on the herbaceous layer in the history of soil conditions (Modrý et al. 2004).

Gap dynamics now only exist in strictly protected areas, because the most of European beech dominated forests have been managed in line with the paradigm of the Central European forestry (Hahn and Fanta 2001). This paradigm is based on very intensive treatment of forest stands by age classes, on prescriptive forest planning and on sophisticated forest management techniques. Natural processes in these forests have been largely ruled out in order to keep timber production. In the past three decades a criticism of this forest management practice has been formulated in relation to the ecological risks and the loss of biodiversity caused by the uniformity and simple homogenous structure of commercial forests. A growing interest for sustainable forest

management (which is aimed at maintaining forest biodiversity) is increasing. The implementation of sustainable forest management should be based on the knowledge of natural processes in primeval forests. It plays an essential role in strictly protected areas of forested landscapes. For example, most parts of the Kékes Forest Reserve (which protects 63 ha of primeval European beech montane forest ecosystem in Hungary) show the characteristic fine-scale mosaic of forest developmental stages *sensu* Korpel (1995). Standovár (et al. 2017) found the very intensive fine-scale dynamics of the beech forest, determined by natural stand dynamics in this strict forest reserve. The above mentioned authors proved that extinction and colonisation episodes even out at the stand-scale, implying an overall compositional stability of the herbaceous vegetation at the stand-scale after 17 years (whereas the abundance of vegetation changed considerably in relation to the partial closure of the canopy). They discovered that fine-scale gap dynamics, driven by natural process or applied as a management method, can warrant the survival of many closed forest specialist species in the long-run. An important decrease in herbaceous species cover in relation to light deficiency from a denser canopy during the process of forest gap dynamics was published by Lysik (2008) in a primeval beech forest in Poland. The author connected these changes with the massive recruitment of beech regeneration in the frame of natural forest dynamics. The denser canopies effect was observed as a decrease in light-demanding species and an increase in shade-tolerant species (Hédli et al. 2010). The species diversity of the herbaceous layer can be also influenced by invasive species, even in primeval forests, as noted by Lysik (2008). Ujházy et al. (2005) found relatively low species turnover in primeval fir-beech forest compared to commercial forests in Slovakia in all three developmental stages of forest dynamics – the growing, optimum and decay stages were differentiated rather by the value of abundance and dominance than by changes in diversity. Applying this theoretical knowledge in the practice of sustainable forest management (using only small regeneration areas) can support the conservation of the diversity of the herbaceous layer and prevent invasive or ruderal species with strong competitive abilities (Kelemen et al. 2012). Thus, the application of retention forestry in the frame of conservation planning for forested protected areas can be considered as a good support tool for integrating conservation targets to forest management practice (Fedrowitz et al. 2014).

Primeval European beech forests have higher stand diversity (at the level of structural and tree species diversity) than commercial forests on comparable sites (Kráľ et al. 2010). All the presented results above obviously support this statement relating to the key importance of knowledge in forest dynamics in stand-scale for conserving forest biodiversity.

The structure of managed and unmanaged European beech-dominated forests (Bílek et al. 2011) and their treefall gap dynamics (Schliemann and Bockheim 2011) have long been subject to ecological research (Kenderes et al. 2008b) that has resulted in defining relevant principles for sustainable forest management (Angelstam et al. 2004). In recent years, research methods have shifted from simple visual estimation (Leibundgut 1993) to the utilization of maps of repeatedly measured trees (Vrška et al. 2001) and dendrochronological analyses (Podlaski 2004), and include studies of

natural regeneration (Barna 2011). Currently, forest growth models are also being increasingly used (Pretzsch 2010).

The near-natural and virgin ecosystems of European beech and fir-beech montane forests are characterized by a long-term cyclical alternating dominance of two main species: Silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.), (Saniga 1999). Some studies show that this phenomenon of long-term cyclical changes is rather a steady trend of the gradual replacement of fir by beech (Janík et al. 2014). A possible explanation of this trend may be the long-term response of forest ecosystems to past human activity, such as the medieval colonization of mountains associated with intensive local exploitation of forests by grazing and litter raking (Samonil and Vrska 2007). Understanding the historical development of mountain forest ecosystems is therefore of great importance for understanding their current state (Agnoletti and Anderson 2000).

Preserved segments of European beech-dominated forests represent valuable natural laboratories (Schultze et al. 2014, Standovár et al. 2017) that are often incorporated into national ecological networks (Jongman 1995) and international systems of conservation areas, such as the Natura 2000 network (Miko 2012). The high environmental value of these conservation areas requires a multidisciplinary approach to develop and assess forest management plans and policy instruments (Brukas and Sallnäs 2012), to evaluate management regimes (Torres-Rojo et al. 2014) and to seek specific forest management alternatives (Götmark 2013).

The main objective of this paper is to show the importance of integrating historical research of forest ecosystems for the assessment of forest management strategy, using an example of protected mountain beech and fir-beech forests of temperate Europe. The particular targets of this paper are:

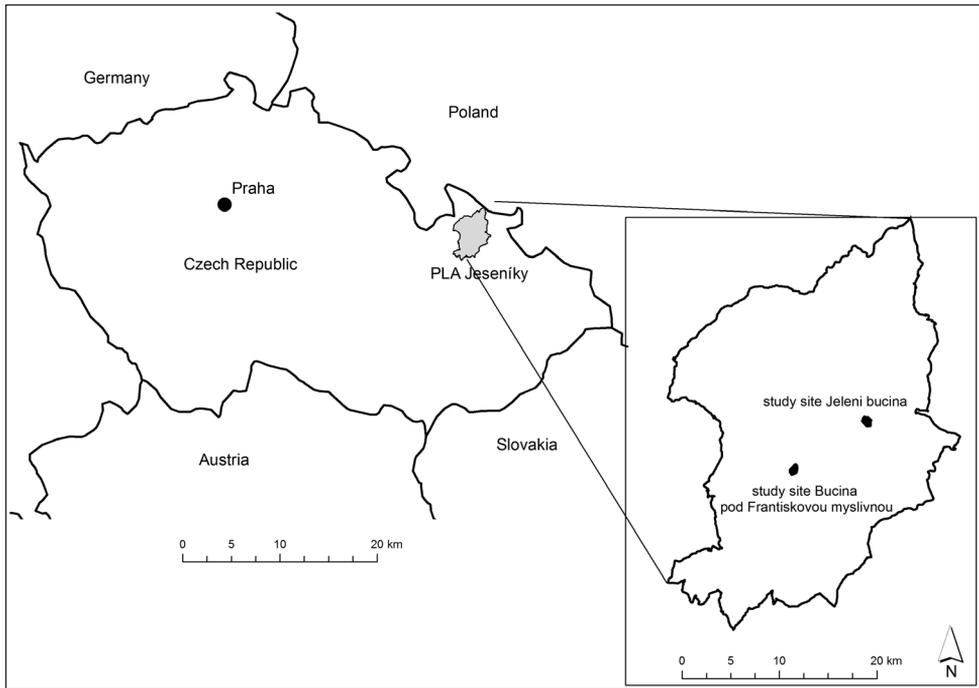
- a) to explain the current state of the beech-dominated forest ecosystem in two study sites using historical analysis of their past,
- b) to predict the likely future trend in the dynamics of forest stands using a growth simulation model,
- c) to review the current forest management plan and decide whether it ensures maintaining the current character of the habitat and thus complies with the Natura 2000 conservation objectives for forest habitats.

## Materials and methods

### Study sites

The research was conducted at two mountain study sites (Fig. 1) in the 5th and 6th forest vegetation zones of the Czech Republic (Machar 2012). Both study sites are part of the core zone of the Jeseníky Mountains Protected Landscape Area (JMPLA).

The Jelení Bučina (JB) study site (45.84 ha) is located at 50°06'N, 17°17'E, 740–920 m above sea level on a mostly steep north-west slope with a gradient of 23 %.



**Figure 1.** Location of Protected Landscape Area Jeseníky and both study sites (Jeleni bucina and Bucina pod Frantiskovou Myslivnou) in the Czech Republic.

The local bedrock geology consists of paragneiss. The soil is very stony with debris, mostly Ranker mesotrophic cambisols with the moder humus type. Most of the study site (91%) is covered by natural beech forest of an old-growth character with small patches of *Tilio-Acerion* ravine forest and minor fragments of *Caricion remotae* forest springs. This forest stands can be considered as forests sensu Korpel (1995) with natural dynamics and high biodiversity. A small part of the study site (9%) is covered by an even-aged, artificial monoculture of Norway spruce (*Picea abies* (L.) Karsten). The forest ecosystem of the JB study site belongs to the *Aceri-Fagetum sylvaticae* phytocoenological association.

The Bučina pod Františkovou Myslivnou (BFM) study site (25.49 ha) is located at 50°03'N, 17°11'E, 1050–1105 m above sea level. This site represents the highest-elevation beech forest in the entire Jeseníky Mountains. At higher altitudes, the beech forest naturally transforms into a natural spruce forest ecosystem (Machar et al. 2014). The BFM study site is located on a highly steep north-east slope with a gradient of 32 %. The local bedrock geology consists of highly weathered paragneiss and migmatites with amphibole. The soil is mostly modal mesotrophic cambisols with the moder humus type. Most of the study site (95%) is covered by natural beech forest admixed with spruce, sycamore maple (*Acer pseudoplatanus* L.), Scots elm (*Ulmus glabra* Hudson) and, very rarely, with fir. This part of the study site can be considered as forest stands with natural dynamics sensu Korpel (1995), which have typical high biodiversity. Adjacent to

the study site are artificial spruce monocultures. The forest ecosystem of the BFM study site belongs to the *Aceri-Fagetum adenostylosum* phytocoenological association.

According to the classification system of the Natura 2000 network, both study sites are classified as “Medio-European subalpine beech woods with *Acer* and *Rumex arifolius*” (habitat code 9140). According to the Habitat Catalogue of the Czech Republic (Chytrý et al. 2010), this habitat type is classified as “Montane sycamore-beech forests” (code L5.2). The borders of both study sites are identical to the borders of nature reserves of the same name. The forest management plan of both reservations for the period of 2013–2022 prescribes a non-intervention protection regime, allowing a spontaneous succession of the forest ecosystem.

## Data collection, verification and processing

### Data sources and analysis of historical development of forest ecosystems in the study sites

To study the historical development of forests in the JB and BFM study sites in the period of 1621–1947, we used the historical documents of the Teutonic Order, a former owner of the studied forests. The set of original documents is stored in the State Regional Archive in Opava in the “Central Administration of the Teutonic Order – Bruntál Estate” collection numbered 1.477–1.543 and forestry maps numbered 5.799–5.802, 5.945, 5.948 and 5.955 in scale 1:2880. In addition, we used several archive materials from the State Regional Archive in Janovice from the collections “Loučná Estate” and “Velké Losiny Estate”. Since 1947, the forests in both study sites have been owned by the state. Valuable historical data for this period were found in the forest management plans deposited in the archives of the Forest Management Institute in Brandýs nad Labem. Recent data necessary for the analysis were taken from the forest management records deposited at the JMPLA administration office.

### Prediction of future dynamic of forest ecosystems in the study sites

To predict the future forest development in the JB and BFM study sites, we used the SIBYLA growth simulation model (Fabrika and Dursky 2006) modified for the specific conditions of the Czech Republic based on a previously created climatic model (Simon 2007).

At both study sites research plots were defined in such a way that they reflected the characteristic conditions of the forest in the study sites and their typical tree species composition (Table 1). The centre of each research plot was recorded with GPS to allow a potential research repetition. The research plots (100×100 m) were selected using the FieldMap software (IFER-Monitoring and Mapping Solutions Ltd.).

All trees wider than 5 cm of DBH were located and marked in a rectangular coordinate system. The following parameters were measured: diameter of the tree trunk at 1.3 m (diameter at breast height,  $d_{1.3}$ ), total height of the tree (m), height of green tree top setting, and social position. We employed the dendrometric measurements from

**Table 1.** Forest stand characteristics for the Jeleni Bucina (JB) and Bucina pod Frantiskovou Myslivnou (BFM) study sites as used for the growth simulation model.

Study site	GPS coordinates	Type of forest ecosystem	Tree species composition (% proportion in the forest stand)
JB	50.06633°N, 17.17945°E	Highly heterogeneous mountain beech forest with patches of natural regeneration	Canopy layer in the disintegration stage: BK 60, KL 20, JL 10, SM 10 Understory formed by isolated patches of natural beech regeneration: BK 100
BFM	50.03446°N, 17.11800°E	Highly heterogeneous mountain beech forest with extensive natural regeneration and admixture of fir	Canopy layer in the optimum stage: BK 94, KL 3, JL 1, SM 1, JD 1 Understory formed by patches of natural regeneration diffused over the entire site: BK 96, JD 4

Used abbreviations of tree species: BK – *Fagus sylvatica*, KL – *Acer pseudoplatanus*, JL – *Ulmus glabra*, SM – *Picea abies*, JD – *Abies alba*.

all research plots to create stand height curves, using the non-linear Naeslund regression height function.

In 2012, we carried out visualization and simulation of the future forest development under a non-intervention management (i.e. spontaneous forest development in relation to conservation targets of Natura 2000 sites) using a growth simulation model. The growth simulation was based on a mortality model, consisting of two components: probability of tree necrosis (Dursky 1997) and competition threshold (Pretzsch et al. 2002). We simulated future forest development for the periods of 25, 50 and 80 years, and calculated the development of the leaf area index (LAI), an important indicator of natural beech regeneration.

For both study sites we predicted changes in tree diameter diversity of the beech stands (excluding individuals originating from natural regeneration) and changes in their standing tree volumes ( $\text{m}^3 \cdot \text{ha}^{-1}$ ). Further, we evaluated the development of tree species composition, representation, and horizontal and vertical structure using the following structural indices: Clark-Evans aggregation index (Clark and Evans 1954), standardized Arten-profile index (Pretzsch 2005) as a relative rate of diversity, and Pielou segregation index (Pielou 1977).

### Linking historical research with growth simulation model to assess forest management strategies in the study sites

The assessment of forest management strategies currently implemented in the JB and BFM study sites is based on combining research of historical development of the studied ecosystem and interpretation of future development of main edifiers predicted by the growth simulation model. The historical research helps to objectively explain the current state of the forest ecosystem determined by the forest management and other human activity carried out in the study sites. The growth simulation model of future forest development predicts the structure of woody vegetation over defined time periods in the future based on specific management strategies delineated in the protected areas management plan.

The final synthesis based on the results of both analyses (historical research and growth simulation) allows the assessment of whether the spontaneous (succession) development of the ecosystem resulting from the current forest management plan ensures maintaining the existing character of the mountain beech forest habitat as defined by Natura 2000 (Moravec et al. 2000). This synthesis then allows the suggestion of possible adjustments in the forest management, in order to comply with the protected area mission that is, retaining defined habitat character and biodiversity as defined by the Habitats Directive (Roth 2003).

## **Results**

### **History of forest ecosystems in the JB and BFM study sites**

Until the 12<sup>th</sup> century, the Jeseníky Mountains were part of the “borderline forests”, an unpopulated and forested border mountain chain that formed a natural defense of lowland areas of the Bohemian Kingdom, intensely inhabited since the Neolithic period (Bouzek 2011). The first colonization efforts in the Jeseníky Mountains associated with anthropogenic impacts date back to the 15<sup>th</sup> century, when the exploitation of iron ore and precious metals started (Hosek 1970). At the end of the 17<sup>th</sup> century, the alpine meadows above the tree line were first used for cattle and sheep grazing during the summer months (Anonymous 1689). Sheep grazing on the alpine pastures was most intense in the 19<sup>th</sup> century on the eastern slopes of the Bruntál Estate, as evidenced by the name of today’s recreational site – Ovčárna (“sheep stable”). Mowing and harvesting of hay in the 19<sup>th</sup> century was another significant human activity that also extended into the naturally sparse forest of the tree line areas. For instance, 50–70 car loads (circa 250–280 quintals) of hay were harvested annually on the grounds of the Bruntál Estate (Anonymous 1866). In contrast, the alpine beech forests and climax spruce forests below the tree line were only affected by selective logging and had the character of an old-growth forest by the mid 18<sup>th</sup> century. In 1750, the forests on the Loučná Estate (which included the area of today’s BFM study site) were described as being full of decaying wood and many fallen trees, making the passage for both man and livestock dangerous and, in some places, completely impossible. Moreover, these forests allegedly provided a safe shelter for large wild animals such as bears, wolves and lynxes (Anonymous 1750). The alpine forests of the Jeseníky Mountains began to be more significantly affected by the selective logging only at the end of the 18<sup>th</sup> century due to the high demand for wood needed for the intensively developing iron industry (ironworks and forges) in the lower areas of the mountain region. Exploitation of the alpine forests by logging had a great impact as the forest stands did not have large timber volumes – the “Josefsky Cadastre” from 1786 (Opsal et al. 2016) shows that the forests had about 180 m<sup>3</sup> of timber in harvest age per hectare. The high demand for wood by the iron industry led to a gradual transition from selective logging to clear-cut logging. The original old-growth forests on the Bruntál Estate (including the area

of today's JB study site) were completely harvested by selective logging around 1750, but they regenerated naturally. Between the years 1778–1808, a repeated harvest took place throughout the Bruntál Estate with almost no subsequent artificial restoration, leaving the stands to be spontaneously renewed by natural regeneration. Based on the economic interests of the Estate owner (the Teutonic Order) in timber harvesting, a first forest management plan was formulated in 1803 by Jan Vavřinec Knappe (Knappe 1803). Forest districts were divided in smaller units in order to reduce the annual harvest volumes. In 1803, stand No. 401 B, forming today's nature reserve and the JB study site, was described as a 50-year old forest stand of uneven stocking level, with beech as a predominant species (one third of all tree individuals). One sixth of the vegetation consisted of sycamore maple, another sixth of spruce, and the remaining third consisted of goat willow. Fir was present only as a rare admixture. The next forest management was carried out in 1827 following identical principles (Krones 1827). There was no more evidence of the goat willow on the site in the later forest management plan in 1862 (Anonymous 1862). When the forest reached its harvesting age, a harvest plan was created to schedule timber extraction using the shelter-wood cutting method (to support natural regeneration). However, the harvest plan was probably never fully implemented due to a strong windstorm that substantially damaged the forest in 1868, and uprooted mainly the spruce trees (Anonymous 1875). Frequent wind-throws in the following years slowly lowered the forest stocking level down to 0.6–0.8 in 1884. In 1910, the given forest stand was attached to the adjacent forests dominated by spruce (partly outside of the JB study site). The newly formed timberland (marked as No. 60) had an area of 34.4 ha, was 140 years old, and consisted of beech (60 %) and spruce (40 %) (Anonymous 1910). Between 1910 and 1919, a significant number of spruces were removed due to health reasons, so the species practically vanished from the site. In the subsequent period up until the Second World War, the forest management plans prescribed harvesting large volumes of beech. In fact, however, such harvests were rarely carried out, with the exception of stand thinning in 1939 (harvest volume of mere 300 m<sup>3</sup>) to make space for the naturally regenerating beech that forms the basis of today's JB study site. From this year on, no other planned harvests took place. But after 1950, fir trees were selectively harvested in the JB study site and the adjacent areas. In 1960, the forest in the JB study site was ranked as an overaged stand dominated by beech, with 95 % canopy cover in the southern part (Anonymous 1960). At that time, the establishment of a nature reserve was discussed and thus the forest management plan prescribed "conservation management activities" (i.e. non-intervention management) that have been enforced on the site up to the present. The forest stand in the Jelení Bučina (JB) study site was officially proposed for legal protection in 1970 (as a "beech old-growth forest"), but the reserve was not declared until 2001. In terms of historical development, the current forest ecosystem in the study site is not a primary old-growth forest, but, for the most part, a remnant of the first generation forest following such a primary old-growth forest, resulting mostly from natural regeneration.

Historical development of the BFM study site was essentially similar. At the turn of the 19th century the site was covered by an old forest stand dominated by beech,

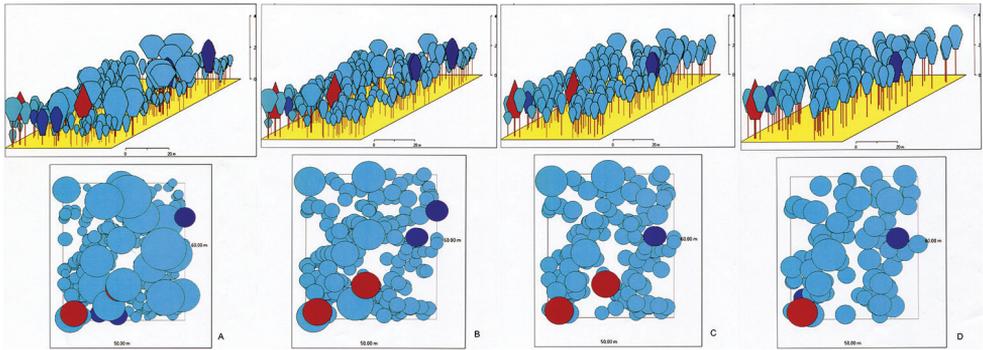
admixed with spruce, sycamore maple and elm. Until the end of the 18th century, selective logging was applied to support natural regeneration of beech. Around 1800, the old trees were almost completely harvested but it is not known whether it was a deliberate timber extraction or a forced harvest after a windstorm (Pechanec et al. 2015a). At the beginning of the 19th century, only few isolated free-standing trees remained from the original forest. The understory, which naturally regenerated after the radical harvest, later formed the canopy layer of today's forest stand in the BFM study site. In 1856, the regenerated saplings already formed an extensive young beech stand. Beech has regenerated naturally in gaps created by fallen old trees. Sporadically, the open gaps were also used for sowing and planting spruce, using seeds of local origin. Spruce was being introduced for economic reasons and its proportion in the forest was gradually increasing. In 1894, the forest in the BFM study site consisted of beech (70 %) and spruce (30 %), admixed with sycamore maple. However, spruce was being greatly affected by the local abiotic factors (especially windstorms), so its proportion in the study site had reduced to a mere admixture by 1952. In 1955, the Ministry of Culture declared the "Bučina pod Františkovou Myslivnou" a nature reserve to protect the 160–180 year old "sycamore-beech old-growth forest". Since that time, no deliberate timber extraction and artificial regeneration has been carried out, with the exception of a thinning harvest in the spruce stands, which were attached to the reserve due to land consolidation. The current forest in the BFM study site has a visual character of an "old-growth forest", although it is in fact a second generation forest after the primary old-growth forest. The forest is of high local genetic value, as it resulted from natural regeneration – similarly as in the JB study site.

The main findings from the historical analyses of both study sites can be generalized for Central European mountain beech forests as follows:

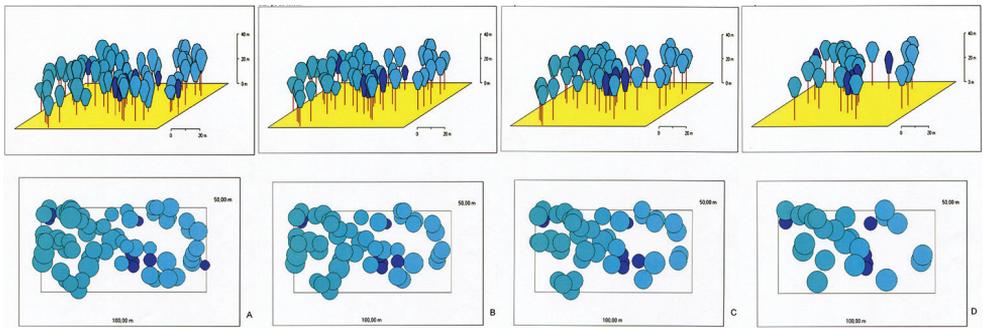
- A) A decrease in the occurrence of fir and a stable dominance of beech in natural forests is obvious during the long-term history of forest stands.
- B) Despite the influence of human activity, most beech forests in protected areas can be considered as natural forests with natural dynamics.
- C) In fully protected areas we can identify the first generation forest stands following former primary old-growth forest, resulting mostly from natural regeneration with a high potential for maintaining natural forest dynamics (and biodiversity) under the theory of the small development cycle.

### **Predicting future dynamics of forest ecosystems in the JB and BFM study sites**

Visualization of the growth simulation results for the JB study site shows that "non-intervention management" induces significant changes in the forest structure (compared to the current state) already in the first forecast horizon (25 years) (Fig. 2): The canopy layer of the mountain beech forest gradually thins out. For the second forecast horizon (50 years), the growth simulation shows a development trend to-

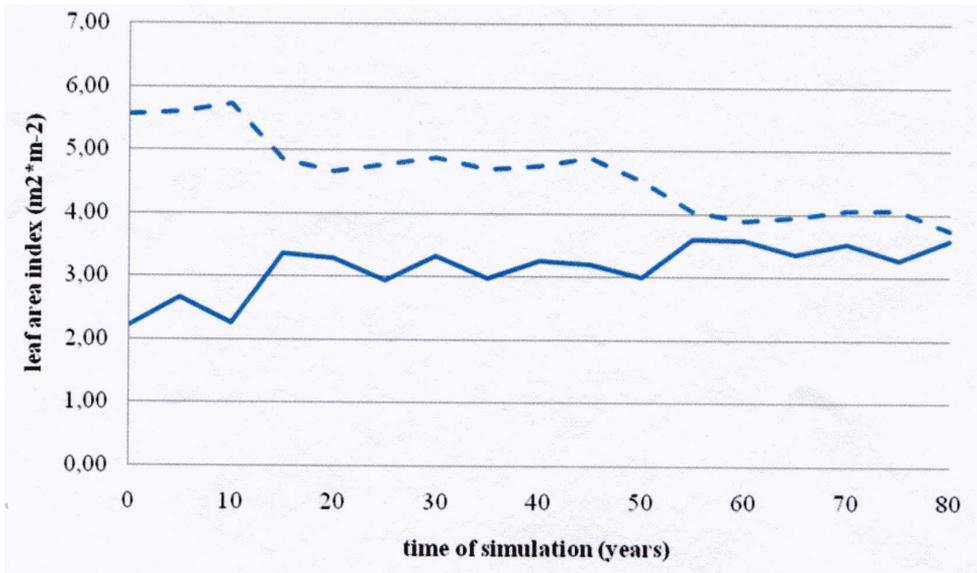


**Figure 2.** Growth simulation model for the Jeleni Bucina study site: current state (A) and future forest development for the periods of 25 years (B), 50 years (C), 80 years (D) (light blue: *Fagus sylvatica*, dark blue: *Acer pseudoplatanus*, red: *Picea abies*).



**Figure 3.** Growth simulation model for the Bucina pod Frantiskovou Myslivnou study site: current state (A) and future forest development for the periods of 25 years (B), 50 years (C), 80 years (D) (light blue: *Fagus sylvatica*, dark blue: *Acer pseudoplatanus*).

wards reduction of the forest stocking level and expansion of vacant bare gaps that provide space for natural regeneration of beech. The forest transitions from the disintegration stage to the growth stage, manifests clearly in the forecast horizon of 80 years. The growth simulation for the BFM study site shows a very similar trend (Fig. 3). The results of growth simulations for the diversified mountain beech forests in both study sites identically indicate that the trend of the gradual forest development leads to a partial shift in forest stages. This corresponds with the theoretical model of the small forest development cycle. The non-intervention management regime in both study sites advances the dominance of beech (Figs 2 and 3). In contrast, an increase in the proportion of sycamore maple, elm or fir does not seem very likely. The changes in leaf area index (LAI) for both study sites are shown in Figure 4. The initial values of LAI for the JB and BFM study sites calculated by the growth simulation model are 2.2 and 5.6, respectively. The long term development of LAI on both sites follows an identical trend – in 50 years, the LAI is equal for both sites as they reach the



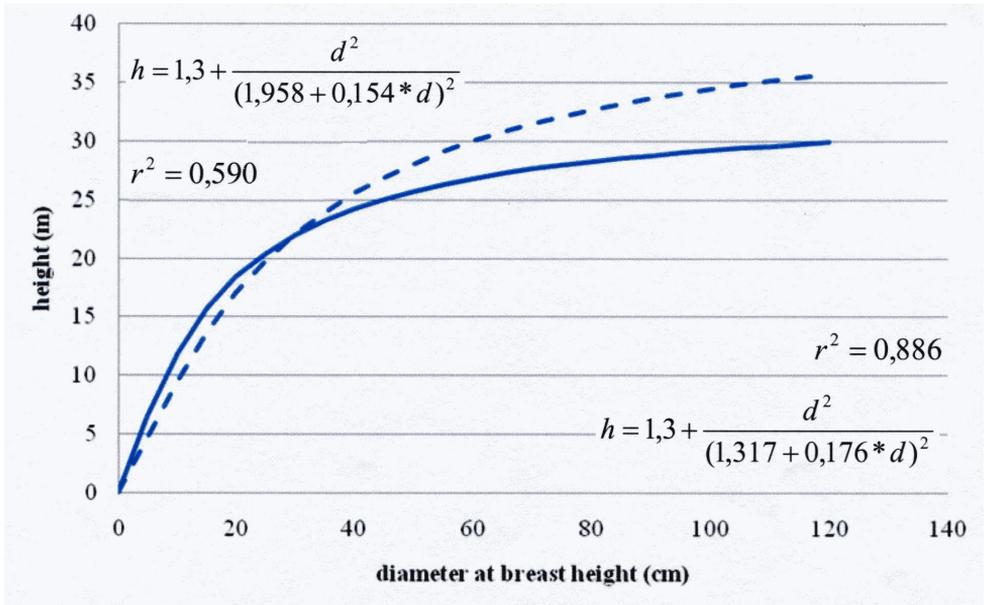
**Figure 4.** Time development of the leaf area index in study site Jeleni Bucina (solid line) and Bucina pod Frantiskovou Myslivnou (dashed line) for prediction period of 80 years.

growth stage with a dominance of beech which is tolerant to reduced light conditions for natural regeneration (Fig. 4).

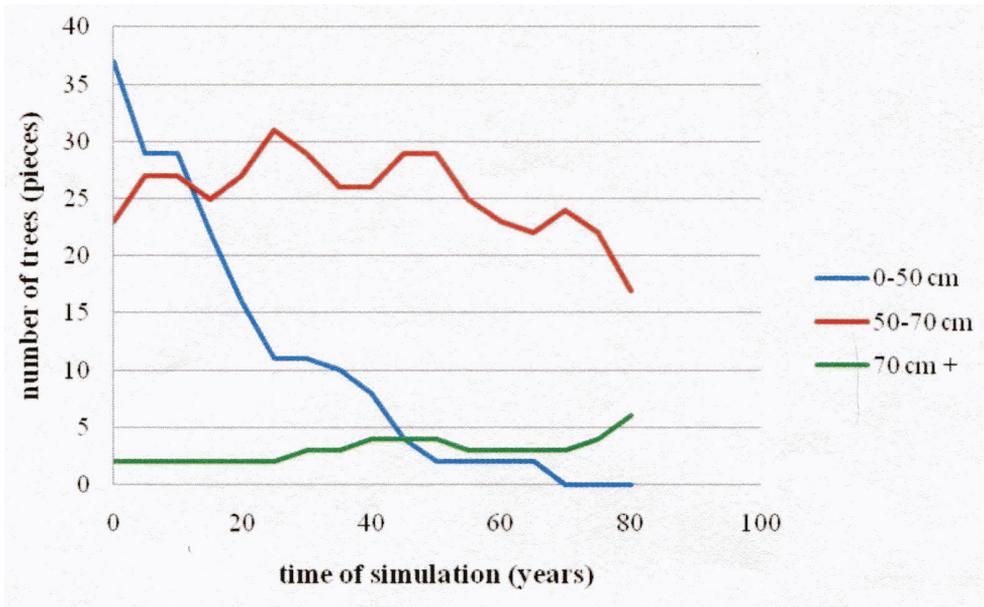
Figure 5 shows a graphical representation of the Naeslund height function for both study sites. Forest stands in the study sites have slightly different spatial structure (forest canopy cover in the BFM study site is more open and trees are higher than in the JB study site), which is reflected in the slight phase shift of the height function curve between the two sites (Fig. 5). Under the non-intervention regime, the proportion of trees with the smallest DBH in the BFM study site decreases (these individuals “move” to classes with higher DBH – see Fig. 6). In contrast, the proportion of individuals with DBH >50 cm remains remarkably stable in time (Fig. 6), which is important both in terms of maintaining the existing habitat character and stable state of the forest stand, as well as in terms of the potential natural regeneration. In the JB study site (Fig. 7), the prediction indicates a decrease of trees in the understory as compared to the status quo. Similarly as in the BFM study site, the proportion of large trees remains stable.

The long-term trend of spontaneous transition of forest ecosystems on both study sites from the disintegration stage to the growth stage is documented by the timber stocks prediction model (Fig. 8). Over the entire simulation period of 80 years, the total timber stocks in the JB and BFM study sites will decrease by 20.7 % (34.5 m<sup>3</sup>) and 25.2 % (45.7 m<sup>3</sup>), respectively.

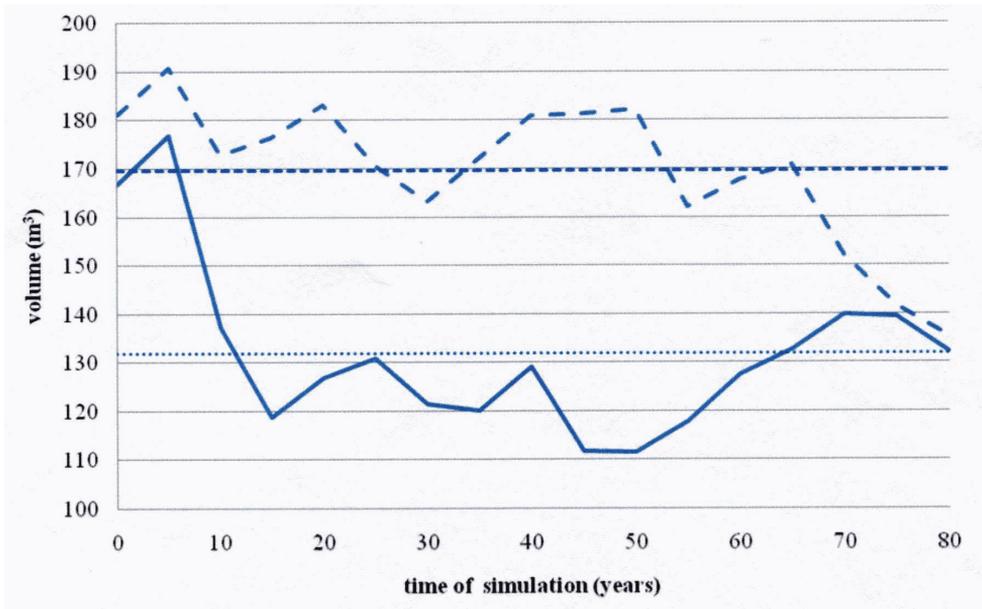
Table 2 provides an overview of three structural indices used in the study. The horizontal structure of the forest stands according to the Clark-Evans aggregation index has



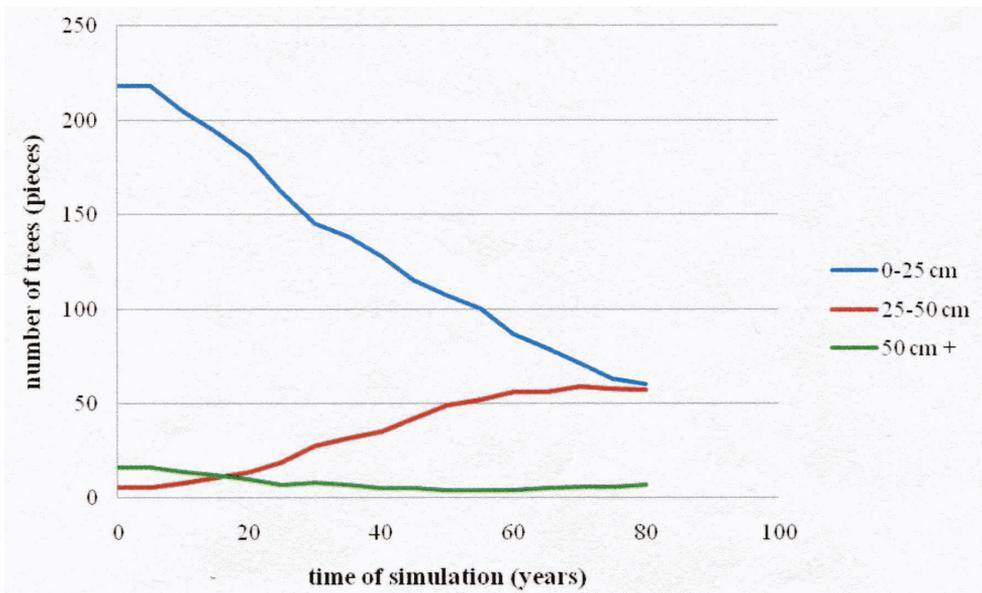
**Figure 5.** Naeslund height function for both study sites: Jeleni Bucina (solid line) and Bucina pod Frantiskovou Myslivnou (dashed line).



**Figure 6.** Prediction of time changes in tree diameter diversity (cm) of the beech stands in study site Bucina pod Frantiskovou Myslivnou.



**Figure 7.** Prediction of time changes in tree diameter diversity (cm) of the beech stands in study site Jeleni Bucina.



**Figure 8.** Prediction of time changes in standing tree volumes ( $m^3 \cdot ha^{-1}$ ) for both study sites: Jeleni Bucina (solid line) and Bucina pod Frantiskovou Myslivnou (dashed line).

**Table 2.** Indices prediction on the Jeleni Bucina (JB) and Bucina pod Frantiskovou Myslivnou (BFM) study sites after spontaneous development.

Time of simulation	Index					
	Clark-Evans index		Arten-profil index		Pielou segregation index	
	JB	BFM	JB	BFM	JB	BFM
0	0,880	0,852	0,574	0,463	0,437	0,442
5	0,880	0,852	0,578	0,467	0,434	0,448
10	0,886	0,865	0,615	0,489	0,483	0,498
15	0,923	0,855	0,623	0,469	0,533	0,515
20	0,942	0,860	0,618	0,474	0,527	0,522
25	0,953	0,864	0,592	0,470	0,492	0,508
30	0,967	0,897	0,613	0,498	0,525	0,545
35	0,963	0,897	0,600	0,498	0,536	0,548
40	0,960	0,897	0,588	0,488	0,527	0,548

a slight tendency towards lower aggregation. The trend is rather clear for the JB study site, but indistinct for the BFM study site. The spatial diversity of the forest stands (according to the Arten-profile index) on both study sites is medial with a very slight increase as a result of the decline of the parent stand followed by natural regeneration in the process of transitioning from the disintegration to the growth stage. The Pielou segregation index indicates that the spontaneous forest development of beech stands on both study sites tends to lead to a more regular arrangement of trees (Table 2).

The main conservation target of the management plan for both nature reserves as well as Natura 2000 sites (comprising the JB and BFM study sites) is to maintain the current character of the habitat, as required by the European Union Habitat Directive No. 92/43/EEC. From this perspective, it is notable that the growth simulation model predicts changes in the spatial structure and shifts in the development stages of modeled forest ecosystems under the non-intervention regime for the next 80 years (see 3.2), but it does not assume any significant changes in the character of the habitat code 9140 as defined by the Natura 2000 classification system.

## Discussion and conclusion

As a consequence of changing climatic conditions in Europe (CO<sub>2</sub> content, air temperature, precipitation, heat waves and drought episodes) it is expected that European beech forests will change in the future (Bošela et al. 2016; Machar et al. 2017a). According to present knowledge, beech forests will probably remain the most important natural forests in temperate Europe during this century (Lindner et al. 2014). Some of the most important predictions regarding European beech forest under climate changes are the following: (1) The geographical area of European beech will shift northwards and will reach to higher altitudes in the mountains (Garamvoelgyi and Hufnagel 2013). (2) The dominance of European beech in temperate European deciduous for-

ests will be broken in some cases, because European beech tends to retreat in upland and submontane landscapes where the summer seasons will become drier in the future (Saltré et al. 2015). (3) Increasing CO<sub>2</sub> content can increase the biomass (and wood production) of beech stands in newly occupied areas at higher altitudes (Machar et al. 2017b). Králíček et al. (2017) confirmed these results by founding of strong correlation between the radial increment of European beech and the temperature in mountain areas. Long-term simulations of climate change's impact on forest dynamics in Silver fir-European beech stands in Dinaric Mountains in Slovenia (Mina et al. 2017) revealed that European beech will be favoured by higher temperatures in contrast to drought-induced growth reduction in Silver fir. But generally there is a knowledge gap on the details of the floristic structure in the future beech forest communities under changing climate conditions.

Predicting future forest dynamics in stand-scale is an essential component of sustainable forest management (Thurnher et al. 2017). The general shift from forest management aimed at pure forest stands (coniferous monoculture) to sustainable forest management aimed at multifunctional uneven-aged mixed-species forests requires modern tools for yield projections which predict future stand development for different management regimes, including conservation targets (Simon et al. 2015). As a result, single-tree growth simulators have been developed. Tree growth simulators predict the future growth of forest in stand-scale and can be used as support tools for conservation forest biodiversity. An important advantage of tree growth simulators are there flexibility, based on using forest inventory data as inputs for modelling of silvicultural management scenarios in order to produce management plans, which can be used for forested protected areas. A combination of routine forest inventory data and the set of functions implemented in the transparent forecast system can be an important support tool for conservation planning in the frame of conservation forest biodiversity. Growth simulation models for the prediction of future forest development represent a promising tool for sustainable management of forest ecosystems (Pretzsch et al. 2015, Simon et al. 2014). However, growths models have not yet been fully integrated into the forest management practice (Porté and Bartelink 2002, Machar et al. 2016) and are rarely used to assess the forest management strategies in conservation areas (Sodtke et al. 2004). The advantage of growth simulation models lies in reasonably accurate predictions of the future character of forest stands under variable growth conditions and types of forest management (Kolström 1998). We believe that the combination of a growth simulation model with the analysis of historical forest development could be more widely used, especially to assess management plans for conservation areas that consist of forest ecosystems (Idle and Bines 2005, Machar 2010). Understanding the historical development of forest stands can significantly improve our understanding of their current state (Honnay et al. 2004).

The multidisciplinary combination of the two different methods (from social and natural sciences) helps to make the assessment of forest management strategies in conservation areas more objective, as it enables the prediction of likely development of forest stands under specific management plans in a specific nature reserves (Peng 2000).

This is particularly important in the Natura 2000 conservation areas (Parviainen and Frank 2003) because the growth model enables the prediction of the likely future development of forest ecosystems based on the conservation targets of a particular forest management plan (Villard and Jonsson 2009).

Based on the combined results of the growth simulation model and the historical analysis, it is possible to evaluate the current management strategy and suggest potential adjustments in the forest management plan, in order to comply with the mission of a protected area, i.e. retaining the defined habitat character and biodiversity (Pechanec et al. 2015b).

Simulation results for both study sites support the theory that the anthropogenic influence is a major cause of fir decline in European mountain beech forests (Paluch 2007). Our results from historical analyses in both of the study sites confirmed this fact. This finding is important in the frame of historical background of European mountain forests, where generally old-growth forests originally co-dominated by fir and beech appear to be transitioning to forests dominated by beech, regardless of the disturbance history, which suggest that beech expansion may be a robust process (Jaloviari et al. 2017). From the nature conservation point of view, the return of fir as a natural component of mountain beech forest in the nature reserve would be desirable (Kral et al. 2014). As shown by the growth simulation model, increasing the proportion of fir in both study sites would only be possible under a targeted intervention by forest practitioners into the current non-intervention management regime. The fir could be reintroduced in these ecosystems, provided that a planting material of local origin is available and individual protection of seedlings against ungulates is secured (Vacek et al. 2014).

The relative value of LAI depends on the character of assimilation organs, that is, on a forest type, as demonstrated by empirical measurements by Jarvis and Leverenz (1983). The high LAI value for the BFM study site reflects a significant reduction in solar radiation as it passes through highly differentiated vegetation. The calculated initial (i.e. current) LAI value for the JB study site is also relatively high. The LAI value for European temperate forests ranges from 0 (bare areas with no vegetation) to 6 (dense forest stands) (Fabrika and Pretzsch 2011).

The computed shape of stand height curves is characteristic only for a particular stand age, and the curves shift with stand age (Laar and Akca 2007). This fact corresponds with findings presented in this paper for both study sites (Fig 5.) in the Jeseníky Mountains (Senfeldr and Madera 2011).

Differences in altitude occurrence of European beech can be considered as influences of past silvicultural management (Štefančík and Bošela 2014). Also the long forest continuity is an important factor in supporting the forest's specialist organisms (Ódor and Standovár 2001). The relationship between the richness of ancient forest indicator plants and other biodiversity in the case study of macrofungi was presented by Hofmeister et al. (2014). Forest stand structure in Europe is generally the result of the environmental history of a phytocoenosis and includes anthropic influences. The study of the disturbances and structural dynamics of forests in the past is very important for

conservation efforts in fully protected areas, as shown by Bianchi et al. (2011) in beech forests in the Apennines. Fully-protected natural forest reserves with long-term forest continuity are living nature laboratories, where the process of forest dynamics can be investigated over long time periods. Thus historical reconstructions of past changes in forest dynamics and human management activities in forest stand-scale can be very a important tool for forest management that attempts to emulate natural forest dynamics in order to conservation forest biodiversity, as proved Firm et al. (2009) based on study of the disturbance history of mountain forests in the Slovenian Alps.

The historical analysis of forest development on both study sites revealed that the current structure of forest stands is strongly influenced by the former management. If the modification of the tree species composition is desired for conservation purposes, in order to get closer to the theoretical assumption of potential vegetation, then some form of management intervention will be necessary – e.g. the artificial reintroduction of fir that disappeared due to anthropogenic activities in the past (see section 3.1).

For both study sites, the growth simulation model indicates changes in forest development over an 80-year time horizon. These future growth changes correspond with the theoretical model of the small development cycle of European temperate forests. They are significant in terms of biodiversity protection, as the long-term spontaneous development of forest ecosystems leads to the creation of valuable habitats for numerous endangered species (Sebkova et al. 2011). In the long term, non-intervention forest management will undoubtedly contribute to an increase of dead wood material in the ecosystem, and thus affect the biodiversity of organisms dependent on various forms of decomposing wood and dying old trees (Vandekerkhove et al. 2009).

Based on the synthesis of the historical research and the growth simulation model, we conclude that in the next 80 years the current non-intervention forest management, which is based on spontaneous (succession) development of the ecosystem, does not contradict the Natura 2000 requirement of protecting this habitat type. From this perspective, the forest management plan for the JB and BFM study sites (and the reserves in which they are located) does not require any corrections in the context of their conservations goals, that is, maintaining the habitat character and biodiversity.

The historical research revealed that both study sites (although having a visual character of an old-growth forest and therefore being protected as nature reserves and Natura 2000 sites) are in fact a second-generation forest following the previous primary old-growth forest. The growth simulation model for both study sites predicts a partial shift in forest stages, corresponding with the theoretical model of the small development cycle of European temperate forest. These future growth changes in the forest ecosystem are significant in terms of biodiversity protection, as the long-term spontaneous development of forest ecosystems leads to the creation of valuable habitats for numerous endangered species.

The studied forest ecosystems are part of the European network of nature protection areas – Natura 2000. The forest management strategy applied in both of the study sites, resulting from the categorization of protected areas by the IUCN (Dudley 2008), is a non-intervention management (IUCN Category Ia – Strict

Nature Reserve). The presented results show that the non-intervention management for mountain beech forest in the next 80 years complies with the Natura 2000 conservation targets to maintain the existing character of the habitat. The multidisciplinary research helps to make the assessment of forest management (in any geographical and environmental conditions) more objective, provided that basic historical and dendrometric data about the studied forest ecosystem are available. The application of this multidisciplinary approach is therefore particularly appropriate for assessing the suitability of selected management strategies in protected areas. The results of this study suggest that combining the research on historical development with a forest growth simulation can be used as a suitable decision-support tool to assess management strategies for forest habitats in protected areas worldwide.

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## **References**

- Agnoletti M, Anderson S (2000) *Methods and Approaches in Forest History*. CABI Publishing, Cambridge, 1–368.
- Angelstam P, Kuuluvainen T (2004) Boreal forest disturbance regimes, successional dynamics and landscape structures: A European perspective. *Ecological Bulletins* 51: 117–136.
- Angelstam P, Persson R, Schlaepfer R (2004) The sustainable forest management vision and biodiversity – barriers and bridges for implementation in actual landscapes. *Ecological Bulletins* 51: 29–49.
- Anonymous (1689) Register of the Velké Losiny Estate. State Regional Archive Janovice, signature 56/22. Unpublished archive document.
- Anonymous (1750) Obrigkeitliche Bekanntnis-Tabelle der Herrschaft Wiesenberg. State Regional Archive Janovice, signature 5. Unpublished archive document.
- Anonymous (1862) Forst-Revier Ludwigsthal, Revision des Waldstandes. State Regional Archive Opava, signature 1.477 a 5.799. Unpublished archive document.
- Anonymous (1866) Forest Management Plan for the Hubertov District. State Regional Archive Opava, signature 1.423. Unpublished archive document.
- Anonymous (1875) Forstverwaltung Huberstkirch, Einrichtung vom Forstreviere Ludwigsthal. State Regional Archive Opava, signature 1.479 a 5.800. Unpublished archive document.
- Anonymous (1910) Forsterwaltung Würbenthal. State Regional Archive Opava, signature 1.541 a 5.945. Unpublished archive document.

- Anonymous (1960) Forest Management Plan for the Ludvíkov district in 1960–1969. Forest Management Institute, Olomouc branch. Work document for internal use.
- Barna M (2011) Natural regeneration of *Fagus sylvatica* L.: a Review. *Austrian Journal of Forest Science* 128(2): 71–91. Accession Number: WOS:000292738600001
- Bianchi L, Bottacci A, Calamini G, Maltoni A, Mariotti B, Quilghini G, Salbitano F, Tani A, Zoccola A, Paci M (2011) Structure and dynamics of a beech forest in a fully protected area in the northern Apennines (Sasso Fratino, Italy). *iForest* 4: 136–144. <https://doi.org/10.3832/ifor0564-004>
- Bílek L, Remes J, Zahradník D (2011) Managed vs. unmanaged. Structure of beech forest stands (*Fagus sylvatica* L.) after 50 years of development. Central Bohemia. *Forest Systems* 20(1): 122–138. Accession Number: WOS:000289657600010
- Bohn U, Neuhäusl R, Gollub G, Hettwer C, Neuhäuslová Z, Schlüter H, Weber H (2002) Map of the Natural Vegetation of Europe. Scale 1:2 500 000. Landwirtschaftsverlag, Münster.
- Bošela M, Štefančík I, Petráš R, Vacek S (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agricultural and Forest Meteorology* 222: 21–31. <https://doi.org/10.1016/j.agrformet.2016.03.005>
- Bouzek J (2011) Prehistory of the Bohemian Lands in the European Context. Triton, Prague, 1–173.
- Brukas V, Sallnäs O (2012) Forest management plan as a policy instrument: Carrot, stick or sermon? *Land Use Policy* 29. <https://doi.org/10.1016/j.landusepol.2011.10.003>
- Chytrý M, Kučera T, Kočí M, Grulich V, Lustyk P (2010) Habitat Catalogue of the Czech Republic. Agency of Nature Conservation and Landscape Protection, Prague, 1–445.
- Clark PJ, Evans FC (1954) Distance to nearest neighbour as a measure of spatial relationship in populations. *Ecology* 35: 445–453. <https://doi.org/10.2307/1931034>
- Degen T, Devillez F, Jacquemart AL (2005) Gaps promote plant diversity in beech forests (*Luzulo-Fagetum*), North Vosges, France. *Annales Forest Science* 62: 429–440. <https://doi.org/10.1051/forest:2005039>
- Dudley N (2008) Guidelines for Applying Protected Area Management Categories. IUCN, Gland, Switzerland, 8–11. <https://doi.org/10.2305/IUCN.CH.2008.PAPS.2.en>
- Durský J (1997) Modellierung der Absterbeprozesse in Rein – und Mischbeständen aus Fichte und Buche. *Allgemeine Forst und Jagtzeitung* 168(6/7): 131–134.
- Fabrika M, Durský J (2006) Implementing Tree Growth Models in Slovakia. In: Hasenauer H (Ed.) *Sustainable Forest Management. Growth Models for Europe*. Springer, The Netherlands, 315–341. [https://doi.org/10.1007/3-540-31304-4\\_19](https://doi.org/10.1007/3-540-31304-4_19)
- Fabrika M, Pretsch H (2011) Analysis and modelling of forest ecosystems. Technical University, Zvolen, 1–599.
- Fedrowitz K, Koricheva J, Baker SC, Lindenmayer DB, Palik B, Rosenvald R, Beese W, Franklin JF, Kouki J, Macdonald E, Messier C, Sverdrup-Thygeson A, Gustafsson L (2014) Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology* 51: 1669–1679. <https://doi.org/10.1111/1356-2664.12289>
- Firm D, Nagel TA, Diaci J (2009) Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *Forest Ecology and Management* 257: 1893–1901. <https://doi.org/10.1016/j.foreco.2008.09.034>

- Fischer A (1997) Vegetation dynamics in European beech forests. *Annali Di Botanica* LV, 59–76.
- Garamvoelgyi A, Hufnagel L (2013) Impacts of climate change on vegetation distribution no.1. Climate change induced vegetation shifts in the Palearctic region. *Applied Ecology and Environmental Research* 11: 79–122. [https://doi.org/10.15666/aeer/1101\\_079122](https://doi.org/10.15666/aeer/1101_079122)
- Gebert C, Verheyden-Tixier H (2001) Variations on diet composition of red deer in Europe. *Mammal Review* 31: 189–201. <https://doi.org/10.1046/j.1365-2907.2001.00090.x>
- Glatthorn J, Pichler V, Hauck M, Leuschner C (2017) Effects of forest management on stand leaf area: Comparing beech production and primeval forests in Slovakia. *Forest Ecology and Management* 389: 76–85. <https://dx.doi.org/10.1016/j.foreco.2016.12.025>
- Götmark F (2013) Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications. *Forest Ecology and Management* 306. <https://doi.org/10.1016/j.foreco.2013.06.014>
- Hahn K, Fanta J (2001) Contemporary Beech Forest Management in Europe. Research report of the NatMan project.
- Hofmeister J, Hošek J, Brabec M, Dvořák D, Beran M, Deckerová H, Burel J, Kříž M, Borovička J, Běťák J, Vašutová M (2014) Richness of ancient forest plant species indicates suitable habitats for macrofungi. *Biodiversity and Conservation* 23: 2015–2031. <https://doi.org/10.1007/s10531-014-0701-y>
- Holeksa J, Saniga M, Szwagrzyk J, Czerniak M, Staszynska K, Kapusta P (2009) A giant tree stand in the West Carpathians – an exception or a relic of formerly widespread mountain European forests? *Forest Ecology and Management* 257: 1577–1585. <https://doi.org/10.1016/j.foreco.2009.01.008>
- Honnay O, Verheyen K, Bossuyt B, Hermy M (2004) Forest biodiversity: Lessons from history to conservation. CABI Publishing, Wallingford, 1–358. <https://doi.org/10.1079/97808-51998022.0000>
- Hosek E (1970) Development of damages caused by abiotic factors in the forests of Hrubý Jeseník. *Campanula* 1970(1): 13–21.
- Idle ET, Bines TJH (2005) Management planning for protected Areas. Eurosite, English Nature, Peterborough, 1–144.
- Jaloviar P, Saniga M, Kucbel S, Pittner J, Vencurik J, Dovciak M (2017) Seven decades of changes in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. *Forest Ecology and Management* 399: 197–205. <https://dx.doi.org/10.1016/j.foreco.2017.05.036>
- Janik D, Adam D, Hort L, Král K, Šamonil P, Unar P, Vrška T (2014) Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. *European Journal of Forest Research* 133. <https://doi.org/10.1007/s10342-014-0819-1>
- Jarvis PG, Leverenz JW (1983) Productivity of temperate deciduous and evergreen forests. In: Lange OS, Nobel PS, Osmond CB, Ziegler H (Eds) *Physiological Plant Ecology IV*, Springer, The Netherlands, 233–280.
- Jongman RHG (1995) Nature conservation planning in Europe: Developing ecological networks. *Landscape and Urban Planning* 32. [https://doi.org/10.1016/0169-2046\(95\)-00197-O](https://doi.org/10.1016/0169-2046(95)-00197-O)

- Kelemen K, Mihók B, Gálhidy L, Standovár T (2012) Dynamics Response of Herbaceous Vegetation to Gap Opening in a Central European Beech Stand. *Silva fennica* 46: 53–65. <https://doi.org/10.14214/sf.65>
- Kenderes K, Mihók B, Standovár T (2008a) Thirty years of gap dynamics in a central European beech forest reserve. *Forestry* 81: 112–123. <https://doi.org/10.1093/forestry/cpn001>
- Kenderes K, Král K, Vřška T, Standovár T (2008b) Natural Gap Dynamics in a Central European Mixed Beech-Spruce-Fir Old-Growth Forest. *Ecoscience* 16. <https://doi.org/10.2980/16-1-3178>
- Knappe JV (1803) Forest Management Plan for the Bruntál Estate in 1803–1813. State Regional Archive Opava, signature 1.391. Unpublished archive document.
- Kopecký M, Hédl R, Szabó P (2013) Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology* 50: 79–87. <https://doi.org/10.1111/1365-2664.12010>
- Kolström T (1998) Ecological simulation model for studying diversity of stand structure in boreal forests. *Ecological Modelling* 111: [https://doi.org/10.1016/S0304-3800\(98\)00102-1](https://doi.org/10.1016/S0304-3800(98)00102-1)
- Korpel S (1995) *Die Urwälder der Westkarpaten*. Stuttgart, Jena, New York, 310 pp.
- Král K, Janík D, Vřška T, Adam D, Hort L, Unar P, Šamonil P (2010) Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. *Forest Ecology and Management* 260: 2196–2203. <https://doi.org/10.1016/j.foreco.2010.09.020>
- Král K, Valtera M, Janík D, Samonil P, Vřška T (2014) Spatial variability of general stand characteristics in central European beech-dominated natural stands – Effect of scale. *Forest Ecology and Management* 328. <https://doi.org/10.1016/j.foreco.2014.05.046>
- Králíček I, Vacek Z, Vacek S, Remeš J, Bulušek D, Král J, Štefančík I, Putalová T (2017) Dynamics and structure of mountain autochthonous spruce-beech forests: impacts of hill-top phenomenon, air pollutants and climate. *Dendrobiology* 77: 119–137. <https://doi.org/10.12657/denbio.077.010>
- Krones V (1827) Forest Management Plan for the Bruntál Estate in 1827–1836. State Regional Archive Opava, signature 1.544. Unpublished archive document.
- Laar A, Akca A (2007) *Forest Mensuration*. Springer, The Netherlands, 1–383. <https://doi.org/10.1007/978-1-4020-5991-9>
- Leibundgut H (1959) Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. *Schweiz. Z. Forstwes*, 110: 111–124.
- Leibundgut H (1993) *Europäische Urwälder*. Paul Haupt, Bern, 1–174.
- Lindner M, Fitzgerald JB, Zimmermann NE, Reyer C, Delzon S, van der Maaten E, Schelhaas MJ, Lasch P, Eggers J, van der Maaten-Theunissen M, Suckow F, Psomas A, Poulter B, Hanewinkel M (2014) Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *Journal of Environmental Management* 146: 69–83. <https://doi.org/10.1016/j.jenvman.2014.07.030>
- Lysik M (2008) Ten years of change in ground-layer vegetation of European beech forest in the protected area (Ojcow National Park, South Poland). *Polish Journal of Ecology* 56: 17–31.
- Machar I (2010) Attempt to summarize the problems: Is a sustainable management of floodplain forest geobiocenoses possible? In: Machar I (Ed) *Biodiversity and target management*

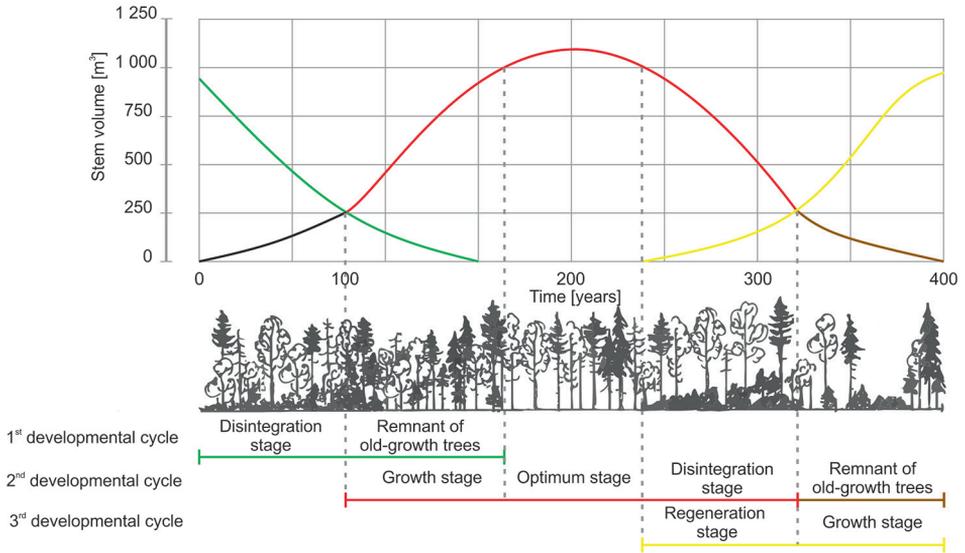
- of floodplain forests in the Morava river basin (Czech Republic). Palacky University, Olomouc, 189–226. Accession Number: WOS 000328003200016
- Machar I (2012) Protection of nature and landscapes in the Czech Republic selected current issues and possibilities for their solution. *Ochrana přírody a krajiny v Ceske republice*, vols I and II. Palacky University, Olomouc, 9–853. Accession Number: WOS:000334387900001
- Machar I, Pechanec V, Brus J, Kilianova H, Kirchner K (2014) Forest management at the upper treeline in Jeseniky Mountains (Czech Republic). In: SGEM (Ed) *International Multidisciplinary Scientific GeoConference-SGEM*, Albena (Bulgaria), June 2014. STEF92 Technology Ltd, 361–366. Accession Number: WOS:000371596300049
- Machar I, Simon J, Rejsek K, Pechanec V, Brus J, Kilianova H (2016) Assessment of forest management in protected areas based on multidisciplinary research. *Forests* 7. <https://doi.org/10.3390/f7110285>
- Machar I, Vlckova V, Bucek A, Vozenilek V, Salek L, Jerabkova L (2017a) Modelling of Climate Conditions in Forest Vegetation Zones as a Support Tool for Forest Management Strategy in European Beech Dominated Forests. *Forests* 8, 3, article no. 82. <https://doi.org/10.3390/f8030082>
- Machar I, Vozenilek V, Kirchner K, Vlckova V, Bucek A (2017b) Biogeographic model of climate conditions for vegetation zones in Czechia. *Geografie* 122(1): 64–82.
- Miko L (2012) Nature and landscape protection in the European context. In: Machar I, Drobilova L (Eds) *Nature and Landscape Protection in the Czech Republic*. Palacky University (Olomouc): 43–49. Accession Number: WOS:000334387900005
- Mina M, Bugmann H, Klopčič M, Cailleret M (2017) Accurate modelling of harvesting is key for projecting future forest dynamics: a case study in the Slovenian mountains. *Regional Environmental Changes* 17: 49–64. <https://doi.org/10.1007/s10113-015-0902-2>
- Modrý M, Hubený D, Rejsek K (2004) Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. *Forest Ecology and Management* 188: 185–195. <https://doi.org/10.1016/j.foreco.2003.07.029>
- Moravec J, Husová M, Chytrý M, Neuhäuslová Z (2000) *Vegetation Survey of the Czech Republic. Volume 2. Hygrophilous, mesophilous and xerophilous deciduous forests [in Czech]*; Academia, Praha, 1–319.
- Nozicka J (1957) Overview of the development of our forests. *SZN*, Prague, 1–246.
- Ódor P, Standovár T (2001) Richness of bryophyte vegetation in near-natural and managed beech stands: effects of management induced differences in dead wood. *Ecological Bulletins* 49: 219–229.
- Oprsal Z, Kladiivo P, Machar I (2016) The role of selected biophysical factors in long-term land-use change of cultural landscape. *Applied Ecology and Environmental Research* 14(2): 23–40. Accession Number: WOS:000375222100002
- Paluch JG (2007) The spatial pattern of a natural European Beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forests: A patch-mosaic perspective. *Forest Ecology and Management* 253. <https://doi.org/10.1016/j.foreco.2007.07.013>
- Parviainen J, Bucking W, Vandekerckhove K, Schuck A, Paivinen R (2000) Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-Cost-Action E4). *Forestry* 73: 107–118. <https://doi.org/10.1093/forestry/73.2.107>

- Parviainen J, Frank G (2003) Protected forests in Europe approaches – harmonising the definitions for international comparison and forest policy making. *Journal of Environmental Management* 67. [https://doi.org/10.1016/S0301-4797\(02\)00185-8](https://doi.org/10.1016/S0301-4797(02)00185-8)
- Pechanec V, Machar I, Kirchner K, Brus J (2015a) Ecosystem evaluation in the frame of environmental impact assessment. Case study from the Czech Republic. In: SGEM (Ed.) *International Multidisciplinary Scientific GeoConference-SGEM*, Albena (Bulgaria), June 2015. STEF92 Technology Ltd, 223–230. Accession Number: WOS:000370813400029
- Pechanec V, Brus J, Kilianova H, Machar I (2015b) Decision support tool for the evaluation of landscapes. *Ecological Informatics* 30. <https://doi.org/10.1016/j.ecoinf.2015.06.006>
- Peng C (2000) Growth and yield models for uneven-aged stands: Past, present and future. *Forest Ecology and Management* 132. [https://doi.org/10.1016/S0378-1127\(99\)00229-7](https://doi.org/10.1016/S0378-1127(99)00229-7)
- Pielou EC (1977) *Mathematical Ecology*. Willey, New York, 1–385.
- Podlaski R (2004) A development cycle of the forest with fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.) in its species composition in the Swietokrzyski National Park. *Journal of Forest Science* 50: 55–66.
- Porté A, Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling* 150: [https://doi.org/10.1016/S0304-3800\(01\)00476-8](https://doi.org/10.1016/S0304-3800(01)00476-8)
- Pretzsch H (2005) Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). Evidence from long-term experimental plots. *European Journal of Forest Research* 124: <https://doi.org/10.1007/s10342-005-0068-4>
- Pretzsch H (2010) *Forest Dynamics, Growth and Yield*. Springer, Heidelberg, 1–664. <https://doi.org/10.1007/978-3-540-88307-4>
- Pretzsch H, Biber P, Dursky J, von Gadow K, Hasenauer H, Kändler G, Kenk K, Kublin E, Nage J, Pukkala T, Skovsgaard JP, Sotke R, Sterba H (2002) Recommendations for Standardized Documentation and Further Development of Forest Growth Simulators. *Forstwissenschaftliches Centralblatt* 121(3): 138–151.
- Pretzsch H, Forrester DI, Rötzer T (2015) Representation of species mixing in forest growth models. A review and perspective. *Ecological Modelling* 313. <https://doi.org/10.1016/j.ecolmodel.2015.06.044>
- Remmert H (1992) Das Mosaik-Zyklus-Konzept und seine Bedeutung für den Naturschutz. Eine übersicht. *Laufener Seminarbeiträge* 2/92: 45–57.
- Roloff A (1992) Mögliche Auswirkungen des Treibhauseffektes auf die Konkurrenzsituation in Waldökosystemen. *Forstarchiv* 63: 4–10.
- Roth P (2003) European Union legislation on nature protection (Directive 79/409/EEC, Directive 92/43/EEC, Commission Decision 97/266/EC). Ministry of Environment of the Czech Republic, Prague, 1–181.
- Rubner K (1925) Das Urdwaldproblem. *Forstarchiv* 1: 145–151.
- Rugani T, Diaci J, Hladnik D (2013) Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. *PloS One* 8: e52641. <https://doi.org/10.1371/journal.pone.0052641>
- Salré F, Duputié A, Gaucherel C, Chuine I (2015) How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. *Global Change Biology* 21: 897–910. <https://doi.org/10.1111/gcb.12771>

- Samonil P, Vrska T (2007) Trends and cyclical changes in natural fir-beech forests at the north-western edge of the Carpathians. *Folia Geobotanica* 42. <https://doi.org/10.1007/BF02861699>
- Saniga M (1999) Structure, Production and Regeneration Processes of the Dobročský Prales. Technical University, Zvolen, 1–64.
- Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. *Forest Ecology and Management* 261. <https://doi.org/10.1016/j.foreco.2011.01.011>
- Schmidt-Vogt H (1985) Struktur und Dynamik natürlichen Fichtenwälder in der Nadelwaldzone. *Z. f. Forstwesen* 136(12): 977–974.
- Schultze J, Gärtner S, Bauhus J, Meyer P, Reif A (2014) Criteria to evaluate the conservation value of strictly protected forest reserves in Central Europe. *Biodiversity Conservation* 23. <https://doi.org/10.1007/s10531-014-0787-2>
- Sebkova B., Samonil P., Janik D, Adam D, Kral K, Vrska T, Hort L, Unar P (2011) Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management* 262. <https://doi.org/10.1016/j.foreco.2011.05.028>
- Senfelder M, Madera P (2011) Population Structure and Reproductive strategy of Norway spruce (*Picea abies* L. Karst) above the Former Pastoral Timberline in the Hruby Jeseník Mountains, Czech Republic. *Mountain Research and Development* 31(2). <https://doi.org/10.1659/MRD-JOURNAL-D-10-00073.1>
- Simon J (2007) Method of creation of forest management plan based on imaging analysis. In: Vacek S (Ed) *Management of Natural Forests*. Lesnická práce, Kostelec nad Černými Lesy, 138–140.
- Simon J, Machar I, Bucek A (2014) Linking the historical research with the growth simulation model on hardwood floodplain forests. *Polish Journal of Ecology* 62(2): 273–288. <https://doi.org/10.3161/104.062.0208>
- Simon J, Machar I, Brus J, Pechanec V (2015) Combining a growth simulation model with acoustic wood tomography as a decision support tool for adaptive management and conservation of forest ecosystems. *Ecological Informatics* 30: 309–312. <https://doi.org/10.1016/j.ecoinf.2015.08.004>
- Skokanova H, Eremiasova R (2013) Landscape functionality in protected and unprotected areas: Case studies from the Czech Republic. *Ecological Informatics* 14. <https://doi.org/10.1016/j.ecoinf.2012.11.007>
- Sodtke R, Schmidt M, Fabrika M, Nagel J, Dursky J, Pretzsch H (2004) Anwendung und Einsatz von Einzelbaummodellen als Komponenten von entscheidungsunterstützenden Systemen für die strategische Forstbetriebsplanung. *Forstarchiv* 75: 51–64.
- Splechtna BE, Gratzner G, Black B (2005) Disturbance history of a European old-growth mixed species forest – a spatial dendro-ecological analysis. *Journal of Vegetation Science* 16: 511–522.
- Standovár T, Kenderes K (2003) A review of natural stand dynamics in beech woods of east central Europe. *Applied Ecology and Environmental Research* 1: 19–46. <https://doi.org/10.15666/aeer/01019046>

- Standovár T, Ódor P, Aszalós R., Gálhidy L (2006) Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. *Community Ecology* 7(2): 199–209. <https://doi.org/10.1556/ComEc.7.2006.2.7>
- Standovár T, Horváth S, Aszalós R (2017) Temporal changes in vegetation of a virgin beech woodland remnant: stand-scale stability with intensive fine-scale dynamics governed by stand dynamics events. *Nature Conservation* 17: 35–56. <https://doi.org/10.3897/nature-conservation.17.12251>
- Štefančík I, Bošela M (2014) The influence of different thinning methods on quantitative wood production of European beech on two eutrophic sites in Western Carpathians. *Journal of Forest Science* 60: 406–416.
- Thurnher C, Klopff M, Hasenauer H (2017) MOSES – A tree growth simulator for modelling stand response in Central Europe. *Ecological Modelling* 352: 58–76. <https://dx.doi.org/10.1016/j.ecolmodel.2017.01.013>
- Torres-Rojo JM, Vilcko F, von Gadow K (2014) Evaluating management regimes for European beech forests using dynamic programming. *Forest Systems* 23(3). <https://doi.org/10.5424/fs/2014233-05296>
- Ujházy K, Križová E, Vančo M, Freňáková E, Ondruš M (2005) Herb layer dynamics of primeval fir-beech forests in central Slovakia. In Hamor F, Commarmot B (Eds) *Natural forests in the temperate zone of Europe – Values and Utilisation Conference Proceedings (2005)* Swiss Federal Research Institute WSL (Birmensdorf) and Carpathian Biosphere Reserve, Rakhiv, 142–143.
- Vanbergen AJ, Woodcock BA, Watt AD, Niemelä J (2005) Effect of land-use heterogeneity on carabid communities at the landscape level. *Ecography* 28: 3–16. <https://doi.org/10.1111/j.0906-7590.2005.03991.x>
- Vacek Z, Vacek S, Bilek L, Kral J, Remes J, Bulusek D, Kralicek I (2014) Ungulate impact on natural regeneration in spruce-beech-fir stands in Cerny Dul nature reserve in the Orlické Hory mountains, Case study from Central Sudetes. *Forests* 5. <https://doi.org/10.3390/f5112929>
- Vacek S, Černý T, Vacek Z, Podrázský V, Mikeska M, Králíček I (2017) Long-term changes in vegetation and site conditions in beech and spruce forests of lower mountain ranges of Central Europe. *Forest Ecology and Management* 398: 75–90. <https://dx.doi.org/10.1016/j.foreco.2017.05.001>
- Vandekerkhove K, De Keersmaecker L, Menke N, Meyer P, Verhelde P (2009) When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *Forest Ecology and Management* 258. <https://doi.org/10.1016/j.foreco.2009.01.055>
- Villard MA, Jonsson BG (2009) *Setting Conservation Targets for Managed Forest Landscapes*. Cambridge University Press, New York, 1–411.
- Vrška T, Hort L, Odehnalová P, Adam D, Horal D (2001) The Razula virgin forest after 23 years (1972–1995). *Journal of Forest Science* 47: 15–37.
- Yamamoto SI (2000) Forest gap dynamics and tree regeneration. *Journal of Forest Research* 5: 223–229.

### Appendix



**Figure A1.** Mosaic of small development cycles in primeval beech-fir mountain forest – adapted from Korpel (1995), Natural Reserve Dobrocsky Prales, Slovak Republic.