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Expansion to abandoned agricultural land forms an integral part of silver fir dynamics

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ABSTRACT

Silver fir (*Abies alba* Mill.) is a tree species distributed mainly in central Europe. It once was a dominant tree species within some forests of this region. The causes for its rapid decline in the past two centuries have not yet been sufficiently explained. It is argued that human activities have been largely responsible for expansions and contractions of silver fir populations. On the basis of the current distribution of silver fir, historical maps and palaeoecological data, we describe the expansion of silver fir forests. We use fine resolution at the landscape level, an approach that has so far been neglected. Our study area lies in the northern part of the White Carpathian Mountains, Czech Republic. The area comprises 7045 ha, 65% of which is covered by forests. This landscape was shaped by early modern colonization from the 16th century onwards and has changed greatly since the decline of its traditional utilization in the 19th and 20th centuries. The area of forests almost doubled from 1838 to 2005 while the area of pastures and arable land decreased. We identified 172 ha of silver fir forests by field mapping, which represent 2.5% of the whole study area and 3.8% of its forested part. We used land use history variables (based on subsequent land cover maps from 1838, 1882 and 1956) and terrain variables (derived from a digital elevation model) in a logistic regression to model the probability of silver fir forest occurrence. Land use history was highly significantly correlated with the occurrence of silver fir forests. Approximately 59% of silver fir forests occur on land used as pastures in 1838, 28% are on former arable land, meadows and fallows, while only 13% have been forested continuously since the 19th century. We know from historical sources that the surrounding forests (now mainly Norway spruce monocultures) were dominated by silver fir up to the 1860s. Silver fir can act as a pioneer species. It can invade former agricultural land, which probably ensures the survival and periodical expansion of silver fir-dominated forests. Although silver fir has been thought to decline under human pressure, we suggest that the opposite may occur at the landscape level.

1. Introduction

Silver fir (*Abies alba* Mill.) is tree species which occurs mainly in Central and Southern Europe (Jalas and Suominen, 1973; Muller et al., 2007). Its distribution range is smaller than that of other common European tree species, which may be the result of migration history from glacial refugia (Konnert and Bergmann, 1995; Terhürne-Berson et al., 2004; Muller et al., 2007). Silver fir often occurs together with European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) (Bohn et al., 2003). It thrives in old-growth stands (Ellenberg, 1988; Vrška et al., 2009) as well as in managed forests (Motta and Garbarino, 2003), occupying a wide ecological range on various substrates from lowlands to the upper montane zone. Boublík (2010) observed that some authors considered all silver fir-dominated stands as natural, while others argued that these stands were natural only in places influenced by ground water. In congruence with the latter opinion about the relatively low competitive capacity of the species, Ellenberg (1988) supposed silver fir forests to be natural at sites where European beech is at a competitive disadvantage.

Although common in the past, silver fir has been declining since at least the 19th century with no obvious cause (but see also Diaci et al., 2010; Klopcic and Boncina, 2011). The limits to the occurrence of silver fir have been most often associated with factors critical for the regeneration of the species, either natural or connected with management and land use history. Silver fir may fail to regenerate under the influence of competitively stronger European beech (Šamonil and Vrška, 2007; Šebesta et al., 2011). It may decline as a consequence of past logging and drought stress (Camarero et al., 2011), due to air pollution (Medwecka-Kornaś and Gawroński, 1990; Bert, 1993) or browsing by ungulates (Senn and Suter, 2003), because of a complex disease (Schütt, 1977) or due to its low genetic variation (Larsen, 1986).

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In spite of the complexity of mechanisms, most hypotheses about silver fir dynamics are based either on observations about the population structure of a few old-growth forests (Korpel', 1995; Vrška et al., 2009; Diaci et al., 2011; Šebesta et al., 2011), or on palaeoecological evidence, mainly pollen and charcoal (Carcaillet and Muller, 2005; Muller et al., 2007). The former approach is limited to ecologically specific and spatially restricted conditions, while the latter reveals large-scale dynamics (Tinner and Lotter, 2006). However, advanced explanations of ecological processes often require the use of independent sources of information. This can be achieved by the combination of several data sources (Rybníček and Rybníčková, 1978; Motta and Garbarino, 2003; Kozáková et al., 2011). A particularly valuable and somewhat neglected source is historical documentation, such as management accounts, taxation surveys and maps. Such archival sources offer spatially and temporally explicit information about tree species and management, allowing an insight into forest dynamics at the scale of decades to centuries (Szabó and Hédl, 2011).

Among historical factors influencing vegetation composition, land use change is of particular importance (Brunet and von Oheimb, 1998; Dambrine et al., 2007; Brown and Boutin, 2009; Kopecký and Vojta, 2009; Svenning et al., 2009). Land use changes are likely to have influenced the dynamics of silver fir populations as well. Recent overall changes in European landscapes include the spreading of urban areas and intensive agriculture and the abandonment of less productive or boundary areas (Vos and Meekes, 1999; Verburg et al., 2009). Abandonment has led to the return of forests to large areas historically cleared for non-forest uses.

We analyzed the dynamics of silver fir forests in an area of the Western Carpathians that has been partly abandoned since the 19th century. We focused on three aspects: (1) To quantify the impact of historical landscape changes, we analyzed a sequence of historical maps, the oldest dating from 1828. Assuming the high importance of land use management for silver fir regeneration, we hypothesized that some present-day silver fir forests have resulted from succession on former agricultural land. (2) In addition, we examined the influence of terrain configuration variables, hypothesizing that they have contributed to changes in the distribution of silver fir forests. (3) To study the dynamics of silver fir over a longer time period than that covered by maps, we analyzed palaeoecological sources.

2. Materials and methods

2.1. Study area

The study area is located in the northern part of the White Carpathian Mountains (Eastern Czech Republic, Fig. 1A), which belongs to the West Carpathians Range. It is delimited as the geomorphological district of Študlovská hornatina (Demek et al., 2006), covering an area of 7045 ha, 17°56′E, 49°5′N in the southwestern edge, and 18°8′E, 49°10′N in the northwestern edge. The military area occupying the northeastern part was excluded from our study. The study area represents the core altitudinal range of silver fir. Elevation ranges from 315 to 817 m.a.s.l. Bedrock is sandstone and claystone of flysch layers (Czech Geological Survey, 2004). Climate is temperate in transition between oceanic and continental, with mean annual temperatures (1961–2000) ranging from 6 to 8 °C and mean annual precipitation from 750 to 1000 mm, following an altitudinal gradient (Tolasz, 2007). *P. abies* L. (Karst.), *F. sylvatica* L., *A. alba* Mill., *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl. are among the main tree species.

The Carpathian Mountains form a vast area with relatively abundant growths of silver fir. It was deeply influenced by early modern colonization. It began between the 10th and 13th centuries in Wallachia (today's Romania) and spread along the Carpathian mountain crescent to the north and west arriving at the study area at the beginning of the 16th century (Štika, 2001). Forests at that time were dominated by mixed stands of *Abies*, *Fagus* and *Picea* in the northern Moravian–Silesian Beskids whereas in the study area *Picea* was rare or absent (Rybníček and Rybníčková, 2008). The new settlers cleared some land and introduced sheep pasturing at higher elevations, sometimes directly in forests. The growing need for wood and cheap wool from Australia led to the decline of sheep pasturing in the 18th and 19th centuries (Materna, 1956; Kunz, 2005).

2.2. Present silver fir forests

We considered all forests with more than approximately 80% of silver fir in growing stock and an area larger than 0.5 ha to be silver fir forests. To establish the extent of present silver fir forests, we used a forest management plan from 1988 available for the whole study area, plans from 1998 available for state forests and some private forests, orthophotomaps and field surveys. First, we extracted all forest stands with at least 10% silver fir from the forest management plans. We set a low percentage boundary, because some larger forest stands consisted partly of silver fir forests and partly of Norway spruce monocultures. We visited all stands and mapped the boundaries of those that met our criteria. Orthophotomaps were used for easily distinguishable boundaries (e.g. forest/pasture), and the GPS receiver Juno ST (Trimble) for others. Fieldwork was carried out in 2008. Forest management plans from 1988 and 1998 were used also to evaluate the age of silver fir forests.

Most of the studied forests belong to the phytosociologial association of species-rich silver fir forests *Galio rotundifolii–Abietetum albae* Wraber 1959, while some to the association of species-poor fir forests *Luzulo-A. albae* Oberdorfer 1957. They are mostly uneven-aged, with an admixture of Norway spruce, Scotch pine, European larch, European beech or other broadleaved species. Common hazel often occurs in the shrub layer. The most common understory species are *Oxalis acetosella*, *Athyrium filix-femina*, *Dryopteris dilatata*, *Dryopteris filix-mas*, *Senecio ovatus*, *Salvia glutinosa* and *Luzula pilosa* on rich and moderately acidic soils. On poor acidic soils, *Luzula luzuloides*, *Vaccinium myrtillus*, *Dryopteris dilatata*, *Oxalis acetosella* and *Polytrichum formosum* are the most frequent understory species.

2.3. Sources on historical human impact

2.3.1. Land use maps from 1838 to 2005

The land use history of the study area was analyzed for five periods extending from the early 19th to the early 21st centuries. Topographical maps from 1838, 1882, 1956, 1980, 1992 and 2005 were used. The map from 1838 was of the so-called Second military mapping of the Habsburg Empire (scale 1:28,800), the map from 1882 was the Third military mapping (scale 1:25,000) (Geoinformatics Laboratory, University of J.E. Purkyne, 2005), and the maps from 1956, 1980 and 1992 were three subsequent Czechoslovak military topographical maps (all scaled 1:25,000) (Skokanová, 2011). The most recent map from 2005 is based on an official Czech digital mapping product called the Fundamental Base of Geographic Data (ZABAGED) provided by the Czech Office for Surveying, Mapping and Cadastre. Six land use categories congruent for all six maps were distinguished: arable land, pasture and meadow, orchard, forest, built-up area and water bodies. These categories were assigned to polygons obtained with manual digitalisation of the maps using ArcGIS 9.2 (ESRI) and the total area for each category in particular years was calculated. We used all maps to evaluate land use development and the first three maps (1838,

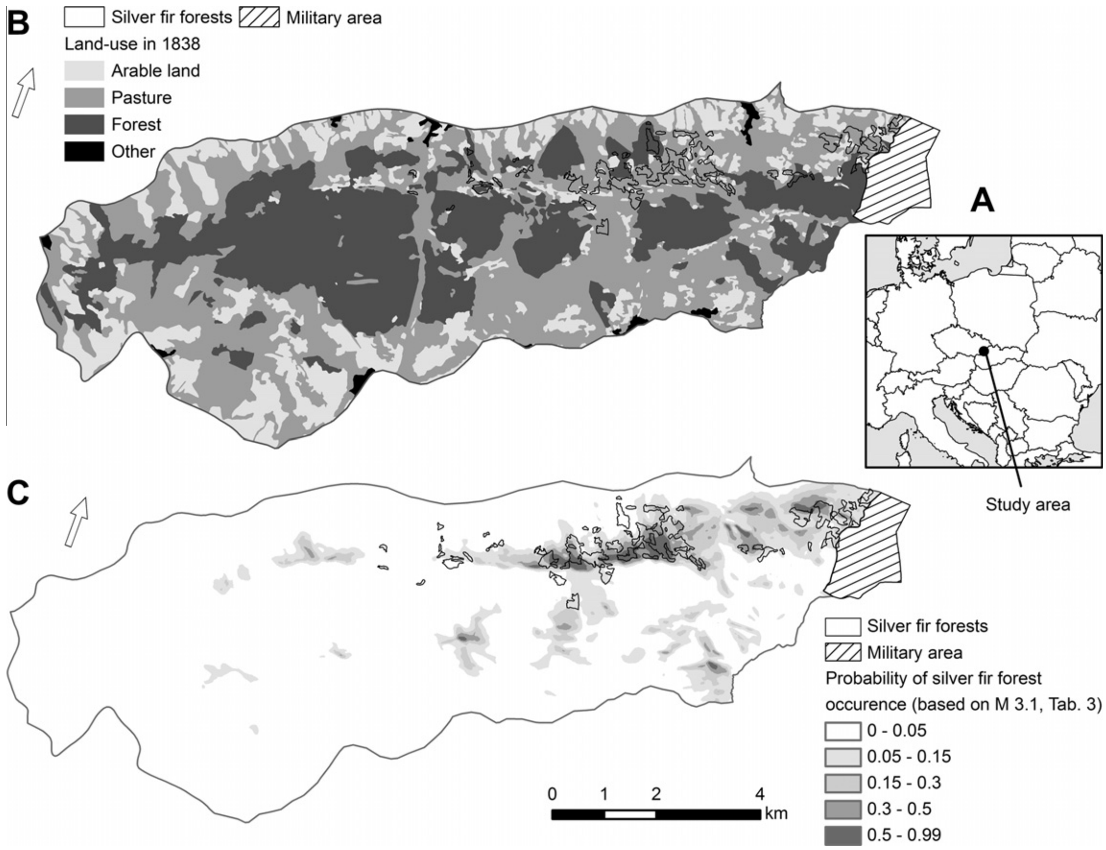

Fig. 1. Localization of study area in the Czech Republic on the border with Slovakia in the White Carpathian Mountains (A). The study area and current silver fir forests superimposed on land use in 1838 according to the Second military mapping (B) and the probability of silver fir forest occurrence based on model 3.1, Table 3 (C).

1882 and 1956) to derive land use variables to analyze the relationship between former land use and present silver fir forest occurrence.

2.3.2. Stable cadastre map from 1828

We also used the maps of the stable cadastre from 1828, scaled 1:2,880 (ČÚZK, 2012). These are taxation maps, made for a different purpose than the military maps. Their focus on land use categories makes them an excellent source on land use ca. 180 years ago. We used these maps for a more specific characterization of land use in the early 19th century regarding areas currently covered by silver fir forests. The legend of this map is more detailed than that of the 1838 map, which enabled us to distinguish pastures from meadows. Furthermore, land use boundaries could be recognized more precisely than in the maps of the military surveys. We distinguished between the following land use categories: arable land (Aecker), pasture (Weiden), meadow (Wiesen), fallow (Rott oder Trisch Aecker) and coniferous forest (Nadelholz Waelder).

2.3.3. Archival forestry management plans

To gain a better insight into the origins of present silver fir forests in the study area, we analyzed the forestry management plans of the Valašské Klobouky district from the middle of the 20th century deposited in the Moravian Archives: 1958 (MZA F387 kniha 55; kniha 56; mapa 208) and 1968 (MZA F387 kniha 58; kniha 59; mapa). Older plans (from 1924 and 1937) showed only those forests that had been present already at the time of Stable cadastre maps and did not cover forests that originated later on agricultural land. We searched for recently established silver fir stands and extracted records about their origin and structure. We focused on whether such stands originated by natural regeneration, were planted or sown.

2.4. Environmental conditions of silver fir forests

2.4.1. Data sources

To analyze the relationship between the occurrence of silver fir forest and land use and terrain-derived variables, we sampled the whole study area using 500 randomly distributed circular sample plots of 200 m diameter. The minimum distance between plots was 200 m. We derived values of land use history variables and terrain-derived variables for each plot. For this purpose, the vector map layers were transformed to raster and sampled using StarSpan version 1.2 (Rueda et al., 2005). The list of all variables used in the statistical analyses with their basic characteristics can be found in Table 1. For categorical variables (land use in 1883, 1882 and 1956, see Section 2.2.1), we calculated the percentage of raster map cells with the presence of a particular land use (forest, pasture and arable land) within the plot. Next, we calculated the distance of each plot from the forest edge in 1838, 1882 and 1956. Negative values were used inside forests, positive values outside forests. We assumed that silver fir forests spread from the original forests after the abandonment of agricultural land, therefore we expected the distance from forest edge variables to explain the occurrence of silver fir forests. For continuous variables (distance from forest edge and terrain-derived) we calculated the average value from the cells within the sample plot.

Three terrain-derived variables were obtained from a digital elevation model (DEM) – elevation, slope and potential global radiation. The DEM was interpolated from contour lines using the RST (regularized spline with tension) method. Contour line data were

Table 1
Variables extracted in 500 randomly distributed circular plots with a 200 m diameter. Pastures include also meadows. Distance from forest edge variables have positive values when inside the forest and negative values when outside the forest.

Variable	Description (unit)	Range	Mean
Fo1838	Cover of forest in 1838 (%)	0–100	42
Fo1882	Cover of forest in 1882 (%)	0–100	51
Fo1956	Cover of forest in 1956 (%)	0–100	67
Fi1838	Cover of arable land in 1838 (%)	0–99	11
Fi1882	Cover of arable land in 1882 (%)	0–100	25
Fi1956	Cover of arable land in 1956 (%)	0–100	20
Pa1838	Cover of pastures in 1838 (%)	0–100	47
Pa1882	Cover of pastures in 1882 (%)	0–100	23
Pa1956	Cover of pastures in 1956 (%)	0–100	13
DistF1838	Distance from forest edge in 1838 (m)	−686 to 1126	74
DistF1882	Distance from forest edge in 1882 (m)	−561 to 962	13
DistF1956	Distance from forest edge in 1956 (m)	−823 to 550	−95
Elev	Elevation (m.a.s.l.)	348–761	510
Rad	Global potential radiation ($MW h \times m^{-2} \times yr^{-1}$)	1.280–2.262	1.849
Slope	Steepness of slope (°)	4.4–26.6	14.2

obtained from the Fundamental Base of Geographic Data of the Czech Republic. All calculations were processed within the GRASS GIS environment (GRASS Development Team, 2007). Potential global radiation was calculated in the r.sun module (Šúri and Hofierka, 2004; Neteler and Mitasova, 2008) as the sum of direct and diffuse radiation for the whole year; the impact of atmospheric conditions was omitted from the calculation, while the effect of terrain shading was included. The resolution of raster maps used for the derivation of values was 5 m, except for the maps of potential global radiation, which had a 10 m resolution.

2.4.2. Data analysis

We used two different statistical methods to assess the effects of land use and terrain-derived variables with respect to the probability of the occurrence of silver fir forests. In both methods the probability of silver fir forests was defined as the area of silver fir forests divided by the area of current forests within the sample plot. Only sample plots where forests currently occur were used for the analysis. First, we used regression trees with a cross-validation procedure to prune the tree. This robust technique (see e.g. De'ath and Fabricius, 2000) enabled us to distinguish the most important variables influencing the occurrence of silver fir forests. All variables listed in Table 1 were used in this analysis.

Second, we used generalized linear models (GLMs) with quasi-binomial family and link function logit (called also logistic regression). We used the quasi-binomial family instead of binomial family because the residual deviance of the final model exceeded the residual degrees of freedom, indicating overdispersion. We used a quasi Akaike information criterion (QAIC) to compare the explanatory power of models resulting from the GLM, where models with lower QAIC are the stronger ones (Burnham and Anderson, 2002). We expected unimodal response curves for some variables (except slope and potential global radiation) and therefore we also tested the significance of quadratic term for each variable. One type of the models was with land use variables, another type with distance from forest edge variables (as in Table 1). Land use variables were correlated with each other. We therefore constructed preliminary models including only one variable and its quadratic term (Table 3). The terrain-derived variables were not significantly correlated with each other. It was therefore possible to use them together in the models. In the final model we combined the best performing land use variables with significant terrain-derived variables. Residuals of the final model were assessed for spatial autocorrelation using Moran's I based correlograms and as it was

Table 2
Pollen site characteristics (Rybníček and Rybníčková, 2008).

Name	Coordinates	Elevation (m.a.s.l.)	Description
Královec	49°07′55″N, 18°01′40″E	560	Very small spring fen – ca. 200–250 m^2, sediments 130 cm deep
Horní Lomná	49°31′14″N, 18°37′51″E	615	Small spring fen – ca. 400 m^2, sediments 100 cm deep
Kubriková	49°29′03″N, 18°40′20″E	790	Small spring fen – ca. 500 m^2, sediments 100 cm deep
Machová	48°49′30″N, 17°02′25″E	460	Small spring fen – ca. 400–500 m^2, sediments 100 cm deep

Table 3
Results from GLM models (quasi-binomial family, link function logit).

Code	Model formula and variable significance	QAIC	Deviance explained	Maximum fitted probability
Land use history variables				
M 1.1	$-3.7 + 0.0085 \times$ DistF1838 (***) $- 1.1 \times 10^{-5} \times$ DistF1838^2 (***)	258.5	0.16	0.118
M 1.2	$-2.9 + 0.0077 \times$ DistF1882 (ns) $- 2.9 \times 10^{-5} \times$ DistF1882^2 (**)	272.9	0.11	0.087
M 1.3	$-2.9 - 0.0152 \times$ DistF1956 (**) $- 11.5 \times 10^{-5} \times$ DistF1956^2 (***)	261.2	0.15	0.083
M 1.4	$-2.4 - 2.8 \times$ Forest1838 (***)	260.3	0.15	0.083
M 1.5	$-2.7 + 2.2 \times$ Forest1882 (**) $- 4.0 \times$ Forest1882^2 (*)	279.2	0.09	0.082
M 1.6	$-5.0 + 7.6 \times$ Forest1956 (ns) $- 6.0 \times$ Forest1956^2 (*)	295.8	0.03	0.072
Terrain-derived variables				
M 2.1	$-64 + 0.19 \times$ Elev (***) $- 1.5 \times 10^{-5} \times$ Elev^2 (***)	222.3	0.28	0.150
M 2.2	$5.3 - 0.49 \times$ Rad (***)	255.9	0.16	0.203
M 2.3	$-2.7 - 0.035 \times$ Slope (ns)	302.6	0.00	0.055
Final model				
M 3.1	$-48 + 0.009 \times$ DistF1838 (***) $- 0.9 \times 10^{-5} \times$ DistF1838^2 (**) $+ 0.16 \times$ Elev (***) $- 12.2 \times 10^{-5} \times$ Elev^2 (***) $- 0.35 \times$ Rad (***)	155.2	0.53	0.647

ns: Not significant.
Codes of variables significance.
*** 0.001.
** 0.01.
* 0.05.

only a minor issue, we kept this classical approach for statistical analysis. All statistical analyses were performed in the R statistical environment version 2.14 (R Development Core Team, 2011), with packages 'tree' (Ripley, 2011) for regression trees, 'MuMIn' (Bartoń, 2012) for QAIC computation and 'ncf' (Bjornstad, 2009) to evaluate spatial autocorrelation.

2.5. Long-term dynamics

To provide an insight into the long-term development of silver fir forests in the study area, we used four pollen profiles from the Moravian Carpathians published by Rybníček and Rybníčková (2008). Pollen data were obtained from the Czech Quaternary Palynology Database PALYCZ (Kuneš et al., 2009). One pollen profile (Královec) is situated directly in the study area. Two (Horní Lomná and Kubriková) are approximately 60 km to the northeast in the Moravian–Silesian Beskids, and the fourth pollen profile (Machová) is situated in the southwest of the White Carpathians approximately 55 km from the study area (Table 2). The temporal development of vegetation composition was visualized using linear graphs of pollen percentage for the past 1200 years (800–2000 AD). We used pollen percentage data of the three most important tree species (*Abies*, *Picea* and *Fagus*), of sedges and grasses (*Cyperaceae* and *Gramineae* – hereafter Graminoids), and of human indicators (*Triticum*, *Secale*, *Centaurea cyanus* and *Plantago lanceolata*). Pollen percentages were based on dry-ground pollen sum.

3. Results

3.1. Land use history

3.1.1. Land use changes from 1838 to 2005

The area of forests almost doubled from 2350 ha in 1838 to 4571 ha in 2005; the area of pastures and meadows decreased from 3175 ha in 1838 to 1421 ha in 2005; and the area of arable land decreased from 1460 ha to 743 ha (Fig. 2). Built-up areas increased more than three times, however, they represent only ca. 3% of the study area. Orchards and water bodies comprise 1.1%. The increase of forests at the expense of agricultural land (arable land, pastures and meadows) is therefore a clear trend. On average, forest area increased by 13.3 ha per year. In 1838, forests were fragmented with approximately 10 larger segments of 40–1110 ha (Fig. 1B) while in 2005 there was one large forest complex.

3.1.2. Land use in current silver fir forests in 1828

The maps of the stable cadastre from 1828 revealed that almost 60% of current silver fir forests are on land which was used as pasture in 1828. However, other types of land use also occurred, such as coniferous forests, fallow land, meadows and arable land (Fig. 3).

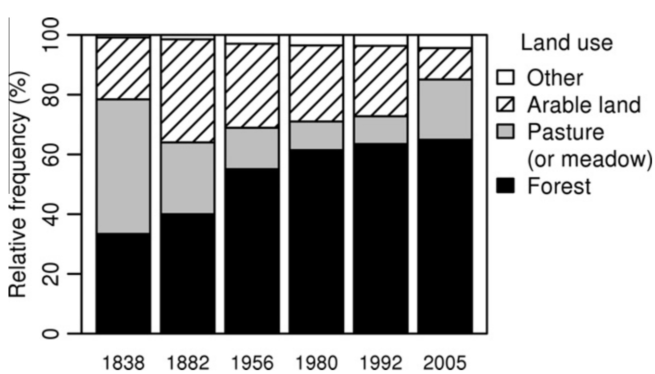

Fig. 2. Development of land use in the study area based on six maps, 1838–2005.

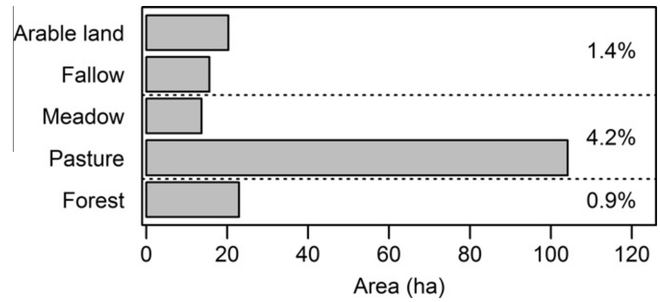

Fig. 3. Land use according to the cadastre map from 1828 in plots where silver fir forests currently occur. Most of these forests were established on former pastures, while only a small portion was a forested land also in 1828. Next to the bars, the percentage of area covered by silver fir relative to total area of respective land use is shown. The second military mapping (1838) was used for these calculations; some categories had to be merged.

In total, 87% of current silver fir forests are on former agricultural land. All former pastures where silver fir forests currently occur are depicted in the 1828 map including a symbol for shrubs or trees, indicating the presence of woody vegetation.

3.2. Environmental conditions of silver fir forests

In total, we found 172 ha of silver fir forests. They covered 2.5% of the study area, which represents 3.9% of all its forests and 5.7% of forests older than 40 years. No stand conforming to our criteria for a silver fir forest (i.e. containing more than 80% of silver fir and larger than 0.5 ha) was younger than 60 years. Most stands were 90–120 years old. The age of the oldest stand was ca. 140 years.

Using regression trees we found that potential global radiation, distance from forest edge in 1838 and distance from forest edge in 1882 were the three most important variables determining the present occurrence of silver fir forests (Fig. 4). These variables resulted from tree pruning. Before tree pruning, two further variables were shown to be important: elevation and slope. The most important variable (at the first node root) was potential global radiation indicating that the silver fir forests tend to occur at sites with lower radiation (e.g. colder northern slopes). The next two nodes are represented by land-use history variables. Silver fir forests occur with higher probability at more than 110 m away from the forest edge

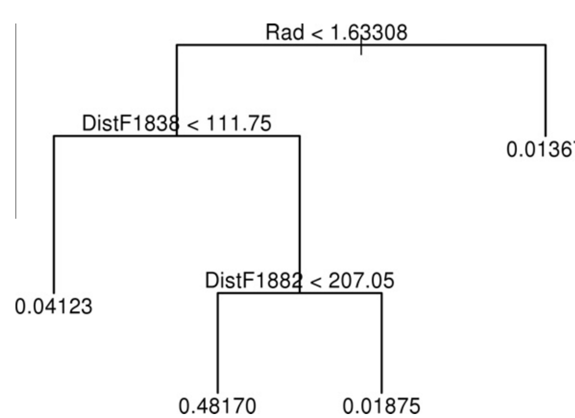

Fig. 4. Pruned regression tree showing the most important environmental variables determining the present occurrence of silver fir forests. The decision criteria are shown on nodes and probabilities of silver fir forest occurrence on the ends of branches. 'Rad' is potential global radiation (MW h × m^{-2} × yr^{-1}), 'DistF1838' is the distance from the forest edge in 1838 (m) and 'DistF1882' is the distance from the forest edge in 1882 (m). After the potential radiation denoting topographical features, historical land use changes (expansion of forest boundaries) were the most important determinant.

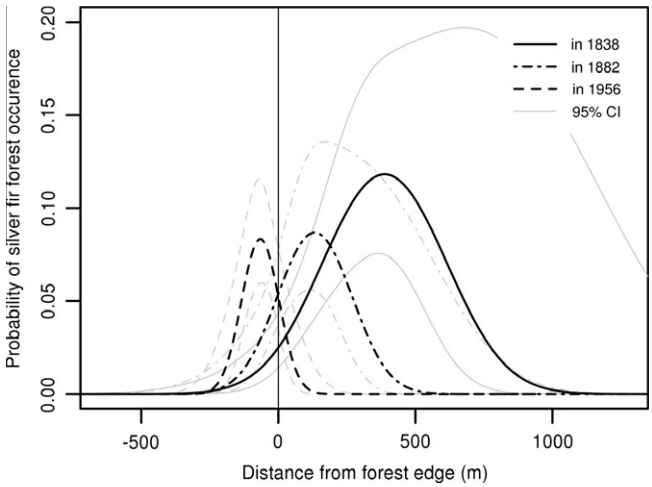

Fig. 5. Probability of the occurrence of current silver fir forests in relation to the distance from the forest edge in 1838, 1882 and 1956 indicates gradual expansion of silver fir to former non-forest land. Negative values are inside the forest at a given date, positive values are outside the forest. Grey lines indicate 95% confidence intervals.

in 1838, and less than 207 m away from the forest edge in 1882 (Fig. 4). This indicates that present silver fir forests developed mostly between these distance limits on former non-forest land.

The GLM analysis provided results similar to the regression tree. Forest cover and distance from forest edge in all particular years (including quadratic terms) significantly ($p < 0.05$) influenced the occurrence of silver fir forests (Table 3, models M 1.1–M 1.6). Distance-based variables performed slightly better than forest cover variables. Distance from the forest edge in 1838 is the best performing variable from this set of models. The highest probability of silver fir forest occurrence today is around 400 m away from the forest boundary in 1838, which means that silver fir forests have originated on former agricultural land. As forests gradually expanded, the distance between silver fir forests and the forest edge decreased in subsequent periods 1882 and 1956 (Fig. 5).

Among terrain-derived variables, elevation and potential global radiation significantly influenced the occurrence of silver fir forests (Table 3, models M 2.1 and M 2.2). Elevation is significant also as the second order polynomial. The highest probability of the occurrence of silver fir forests is around 600 m.a.s.l. Slope was not significant (Table 3, model M 2.3). The final model (Table 3, M 3.1) includes distance from forest edge in 1838, elevation and potential global radiation. All included variables were significant. They explained 53% of the variability in the present occurrence of silver for forests. A map indicating the probability of the occurrence of silver fir forests based on this model superimposed on the current distribution of silver fir forests is shown in Fig. 1C.

3.3. Origins of present silver fir forests

In forestry management plans from the 1960s we found records for 135 ha of current silver fir forests. The analyzed silver fir forests were on average ca. 50 years old in the 1960s; 49 ha were recorded to have originated spontaneously. Some of the youngest forests (in total ca. 1.5 ha) were explicitly described as succession on pasture in the 1958 forestry management plan. They were open stands of silver fir, Scotch pine and silver birch, 5–35 years old, with shrubs of common hazel and common juniper, further emphasizing the former pasture.

1.6 ha of current silver fir forests were recorded to have originated from either spontaneous regeneration or planting. Some silver fir forests (ca. 1 ha) developed under pine or spruce plantations. The management plans did not specify the origins of 82 ha of silver fir forests. Nevertheless, their structure was described as uneven-aged with a great differentiation in heights and DBH. This indicates that they may have originated from spontaneous regeneration. Only 3.6 ha of silver fir forest stands were described as stands with uniform structure indicating plantation. In contrast to silver fir, Norway spruce stands and spruce admixture in silver fir forests were often described as coming from artificial planting.

3.4. Development in the past 1200 years

At Královec, which is located within the study area, there was a prominent peak of *Abies* between 800 and 1350 AD culminating in ca. 1200 AD, and two smaller peaks in 1400 and 1600 AD (Fig. 6). In

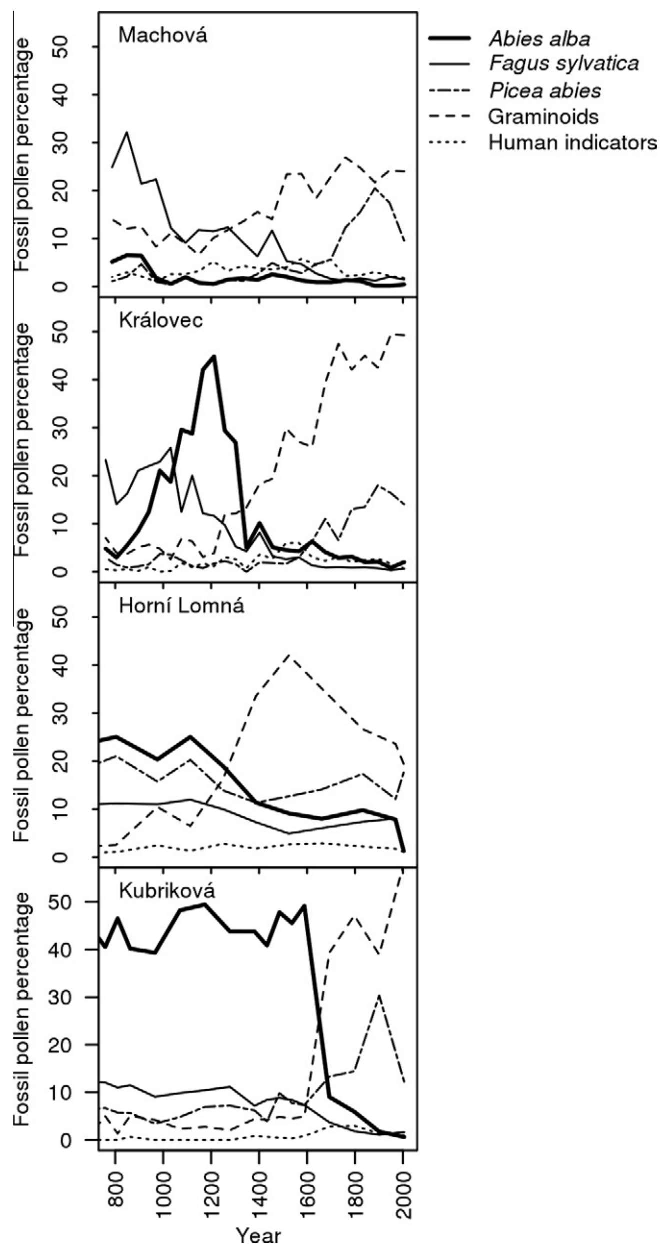

Fig. 6. Percentage of fossil pollen of the main tree species, graminoids, and human indicators between 800 AD and 2000 AD. Pollen profiles were taken from within the study area (Královec) and in the neighbouring mountain ranges (Horní Lomná, Kubriková and Machová). Sites are sorted according to altitude. Pollen percentage was based on the dry-ground pollen sum.

the same period, a gradual increase in Graminoids and decrease in *Fagus* can be observed, probably marking the onset of more intensive land use around 1200 AD. Both *Abies* and *Fagus* have had low pollen percentages since ca. 1400 AD; they have been replaced by the previously infrequent *Picea* since 1600 AD. Around 1600 AD *Abies* became relatively more abundant than *Fagus* although its overall percentage remained relatively low. Landscape abandonment at around 1900 AD may be reflected in a slight decline of human indicators and a relative gain of *Abies* as compared to *Fagus* (Fig. 6). The geographically similar Machová site shows a partly comparable scenario (Fig. 6), except that the abundance of *Abies* remained low throughout the past 1200 years. Instead of *Abies*, *Quercus* was important at this site (not shown in graph).

The vegetation development at two Beskids sites was somewhat delayed in comparison to the two lower elevated sites. In Horní Lomná, *Abies* was relatively abundant until 1100 AD when it started to decrease; in Kubriková it was abundant until 1600 AD when it decreased sharply. At both sites, *Abies* was replaced by *Picea* (Fig. 6). Graminoids recorded steep increases after the *Abies* decline at both sites, exactly as at Královec. Human indicators followed the increase in Graminoids, but their proportion remained generally low. They were more important in Machová and Královec, indicating a more significant impact of agriculture at lower elevations.

4. Discussion

4.1. Landscape abandonment and silver fir expansion

Over the past 170 years, forest cover in the study area increased from one third to two thirds at the expense of agricultural land. This corresponds to the general trend in land use change in the Czech Republic (Bičík et al., 2001) as well as in other places in Europe (e.g. Bender et al., 2005). However, there are differences in the rate of change depending on regional socio-economic patterns. The increase in forested land was higher (1.95 times) in the study area in 1838–2005 than it was in the whole of the Czech Republic (1.15 times) for the period of 1845–1999 (Bičík et al., 2001). The explanation is that modern agriculture intensified in more productive and easily accessible areas, while less productive mountainous regions have been abandoned. Similar trends can be observed in other marginal areas in the Czech Republic (Eremiášová and Skokanová, 2009) as well as elsewhere in Europe (Tasser et al., 2007) and worldwide (Sitzia et al., 2010).

In our study area, this process entailed the abandonment of traditional landscape utilization established by Wallachian settlers in the Early Modern Period. Based on our historical land use analysis and recent silver fir forest distribution, we demonstrated that silver fir probably expanded from forests to abandoned agricultural land (mainly pastures, which were the most frequent land use in the vicinity of the old forests) during the 19th and 20th centuries (cf. Fig. 1). Materna (1956) investigated several historical sources in the northern White Carpathians – *urbaria*, sawmill accounts, cadastres and forest management plans. His results can be summarized in the following four points. (1) Until the end of 19th century, the most important tree species in forests were European beech and silver fir. (2) The first reference to pure silver fir forest is from the 16th century. (3) Norway spruce and Scotch pine are not mentioned at all in sources older than 1836 indicating that they did not play an important role in the study area although they perhaps sporadically occurred. (4) Norway spruce was planted in great amounts from the second half of 19th century as the main commercial timber species. These historical sources support our observations from pollen profiles with the exception of Norway spruce expansion, which is supposed to have happened somewhat earlier based on the pollen data; however, this could be explained by inaccuracies in the dating of pollen profiles.

Although we only rarely found explicit statements about spontaneous succession on agricultural land as the way of establishment of silver fir forests, it is very likely that the majority of the present silver fir forests originated from such a process. Artificial plantation is highly unlikely for most stands as these forests were described as uneven-aged and richly-structured, and almost half of the silver fir forest stands were explicitly stated to have originated through spontaneous regeneration. ‘Spontaneous regeneration’ could refer to regeneration from trees scattered on pastures and trees in adjacent forest or to regeneration of previously planted trees. Of these options, the first one appears to describe silver fir stands in the study area the best. There are ca. 80 years between 1882, when more than half of the silver fir forests were not mapped as forests, and 1956, which is too short a period for plantations to develop into structured forests through spontaneous regeneration. Zajoncová (2007) also described natural succession of silver fir was in the Ščúrnica Reserve situated in our study area. From the stable cadastre maps (1828) we know that pastures were scattered with trees, which could act as sources of diaspores, thus facilitating forest succession on abandoned agricultural land. According to historical sources, there were not many mature spruce forests at the end of the 19th century; Norway spruce therefore could not compete with silver fir in colonizing abandoned agricultural land.

Silver fir is known to foresters as a shade-tolerant species of mature forests (Brzeziecki and Kienast, 1994; Motta and Garbarino, 2003). This may not be the whole truth – our results show that silver fir can behave as a pioneer species present in early succession vegetation. Despite strong disturbances, the species is able to recover its populations repeatedly on the long run (Pèlachs et al., 2009). Although it is sensitive to changing irradiance and drought in the seedling stage (Robakowski et al., 2003), silver fir can successfully colonize abandoned pastures as well as other types of agricultural land (Málek, 1983; Doležal et al., 2004; Bartolomé et al., 2008).

4.2. Long-term dynamics of silver fir

Vegetation development based on fossil pollen showed some common features at all four sites for the past 1200 years. Such common features were the gradual decrease in silver fir and European beech and the increase in Graminoids and Norway spruce. The driving factor seems to have been human influence in the form of deforestation and subsequent landscape management. The timing of the main turnover in vegetation depends on altitude, probably reflecting the advancement of landscape colonization from lower to the higher elevations. At the two lowest elevated sites (Machová and Královec), the assumed colonization impact is apparent in the medieval period from ca. 1000 to 1400 AD, while at the highest elevated Kubriková site the same turnover in pollen could be observed only after 1600 AD, i.e. well after the onset of Early Modern colonization. The intermediate Horní Lomná site stands in between these dates.

Silver fir could expand in certain periods after 1200 AD, as it was shown independently by both palynological and historical evidence. Based on our results, we argue that the dynamics of silver fir historically strongly depended on human activities in two opposing ways:

(1) Silver fir was sensitive to intensive impacts, such as deforestation, the same way as the other natural tree dominant, European beech.

(2) Silver fir benefited from low to moderate human impact, which enabled it to colonize extensively managed and abandoned sites.

We infer that the intensity of historical landscape management could explain the three peaks in silver fir at Královec in ca. 1200, 1450 and 1600 AD, and the increase after 1800 AD. The first peak could also be the result of natural silver fir expansion to the region from the northeast, as hypothesized by Prudič (1990). Later peaks could be the consequences of post-deforestation dynamics including periods of landscape abandonment. The last such peak was revealed independently in our analysis of land use changes. Such changes in forest tree species composition occurring during periods when the landscape was largely deforested may be neglected when focusing on large-scale and long-term development as in Kozáková et al. (2011); however, they may reveal important patterns of species dynamics. It appears that silver fir was able to repeatedly expand during the past millennium and colonize abandoned agricultural land.

An interesting but rather speculative perspective was provided by historical sources. The dynamics of silver fir in the Czech Republic was reconstructed by Málek (1983). Using various historical sources, he quantified the proportion of silver fir in forests back to 1500 AD (for methodology, see Málek 1962, 1979, 1983). However, it is not clear how the estimates of the proportion of silver fir for the whole Czech Republic were arrived at. Assumptions about the expansion of silver fir by 10% from 1200 AD to 1600 AD were based on palynological results as they were available in the 1980s and potential vegetation mapping data. Málek (1983) equalled potential vegetation (including silver fir forests) with vegetation in 1200 AD. These assumptions were uncritically copied by Kozáková et al. (2011: Fig. 2). Their subsequent comparison of pollen (interpreted as regional) and historical (interpreted as local) tree species dynamics is therefore not plausible. Another drawback in their analysis is that regions covered by charcoal and historical data do not overlap (Kozáková et al., 2011: Fig. 3). This leaves the medieval to early modern distribution of silver fir in the Czech Republic an open question.

4.3. Model for silver fir forest dynamics

Human impact is probably crucial for silver fir dynamics. The expansion of silver fir can be directly linked to landscape abandonment in the northern White Carpathians (this study). Similar processes were detected in the Bronze and Iron Ages (as inferred by Kozáková et al., 2011). In regions of recent landscape abandonment, silver fir can be either frequent (Boublík, 2007) or relatively rare (Kopecký and Vojta, 2009), raising questions about locally specific histories. Intensive human impact is argued to lead to silver fir decline in subrecent (Vrška et al., 2009; Diaci et al., 2011) as well as in prehistoric periods (Tinner and Lotter, 2006), while selective logging, litter raking, forest pasturing and other kinds of extensive management may promote the species (Málek, 1983; Motta and Garbarino, 2003; Carcaillet and Muller, 2005; Boublík, 2007; Kozáková et al., 2011). However, so far there is no direct evidence that extensive forms of management constitute a favourable regeneration niche for silver fir. Our results suggest that the relatively high dispersal ability of silver fir may enable the species to escape competition by European beech (compare Tinner and Lotter, 2006; Packham et al., 2012; Szwagrzyk et al., 2012). Such a dynamic equilibrium may constitute a mode of coexistence for these important tree species in Central Europe.

To explain the dynamics of silver fir forests in European landscapes, we suggest an ecological succession model. This model emphasizes periods of expansion by silver fir as an integral part of species ecology.

1. In an intensively managed, mostly deforested landscape silver fir occurs in forest patches (Fig. 7a). It coexists there in a mature state with other species, mainly European beech (Korpel', 1995) providing a flux of diaspores to the surrounding agricultural landscape, where silver fir seedlings are constantly present in suitable places (for tree seedling establishment on grassland see Smit et al., 2006; Dovčiak et al., 2008). Mature silver fir individuals can also occur in pastures (Zajoncová, 2007), providing another important source of diaspores.
2. After the abandonment of areas less suitable for agriculture, the equlibrium changes and forest succession begins (Fig. 7b). Fast

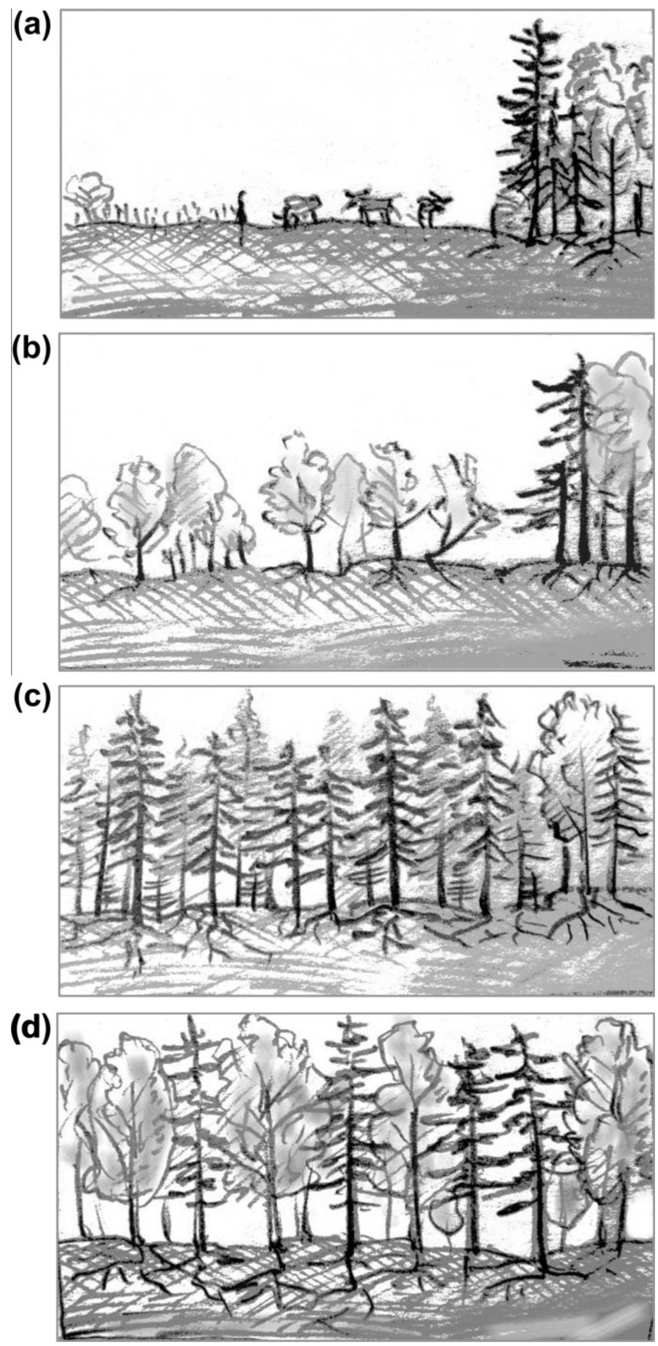

Fig. 7. Succession model for silver fir forests. (a) Agricultural land, mainly pastures, with silver fir in remnants of forests managed for timber and firewood. (b) Early phase of forest succession on abandoned agricultural land dominated by pioneer species including young silver fir. (c) Mid-phase of forest succession dominated by mature silver fir. (d) Old-growth forest dominated by European beech, with silver fir and other species in admixture.

colonizing species, such as silver birch (*Betula pendula* Roth), rowan (*Sorbus aucuparia* L.), common hazel (*Corylus avellana* L.) or species of hawthorn (*Crataegus* spp.). start to dominate on the abandoned land (Bartolomé et al., 2008; Dostálová, 2009; Kopecký and Vojta, 2009). However, silver fir closely follows, behaving as a pioneer species. Soil surface disturbed by former pasturing provide a suitable regeneration niche. This stage may last for about 50 years.

3. Silver fir-dominated forests are the culmination of silver fir succession (Fig. 7c). This phase occurs at ca. 50–150 years from the starting point. Silver fir-dominated forests may not persist much longer than a century. Surviving silver fir individuals continue to the next phase when European beech, which is competitively stronger but disperses more slowly, starts to increase at the expense of silver fir if no management is applied (Vrška et al., 2009; Sitzia et al., 2012). To develop a silver fir-dominated forest, a sufficient flux of diaspores is necessary, thus in abandoned landscapes with a lack of source populations of silver fir, such forests would not develop (e.g. Kopecký and Vojta, 2009).
4. The late successional stage is represented by mixed forests dominated by European beech (Fig. 7d). This follows agricultural land abandonment by ca. 150–200 years and can persist for centuries. Unless favoured by extreme soil conditions, silver fir gives way to competitively stronger European beech (Szwagrzyk et al., 2012); other species can also be present as an admixtion. Such a process of silver fir retraction was observed mainly in Carpathian forest reserves (Šamonil and Vrška, 2007; Šebesta et al., 2011); but not necessarily elsewhere (Klopcic and Boncina, 2011). It is not clear how large the proportion of fir can remain under competition by European beech.

5. Conclusions

The current distribution of silver fir forests in our study region is clearly linked to past land use. Silver fir expanded from old-growth forests to abandoned agricultural land, mainly pastures during the 19th century. Most silver fir-dominated forests resulted from this process. Silver fir populations can escape competition by European beech through utilizing regeneration 'windows' following agricultural abandonment. Expansion on abandoned agricultural land can therefore be a significant element in the dynamics of silver fir. Although it has been argued that silver fir declines under human impact, we suggest that periods of both decline and expansion have underpinned silver fir dynamics.

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