Spatially and temporally disjointed old-growth structures in a southern Swedish beech dominated forest landscape

Marcin Churski and Mats Niklasson

The structure of beech *Fagus sylvatica* dominated stands was investigated in a recently protected 900 ha mixed temperate forest landscape in southern Sweden. The stands ranged from having low biological values with none or few redlisted species to semi-natural stands with high conservational values. We tested the hypothesis that the investigated stands would show a large variation in structures associated with high biological values (age, age structure, variation in stem diameter (dbh) and coarse woody debris (CWD) densities). The number, ages and dbh of living trees and snags, dimensions of CWD (with a minimum diameter of 10 cm and length of 1 m) and the number and ages of stumps were measured on 21 circular plots (0.126 ha). Additionally, on another 39 plots (0.016 ha) the number, ages and dbh of living trees were measured. Age structure analysis revealed a large deficit of the late biostatic phase of a forest cycle (corresponding to trees 150–240 yr old). Few plots were dominated by old-growth attributes (old trees, large trees, snags, CWD). In the remaining plots only small amounts of old and large trees, and CWD were found, clearly reflecting past forest utilization. Past forest management as a type of disturbance has led to the simplification of the forest structure at the stand scale and an uneven distribution of old-growth attributes at the landscape scale. As a consequence, biodiversity rich patches connected to the occurrence of old-growth stand attributes were restricted to few isolated stands. The lack of trees in the late-biostatic phase, in combination with the simplified age structure of stands and discontinuous supply of old-growth attributes may jeopardize future persistence of old-growth related biodiversity.

M. Churski (mchurski@zbs.bialowieza.pl), Polish Academy of Sciences, Mammal Research Inst., Waszkiewicza 1c street, 17-230 Białowieża, Poland. – M. Niklasson, Swedish Univ. of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O. Box 49, SE-230 53 Alnarp, Sweden.

In forests many endangered species depend on old-growth stand structures such as very old and large trees, an abundance of exposed coarse woody debris (CWD), and the occurrence of a specific forest successional stage (Nilsson and Baranowski 1997, Heilmann-Clausen and Christensen 2003, Ranius et al. 2008, Fritz et al. 2009a). In natural old-growth beech forests of the temperate zone all of these attributes exist in a finely patterned, diverse mosaic of developmental phases (Emborg et al. 2000).

In contrast to natural disturbance, forest management usually simplifies stand structure through the reduction of dead wood volumes and the number of old and large trees, by changing tree species composition and by shortening the successional cycle (Christensen and Emborg 1996, Bobiec 1998). In this way, humans have modified southern Swedish beech-oak forests for centuries, especially since the middle of the 19th century, due to intense forestry (Nilsson et al. 2001).

Until the 19th century multiple use of forest prevailed, based mainly on selective cutting of trees for local use and grazing of domestic livestock (Simonsson and Larsson 2007). Since the economical importance of timber increased during the 1900s, intensive forest management was introduced based on clear felling and active replanting of trees, usually conifers. Since about 1920, Norway spruce *Picea abies* has been strongly promoted and has replaced deciduous forest in many places. Many of the remnants of beech-oak forests in southern Sweden have high conservational values reflecting the occurrence of endangered species of invertebrates, lichens and fungi (Berg et al. 1994). The Biskopstorp forest studied here, is now protected as one of the largest semi-natural beech-oak forests in southern Sweden. Earlier studies in this area have revealed the existence of stands with high conservation values connected to old-growth features (Heilmann-Clausen and Christensen 2003, Fritz et al. 2008, 2009a, b, Fritz and Brunet 2010).

In this study, we investigated the amount, distribution and spatial continuity of old-growth associated structural attributes at a landscape level in the beech-dominated stands of the ca 900 ha Biskopstorp reserve. We analyzed the age of 979 living beech trees to obtain a picture of age distributions and regeneration patterns both at stand and landscape scale. Age structures were specifically studied in relation to the presence of old-growth attributes. Such information is valuable for predicting the spatio-temporal development of valuable habitat and will help in the long-term management planning of the area.

Material and methods

Study area

The Biskopstorp forest is located in south-west Sweden, 10 km north of Halmstad (56°48′N, 12°52′E), Halland county (Fig. 1). The climate of the region is maritime temperate. This results in generally moderate weather with average temperatures in January and July being –1.6°C and 15.5°C, respectively. The yearly average precipitation is 1100–1200 mm (Alexandersson and Eggertsson Karlström 2001). The dominant soil type is podzol with mor humus, developed on gneiss bedrock (Fredén 2002). The area is at the northern limit of European deciduous forest within the temperate zone (Ahti et al. 1968).

The forest of Biskopstorp comprises a total area of ca 900 ha (Bengtsson 1999). The landscape is characterized by a diverse topography, and is rich in hills of up to 200 m a.s.l., steep ravines, rocky outcrops and many small streams and lakes. Among previously managed spruce stands, typically planted in the period 1920–1960, there are managed stands and old, semi-natural stands of beech, oaks *Quercus petraea, Q. robur* and black alder *Alnus glutinosa*. The long term reconstruction of the forest history, based on pollen and charcoal analyses, indicates a gradual increase of *Fagus sylvatica* since 1000 AD followed by decline of oak, birch *Betula* spp. and hazel *Corylus avellana* (Karlsson 1996, Björkman 2000, Lindbladh et al. 2008). Deciduous stands with beech, oak, birch and alder cover >50% of the total forest area. Intensive forest management was introduced in the 1920s, comprising the replacement of beech and oak forest with spruce plantations that were managed until the 1990s. In some of the remaining beech stands, a shelterwood cutting system was applied with additional soil scarification.

Sampling design and measurements

In all mixed deciduous stands (n=53) with beech present, a total of 60 circular plots was established consisting of 21 plots with a radius of 20 m (0.1257 ha) and 39 smaller plots

with a radius of 7.07 m (0.0157 ha) – accounting for approximately 2.4% of pure beech stands and 0.4% of the total forest area (Fig. 1) (Bengtsson 1999). One large plot and up to three small plots were set up in each stand. Large plots were established only in beech-dominated stands (>50% beech), and small plots in the remaining stands with beech present. The number of small plots within a stand was dependent on stand size and variation in stand structure, with larger and structurally diverse stands receiving more small plots than uniform stands. Centers of the plots were chosen subjectively to represent the most representative parts of the stands. The number, age and diameter at breast height (dbh) of living trees and snags, dimensions of coarse woody debris (CWD – with a minimum diameter of 10 cm at the thicker end, and a length of 1 m) and the number and age of stumps were measured on 21 large plots. On the 39 small plots the number, age and dbh of living trees were measured. Trees of all species above 2 m in height were classified as living or snags (dead trees) and their dbh was measured. Each tree, snag, log or stump was identified to species. All living beech trees >2 m were cored for aging with a Haglöf increment borer at the lowest possible point, usually at 30–40 cm above forest ground. In total 979 living beech trees were aged. From snags and stumps full or partial cross-sections were collected with a chainsaw. Samples were collected only if the rings were still visible which disqualified decomposed snags and stumps. In total 89 dead beech samples were collected from snags and stumps. All cores and cross-sections were mounted on wooden sticks or boards, dried and polished to a smooth surface with a belt sander up to a 400 grid sand paper. For core samples from healthy (not rotten) trees where tree piths were missed we estimated the pith date after defining the distance to the pith using calculated mean radial growth based on a width of the three oldest rings visible (Brown and Wu 2005, Brown 2006). Only cores with pith present or pith estimated to be located within 20 mm from the oldest present ring of the sample were accepted for further analyses. All samples were cross-dated with the pointer year method to avoid biased age estimation due to missing rings (Stokes and Smiley 1968). The following years had conspicuous narrow rings and were the most useful as pointer years: 1869, 1890, 1911, 1925, 1956, 1960, and 1974. Stands were classified and mapped according to the age and composition features as old-growth beech stands, beech-dominated stands, and oak and spruce-dominated stands.

Data analysis

The landscape scale age structure was based on trees from 39 small plots (0.0157 ha) alone and trees selected within 7.07 m radius from 21 large plots (0.1257 ha) to ensure same plot area weight (Fig. 1). To test for differences in mean diameters between the age cohorts one-way ANOVA was applied. Values are presented as mean ± one stand-
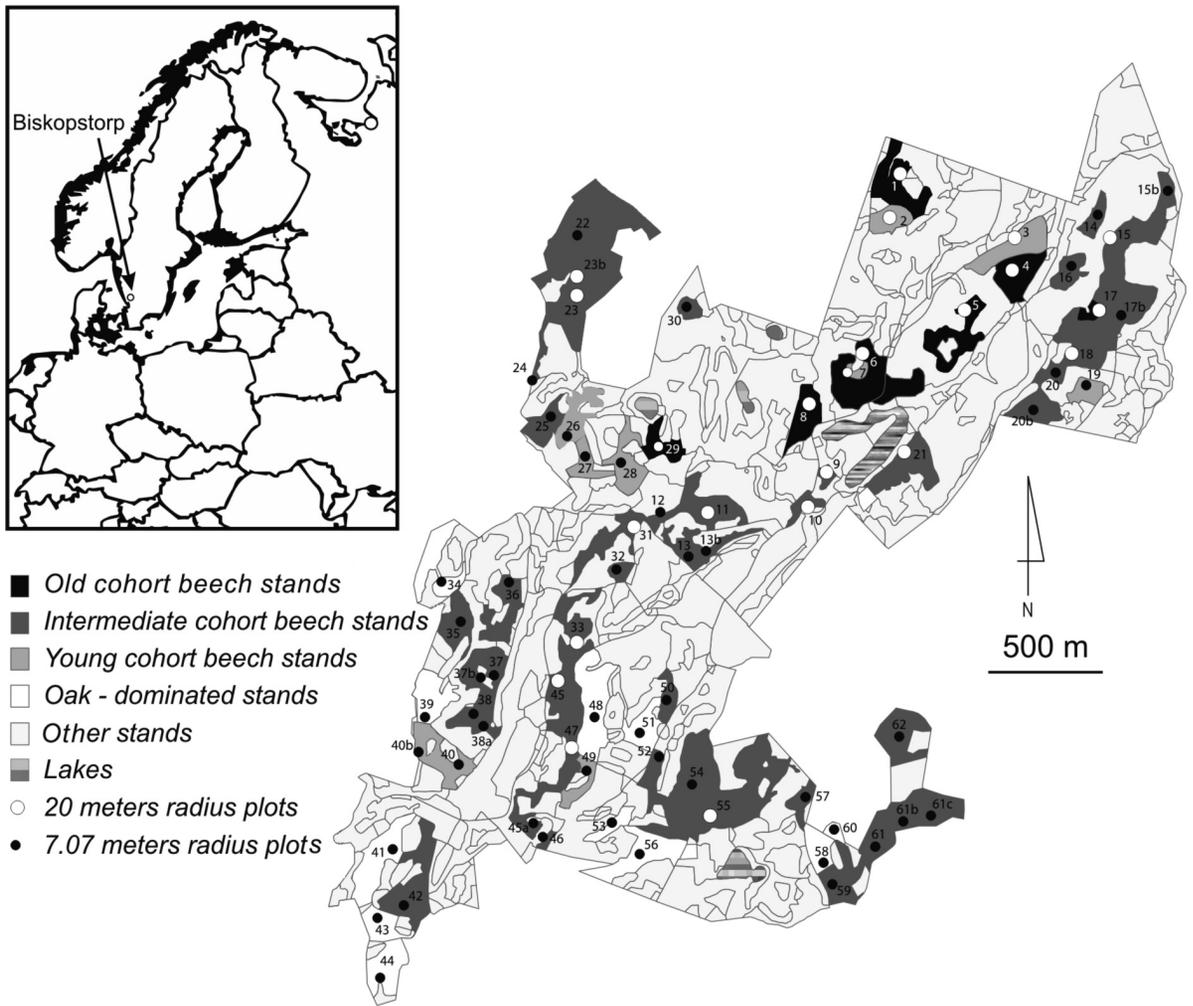
Figure 1. Distribution of beech *Fagus sylvatica* age cohorts and established plots in the Biskopstorp forest study area, southwestern Sweden. The stands are classified based on the oldest trees found on the plots.

ard error (SE). The dbh of the trees in each cohort was log transformed prior to the analysis to achieve normality. To test the difference in mean amounts of old-growth attributes (large trees with dbh >40 cm, snags with dbh >40 cm, CWD with thicker end diameters >40 cm) between the cohorts, a non-parametric Kruskal-Wallis test was applied, due to unequal distribution of valid cases in each cohort and non-normal distribution of the data (Quinn and Keough 2002).

Results

The age structure of living beech trees pooled from all the plots (n=60) showed prominent peaks of regeneration pulses and periods of low recruitment. The age distribution revealed a large deficit of trees between 180 and 240 yr old (Fig. 2). The age structure of dead beech trees (snags and stumps) in general showed a pattern similar to the living trees (Fig. 3). Based on depressions in regeneration that occurred in the periods 1760–1820 and the 1920s, three main regeneration pulses were distinguished: old cohort (>240 yr), intermediate cohort (90–240 yr), and young cohort (<90 yr old) (Fig. 2). The distinction of the young cohort was also based on the intensive logging and replanting activities that begun in the 1910–1920s. At the plot level, beech age structure varied considerably. The majority of the plots were represented by one (42% of the plots) or two (53%) age cohorts. At three plots (no. 1, 4, 8) trees from three cohorts were found (Fig. 4). Only three plots (no. 31, 45, 47), showed continuous beech regeneration over the last 150 yr. No single plot showed continuous beech regeneration since 1750 but five plots with the oldest trees (no. 1, 4, 5, 6, 8) were composed of two well-differentiated cohorts (mainly old and young), separated by over 100 yr of low recruitment (Fig. 4).
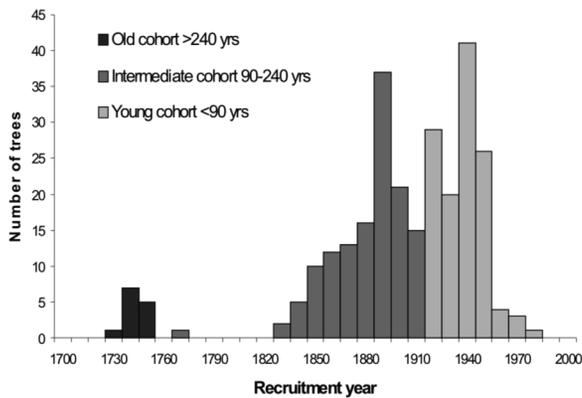
Figure 2. Landscape level age structure of beech *Fagus sylvatica* pooled from all plots with beech present (n=60) based on trees from 39 small plots (0.0157 ha) and trees selected within 7.07 m radius from 21 large plots (0.1257 ha).

The age cohorts differed significantly from each other in respect to mean diameters (ANOVA $F_{2, 814}$=237.24, p < 0.001). The oldest cohort had the highest mean diameter (51.2±1.06 SE), however individual trees with the largest dbh observed belonged to the intermediate cohort (Fig. 5). The dbh of beech trees was positively correlated with age, with age explaining 52% of the variation in dbh (r=0.72, $F_{1, 815}$ = 881.048, p<0.001) (Fig. 5).

Old-growth attributes (large trees, snags, CWD) were found to be unevenly distributed and generally restricted to the plots with the old cohort trees. Plots with trees from the intermediate and young cohorts had significantly lower amounts of large trees (H=7.307, p=0.0259), snags with dbh >40 cm (H=9.175, p=0.0102) and CWD with end diameter >40 cm (H=7.276, p=0.0263) (Fig. 6).

Old, intermediate and young cohorts were unevenly distributed over the study area. The intermediate cohort
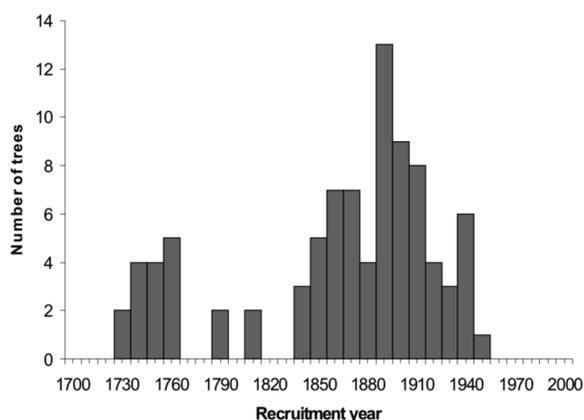

Figure 3. Landscape level age structure of dead beech *Fagus sylvatica* pooled from all plots with beech present (n=60). All samples collected from stumps and snags are presented (n=89) due to the low number of datable material.

was found throughout the area whereas the oldest cohort with highest amounts of old-growth attributes was found in the north. Old beech stands were absent in the south of the Biskopstorp reserve (Fig. 1).

Discussion

Age and stand structures

At the landscape scale, the distinct peaks and the discontinuous pattern of age structure suggests past disturbances that triggered regeneration pulses. The age structure of both living and dead trees showed generally similar patterns. The age analysis revealed that the studied forest is composed of three age cohorts, which differed in terms of development history. The oldest trees reach almost 300 yr in age which is near the upper limit reported for the species in northern Europe (Niklasson and Fritz 2003). The distinct early cohort regenerated between 1720 and 1750 over a large area of the studied site (Fig. 1). There are indications that these trees are a result of human activities rather than natural disturbances (Lindbladh et al. 2008). Historical evidence of large-scale felling operations in the early 1700s in the area has been found although the precise locations of these remain unresolved (Simonsson and Larsson 2007). Some indications of anthropogenic landscape opening in the 1700s are found also in pollen diagrams, where around the 1700s the amount of grass pollen increased together with rapid decrease of beech pollen (Björkman 2000, Lindbladh et al. 2008). This period of intensive forest utilization probably created a strong regeneration pulse, visible on the present age structure as the old cohort. After that period, the recruitment slowed down creating a distinct 100 yr long flat trend in the age distribution (Fig. 2). Periods of low or absent recruitment (1760–1820) may indicate suppression by an external factor (e.g. grazing), filled regeneration space (Eriksson and Jakobsson 1999), i.e. when there is no available space for new saplings to recruit successfully or intensive cuttings. Since the age structures of both living and dead trees showed similar patterns, the period of low recruitment may indeed have been due to recruitment suppression rather than high mortality (both natural and anthropogenic). The collected dead beech samples, due to relatively high decomposition rates of beech wood may under-represent the real mortality processes. Moreover, in late-successional forests shade-tolerant trees (like beech) can persist for several decades under canopy shade (Niklasson 2002), therefore the presented age structure can not be definitely indicative of a disturbance history.

The origin of the young cohort seems to be caused entirely by anthropogenic influence. Intensive forest management was introduced in the 1920s (Simonsson and Larsson 2007) by replacing beech and oak stands with
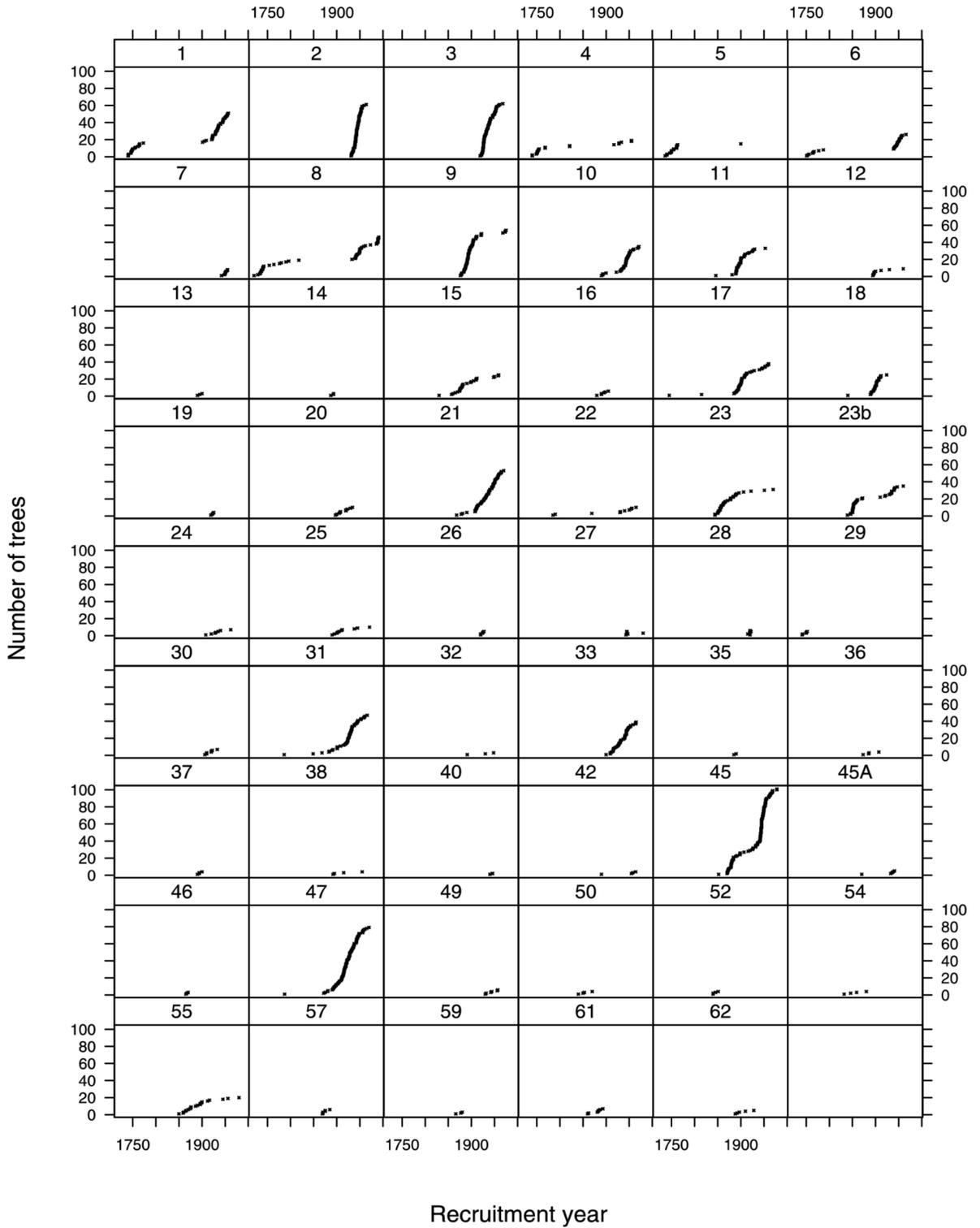
Figure 4. Age structures of living *Fagus sylvatica* trees at plot scale (n=60) plotted as cumulative germination years of the dated trees. In cases where more than one plot was analyzed per stand, the ages from these plots were combined into one graph per stand (8 cases).
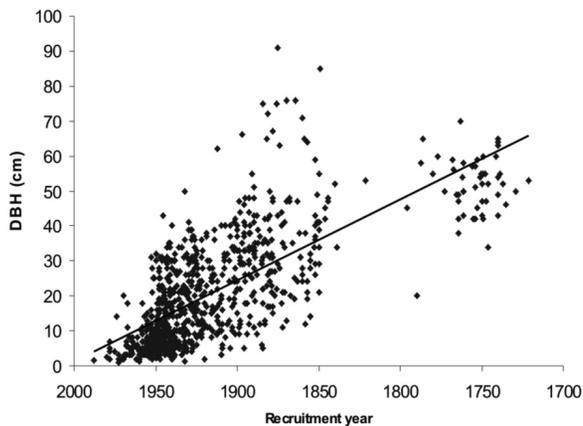
Figure 5. Diameter at breast height (dbh) in relation to age of beech trees (n=817, r^2 = 0.52, r = –0.72, $F_{1, 815}$ = 881.048, p<0.001).

Figure 6. Distribution of old-growth attributes among the cohorts (bars equal to mean + 1 SE).

spruce plantations, with the exception of those stands where shelterwood cuttings were done. This is also visible on the stand scale age structures where several stands show distinct, single cohort structure that originated in the 1910–1920s (Fig. 3).

Alternatively, the irregular age structure of beech at Biskopstorp might have been caused by the natural disturbance regime. Although hurricanes are fairly common in the area, they occur predominantly in winter when deciduous trees are much less susceptible. A striking example of the difference in windthrow susceptibility was given by the hurricane the 8 January 2005 when ca 25% of the Norway spruce monocultures in the reserve were overthrown. In the beech stands however, only occasional trees were broken or uprooted, a pattern observed also in the Fontainebleau forest after the storms in 1996 (Pontailler et al. 1997). Uprootings are obviously rare in the beech stands of the study area (Fuentes et al. 2010). Soilmounds after uprootings may remain for centuries (Faliński 1978) but very few can be found in Biskopstorp (Fuentes et al. 2010, Churski and Niklasson unpubl.). Therefore it seems that the present beech population structure is rather a result of anthropogenic disturbance, mainly past forest utilization.

Substantially low regeneration in the period 1760–1820 is difficult to interpret. In a study of lowland forest in northern Spain, Rozas (2003) argued that intense grazing pressure inhibited establishment of beech regeneration whereas beech recruitment was continuous in periods of forest protection against grazing. If this is the case in Biskopstorp, a combination of grazing and filled regeneration space and selective cuttings may have inhibited stronger regeneration pulses. Periods of rapid recruitment indicate the availability of space for new saplings to establish and recruit. In the Biskopstorp forest a disturbance that might have provided conditions suitable for successful regeneration and recruitment took place in the 1850s,
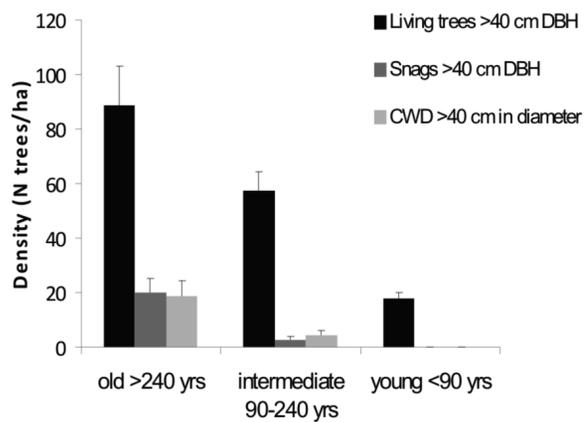
which is indicated by the broad peak in the age structure. The next disturbance that created a regeneration pulse took place in 1920s–1940s, and was most likely connected to active forest management. After that, fast recruitment of beech trees was followed by constantly decreasing regeneration rate. We interpret the disturbance as the onset of a shelterwood management system which at this time was substituting grazing and traditional forest use.

In the studied landscape stem diameter is a poor measure of demographic parameters. The main cause for the low fit is the great plasticity in diameter growth. A large number of trees in the old cohort especially have grown very slowly, with 240 yr old trees being not more than 70 cm in diameter at breast height, while in stands with trees from the intermediate cohort the same size could be reached in less than half the time.

Continuity of old-growth attributes

Old-growth stands in general are known to support more red-listed species than stands in earlier stages of forest development. This is mainly connected to the continuity of forest cover (Fritz et al. 2008), age of trees (Ranius et al. 2008, Fritz et al. 2009a) and age-related number of microhabitats (Fritz et al. 2009b), and amount of dead wood (Nilsson et al. 1995, Brunet et al. 2010). Therefore old-growth stands are the most important for conservation practices. Fritz et al. (2008) showed that beech forests with forest cover continuity for 350 yr or more contain significantly more species of epiphytic lichens and bryophytes than stands lacking continuity. A disturbed forest development cycle in both temporal and spatial scales may limit species dispersal, and continuous regeneration of trees is crucial in maintaining and dispersing species of epiphytic lichens and bryophytes for a time longer than a single generation of trees.

Conclusion

The results of this study show a disjointed pattern of the old-growth attributes (old trees, large snags and CWD) over spatial and temporal scales. Because of the disturbed recruitment cycle in the past and the resulting substantial deficit of late-succesional phases, an important management question arises: how to secure the future of the old-growth-related biodiversity? Focusing on the near future active measures to induce senescence and micro-habitat formation (e.g. rot holes) in vital trees close to old-growth patches could be suitable to maintain habitat availability for epiphytic and saproxylic species.

References

Ahti, T. et al. 1968. Vegetation zones and their sections in northwestern Europe. – Ann. Bot. Fenn. 5: 169–211.

Alexandersson, H. and Eggertsson Karlström, C. 2001. Temperatur och nederbörden i Sverige 1961–1990. Referensnormaler – utgåva 2. – Meteorologi nr 99, 2001, SMHI, Norrköping, in Swedish.

Bengtsson, S. 1999. Biskopstorp – skogstyper, ekologi och skötsel. – Länsstyrelsen Halland, Meddelande 1999:20, in Swedish.

Berg, Å. et al. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat association. – Conserv. Biol. 8: 718–731.

Björkman, L. 2000. Pollenanalytisk undersökning av en torvmarklagerföljd från Trälhultet i Biskopstorps naturreservat, Halmstads kommun. – LUNDQUA Uppdrag 29, Kvartärgeologiska avdelningen, Lunds Univ., in Swedish.

Bobiec, A. 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Bialowieza. – Plant Ecol. 136: 175–187.

Brown, P. M. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. – Ecology 87: 2500–2510.

Brown, P. M. and Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. – Ecology 86: 3030–3038.

Brunet, J. et al. 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. – Ecol. Bull. 53: 77–94.

Christensen, M. and Emborg, J. 1996. Biodiversity in natural versus managed forest in Denmark. – For. Ecol. Manage. 85: 47–51.

Emborg, J. et al. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. – For. Ecol. Manage. 126: 173–189.

Eriksson, O. and Jakobsson, A. 1999. Recruitment trade-offs and the evolution of dispersal mechanisms in plants. – Evol. Ecol. 13: 411–423.

Faliński, J. B. 1978. Uprooted trees, their distribution and influence in the primeval forest biotope. – Vegetatio 38: 175–183.

Fredén, C. E. 2002. Geology. The National Atlas of Sweden. – SNA Förlag, Stockholm.

Fritz, Ö. and Brunet, J. 2010. Epiphytic bryophytes and lichens in Swedish beech forests – effects of forest history and habitat quality. – Ecol. Bull. 53: 95–107.

Fritz, Ö. et al. 2008. Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. – Biol. Conserv. 141: 655–668.

Fritz, Ö. et al. 2009a. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. – Appl. Veg. Sci. 12: 96–106.

Fritz, Ö. et al. 2009b. Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. – Bryologist 112: 488–505.

Fuentes, M. et al. 2010. Tree mortality in a semi-natural beech forest in SW Sweden. – Ecol. Bull. 53: 117–129.

Heilmann-Clausen, J. and Christensen, M. 2003. Fungal diversity on decaying beech logs – implications for sustainable forestry. – Biodivers. Conserv. 12: 953–973.

Karlsson, M. 1996. Vegetationshistoria för en artrik bokskog i Halland – stabilitet eller störning? – Examensarbete nr 1, Southern Swedish Forest Research Centre, in Swedish.

Lindbladh, M. et al. 2008. Close anthropogenic control of *Fagus sylvatica* establishment and expansion in a Swedish protected landscape – implications for forest history and conservation. – J. Biogeogr. 35: 682–697.

Niklasson, M. 2002. A comparison of three age determination methods for suppressed Norway spruce: implications for age structure analysis. – For. Ecol. Manage. 161: 279–288.

Niklasson, M. and Fritz, Ö. 2003. A 400-year-old beech Fagus sylvatica found in Småland, SW Sweden. – Sv. Bot. Tidskr. 97: 150–156, in Swedish with English abstract.

Nilsson, S. G. and Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. – Ecography 20: 491–498.

Nilsson, S. G. et al. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. – Conserv. Biol. 9: 1208–1215.

Nilsson, S. G. et al. 2001. Biodiversity and its assessment in boreal and nemoral forests. – Scand. J. For. Res. Suppl. 3: 10–26.

Pontailler, J. Y. et al. 1997. Storms drive successional dynamics in natural forests: a case study in Fontainebleau forest (France). – For. Ecol. Manage. 98: 1–15.

Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. – Cambridge Univ. Press.

Ranius, T. et al. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. – J. Veg. Sci. 19: 653–662.

Rozas, V. 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech-oak lowland forest in northern Spain. – For. Ecol. Manage. 182: 175–194.

Simonsson, G. and Larsson, K. 2007. Biskopstorp, historisk hävd och framtida skötsel. – Länsstyrelsen Halland, Meddelande 2007:24, in Swedish.

Stokes, M. A. and Smiley, T. L. 1968. An introduction to tree-ring dating. – Univ. of Chicago Press.