Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe

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Summary
Studies of old-growth forests are becoming increasingly important for the improvement of silviculture and for understanding environmental changes. However, in Europe such forests are rare, fragmented and influenced by millennia of human activity. Comparative studies of old-growth forests across Europe are needed to improve knowledge on how direct and indirect anthropogenic factors influence their structure. We analysed structural dynamics in 15 silver fir-beech-Norway spruce old-growth forests in Slovenia, Croatia, Slovakia and Bosnia-Herzegovina. Changes in diameter distributions, stand parameters and regeneration were analysed at intervals of 6–116 years. Most diameter growth at breast height (d.b.h.) distributions approximated a rotated sigmoid shape, which could be explained by differences in growth and mortality rates with respect to d.b.h. class and by disturbance history. Our results suggest that different disturbance types are likely to cause different changes in d.b.h. distributions. For example, overbrowsing, canopy dieback of silver fir and windthrow decreased the density of small, intermediate and large-diameter silver fir, respectively. The slopes of the fitted diameter distribution curves were steeper for beech than for silver fir, which could be explained by their different life strategies. Despite disturbances, growing stocks remained stable over the long term. A synchronous silver fir decline was confirmed. It was more pronounced in Slovenia and Slovakia, both of which experienced more SO₂ pollution and had higher ungulate densities. The silver fir sapling stage was often totally absent in both countries. Our results suggest that anthropogenic disturbances, especially air pollution and overbrowsing (resulting from human-induced increases in deer density), significantly influenced the coexistence of silver fir and beech; asynchronous, patchy changes in species mixture have been replaced by large-scale synchronous changes.

Introduction
Research on old-growth forests is essential for understanding forest ecosystem functioning and for the development of forest management strategies. Their structural dynamics depends on disturbance patterns (White and Pickett, 1985). In recent decades, much research in old-growth forests has focused on natural disturbances. However, over several centuries, the natural disturbance regime has been severely altered by forest fragmentation, changes in fire regime, fauna extinctions, the introduction of forest management into the forest matrix surrounding old-growth, forest road infrastructure, and, in the last few decades, by overbrowsing, air pollution and climate change (Nowacki and Abrams, 1994; Uotila et al., 2002; Oulehle et al., 2010). Present-day old-growth forest structures are often a result of complex interactions between natural and anthropogenic disturbances (McLachlan et al., 2000). In Europe, old-growth forests have been significantly influenced by millennia of civilization. Thus, studies of
anthropogenic disturbance history could reveal new perspectives on European old-growth forests.

Mixed silver fir (Abies alba Mill.), beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.) mountain forests represent one of the major forest types in Eastern and Southeastern Europe (Horvat et al., 1974; Ellenberg, 1988). They are well preserved since they have been influenced by humans to a lesser extent than lowland or high mountain forests have (Korpel, 1995; Ficko et al., 2011). The majority of European temperate old-growth forests lie in this region (Leibundgut, 1982), while small-scale, uneven-aged silvicultural systems are typical of managed forests (Mlinsek, 1972; Matic, 1983; Korpel et al., 1991). The majority of mixed mountain forests have experienced changes in structure and composition over the last few hundred years. From the beginning of regular management, conifers have been promoted by silvicultural measures, charcoal burning, the production of potash, localized forest litter collection and grazing and decreasing densities or extinction of ungulates (Matic, 1983; Kordis, 1993; Vrška et al., 2009). Therefore, the proportion of silver fir (hereafter fir) in the growing stock in Eastern and Southeastern Europe peaked soon after World War II (WWII) (Korpel, 1995; Klopčič et al., 2010). Later, its proportion started to decline, probably due to the interplay of several factors, such as changes in forest management (abandonment of the selection system, intensified cutting regimes, forest microclimate changes induced by construction of skid trails and forest roads), overbrowsing and canopy dieback of silver fir. However, an increase in beech in mixed old-growth forests may have started as long as 60 years ago (Safar, 1951, p. 302) and has been more noticeable in recent decades, indicating the importance of indirect human disturbances or natural processes (Korpel, 1995; Vrška et al., 2009). Therefore, a comparative study of mixed old-growth forests could verify whether these processes have been significant on a larger scale. This would help to distinguish the natural, direct and indirect anthropogenic factors influencing compositional and structural changes.

The long-term influence of heavy air pollution on old-growth forests in Eastern and Southeastern Europe has not been given a great deal of attention (Oulehle et al., 2010) although SO₂ emissions in this area have been reported to be among the world’s highest (Stern, 2006). Since old-growth forests are often game reserves, the elimination of palatable species by overbrowsing has become a key factor in species coexistence over the last few decades in many European regions (Korpel, 1995; Linder et al., 1997; Kenderes et al., 2008; Vrška et al., 2009; Diaci et al., 2010). Fir combines certain features that make it very vulnerable to browsing: it is one of the most palatable species, it grows very slowly in shaded conditions, and it recovers poorly from browsing damage (Gill, 1992; Motta, 1996). The significant differences in ungulate densities between countries in Eastern and Southeastern Europe make comparisons particularly interesting.

Stand parameters such as growing stock, basal area and tree density are basic inventory parameters in old-growth forests and are therefore often recorded. However, in Europe, such parameters have not often been used in integrative and comparative research. Because of the rarity and fragmentation of old-growth forests, this research is especially important (Leibundgut, 1982; Korpel, 1995; Vrška et al., 2009). Their spatiotemporal variability reflects the interplay between natural and anthropogenic factors on old-growth structure. These parameters, in particular, become more valuable when integrated with other characteristics such as diameter distributions, regeneration and disturbance history.

Spatiotemporal changes in diameter at breast height (d.b.h.) distributions are important in old-growth research since they help to trace past disturbances; understand regeneration, growth and mortality patterns; predict future development of stands and reveal the competitive relationship between tree species (Schmelz and Lindsey, 1965; Goff and West, 1975; Aldrich et al., 2005; Wang et al., 2009). Namely, in tree populations, size, social status and age considerably influence demographic processes. For d.b.h. distributions of old-growth forests close to their demographic equilibrium, several shapes can be characteristic (Goff and West, 1975; Lorimer, 1980; Leak, 1996; Shimano, 2000; Westphal et al., 2006): negative exponential (NE), negative power function (NP), increasing Q (IQ) and rotated sigmoid (RS). The biological reason behind the distribution shapes is linked to their reduction rate (Q) with increasing d.b.h. class; it can be constant (NE), decreasing (NP), increasing (IQ) or variable (RS). IQ and RS shapes could also indicate past disturbances or management (Leak, 1996), while a unimodal shape (UNI) indicates heavier disturbance or succession (Aldrich et al., 2005; Janowiak et al., 2008). Old-growth stands are often composed of several species, which may add to the complexity of distribution shapes. Many studies of the d.b.h. structures of old growth forests have been done and many have focused solely on d.b.h. structures (overview Westphal et al., 2006). However, because of the many possible factors influencing d.b.h. distributions, they should always be interpreted in relation to other structural parameters or knowledge on the disturbance history of the forest in question (Lorimer, 1980; Goodburn and Lorimer, 1999).

The overall objective of the study was to describe the change in stand structure and composition and to discuss these changes in relation to the natural and anthropogenic disturbance history, especially air pollution and overbrowsing resulting from human-induced increases in deer density. The aims of the study were to (1) examine whether mixed old-growth forests from different geographical regions in Eastern and Southeastern Europe have experienced similar structural and compositional changes in the past few decades; (2) compare the relevance of natural and anthropogenic factors influencing composition and structure; (3) anticipate future developmental trends and (4) develop recommendations for old-growth management.

Methods

Study area and disturbance history

The study included 15 old-growth forests in four countries: Bosnia and Herzegovina (BiH), Croatia (CRO), Slovakia
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Field methods

Diameter distribution data was obtained from callipering whole reserves in mainly 10-year intervals (seven reserves), from larger permanent plots (five reserves) and from combinations of permanent plots and systematic sampling (three reserves; Table 3). However, all permanent plots and the total of the areas of the systematic sampling plots were larger than 0.9 ha. In BiH, Croatia and Slovenia, the lower d.b.h. limit was set at 10 cm, with 5-cm d.b.h. classes, while in Slovakia, the lower limit was set at 8 cm, with 4-cm d.b.h. classes. Volume was calculated by the volume tables that are typically used for old-growth research in each country. The data on regeneration was obtained for the same areas as the data on stand structure and was available for nine reserves. Common size classes were seedlings (older than 1 year and lower than 0.5 m) and saplings (0.5 ≤ h < 3–4 m).

Data analysis

Diameter distributions were fit with multiple linear regressions, following the methodology presented in Leak (1996). The dependent variable was the base 10 logarithm of trees per hectare and the independent variables were all possible combinations of the d.b.h. class midpoint, the midpoint squared or the midpoint cubed. The procedure for

| Research site                  | Area (ha) | Latitude (°) | Longitude (°) | Altitude (m) | Beec/silver fir | Beech/silver fir d.b.h. class midpoint | Beech/silver fir d.b.h. class midpoint squared | Beech/silver fir d.b.h. class midpoint cubed |
|-------------------------------|-----------|---------------|---------------|--------------|----------------|----------------------------------------|------------------------------------------------|-----------------------------------------------|
| Rajhenavski Rog                | Pecka     | 52.1          | 45° 40' N     | 15° 01' E    | 1760           | 6–7                                    | 6–7                                            | 6–7                                           |
| Krokare                       | Krokar    | 59.5          | 45° 33' N     | 15° 00' E    | 1760           | 6–7                                    | 6–7                                            | 6–7                                           |
| Strmec                        | Strmec    | 16.6          | 45° 38' N     | 15° 00' E    | 2000           | 6–7                                    | 6–7                                            | 6–7                                           |
| Lucka Bela                    | Lucka Bela| 20.0          | 46° 20' N     | 15° 00' E    | 2300           | 6–7                                    | 6–7                                            | 6–7                                           |
| Bukov Vrh                     | Bukov Vrh | 9.5           | 46° 29' N     | 15° 00' E    | 2000           | 6–7                                    | 6–7                                            | 6–7                                           |
| Somik                         | Somik     | 100.5         | 49° 30' N     | 15° 00' E    | 1700           | 6–7                                    | 6–7                                            | 6–7                                           |
| Trstionica                    | Trstionica| 1530          | 45° 30' N     | 15° 00' E    | 1700           | 6–7                                    | 6–7                                            | 6–7                                           |
| Pljesivica                    | Pljesivica| 1770          | 45° 30' N     | 15° 00' E    | 1700           | 6–7                                    | 6–7                                            | 6–7                                           |
| Igman                         | Igman     | 2000          | 45° 30' N     | 15° 00' E    | 1700           | 6–7                                    | 6–7                                            | 6–7                                           |
| Dobroc                        | Dobroc    | 1530          | 45° 30' N     | 15° 00' E    | 1700           | 6–7                                    | 6–7                                            | 6–7                                           |

Table 1: Characteristics of the 15 old-growth forests, including their ecological variables

*Stand key is used further in the text and figures.

Proportions of other species were below 2%, their proportions were added to the main species, and in other cases the sum of proportions is lower than 100%.

(57) and Slovenia (SI). Their area varied in size from 10 to 660 ha, while the majority were ~50 ha in size (Table 1). All of the forests were in the mountain to upper mountain vegetation belt. The bedrock consisted partially of carbonate and partially of acidic silicate rock; however, all of the old-growth sites were classified as the fir-beech-Norway spruce type according to Braun-Blanquet typology (Braun-Blanquet, 1964). The most recently recorded proportion of beech in the growing stock of these forests varied from 18 to 93 per cent. All forests are protected by law. Forest histories, especially past disturbances, were studied by an overview of the available literature and by a detailed formalized questionnaire sent to all co-authors. It included 11 disturbance categories: overviewing on tree regeneration by wild ungulates, canopy dieback of silver fir, canopy dieback of Norway spruce (hereafter spruce), windthrow, fir bark beetle (native species: genera *Pityokteines* and *Cryphalus*), spruce bark beetle (native species: genera *Ips* and *Pityogenes*), felling, charcoal or potash production, grazing by domestic animals, proximity of forest roads and other. Canopy dieback of fir and spruce denotes the dieback from the 1960s to 1990s which was mainly attributed to elevated SO2 emissions as reported from several reserves (e.g. Korpel, 1995; Daci et al., 2010). The disturbance intensity was scored on a scale from 0 (no disturbance) to 3 (severe disturbance). Scores were based on quantitative indicators for disturbance intensity and literature sources, e.g. the year of the event, ungulate density, the volume of damaged or killed trees, the quantity of and trends in SO2 emissions and general forest health status (Table 2).
selecting the best-fitting model and diameter distribution shapes to use for classification followed the methodology described in Janowiak et al. (2008). The highest adjusted $R^2$ and lowest root mean square error values were used as a basis for selection of the best-fitting model from all significant models ($P < 0.05$). If shapes were inconsistent or variable (Janowiak et al. 2008), the second best-fitting model was used. Out of 49 fits, 3 per cent of the cumulative distributions were variable shapes, and out of 96 fits, 8 per cent of species-specific distributions were variable shapes. A chi-square test of independence was applied to determine whether the d.b.h. distributions varied between different old-growth forests, species, before and after 1980 (significant increase of anthropogenic disturbances: e.g. SO$_2$ emissions and overbrowsing) and successive inventories of the same old-growth forest (for cumulative and species specific data). The differences in intercepts and the slopes of the fitted regression lines (between d.b.h. class midpoints and log n) were tested with an analysis of covariance. In order to linearly approximate the most frequent RS shape, the d.b.h. interval was divided into three sections: (1) d.b.h. $\leq 30$ cm, (2) 30 cm < d.b.h. $\leq 55$ cm and (3) d.b.h. > 55 cm. Additionally, differences in slopes and intercepts for pooled unsectioned data were tested. Cochran’s C test was applied to test the assumption of the homogeneity of variances, and residuals were visually inspected for any trends. To compare dependent samples, a nonparametric Wilcoxon test was applied.

Results

Disturbance history

All scores for individual disturbances from the questionnaire were summed for individual old-growth forests (Table 2), and they were classified into two groups with boundaries set as medians of all score sums: less disturbed forests (rank = 1) and more disturbed forests (rank = 2). The four most disturbed old-growth forests were in Slovenia (PE, LB) and Slovakia (DO, BA). All these forests experienced overbrowsing and fir canopy dieback, and some experienced repetitive windthrows or bark beetle outbreaks on spruce. All five of the least overall disturbed old-growth forests, CU, DT, IG, PL and TR, were in Croatia and BiH and had significantly lower impacts of ungulate browsing and fir canopy dieback. Comparison between disturbance categories based on the proportion of received scores per disturbance of the score total revealed that by far the most frequent and intensive disturbance was overbrowsing (25 per cent), followed by windthrow (18 per cent), fir canopy dieback (17 per cent), felling (15 per cent), proximity of forest roads (7 per cent), charcoal burning (6 per cent) and bark beetle on spruce (5 per cent). However, some disturbance categories were more closely linked to specific countries. For example, overbrowsing and fir canopy dieback were specifically linked to Slovenia and Slovakia, while others were more equally or randomly distributed. Individual stumps were recorded in all old-growth forests,
yet most fellings occurred in the period following WWII, and they were usually located at the old-growth borders. Grazing by domestic animals (3 per cent), spruce canopy dieback (2 per cent) and bark beetle outbreaks on fir (0 per cent) were less important disturbances overall. Other disturbances (2 per cent) were mentioned in two cases, namely the harvesting of small-diameter woody debris (TR) and reports from WWII on partisan warfare and a hospital (PE). The average distance from reserves to a forest road was ~370 m. However, seven old-growth forests shared one of the borders with a forest road, while the longest distance to a forest road was from forest SA (~2000 m).

**Diameter distribution shape**

We fitted curves to 49 cumulative d.b.h. distributions, 49 beech d.b.h. distributions and 47 fir d.b.h. distributions. Fewer fits for fir were due the insufficient number of fir trees in forest SA in the last two inventories in 1991 and 2001. The most frequent shape of the cumulative d.b.h. distributions was the RS shape, followed by the IQ, NE and UNI shapes (Figure 1; Table 4). Similar results were also obtained for shape frequency derived from the pool of all individual species-specific d.b.h. distributions (N = 96), although with slightly less RS and IQ shapes and more NE shapes. The RS shape was also the most frequent shape when d.b.h. distributions for beech and fir were analysed separately (Figure 2). However, for fir, the NE shape was the second most frequent, and for beech, the IQ shape was the second most frequent, closely followed by the UNI shape. For the chi-square test of independence, shapes with lower frequency than 5 (CO and UNI) were merged into one group. The shapes and tree species were not related (chi-square = 2.742, P = 0.4331). All fitted shapes explained more variance in beech than in fir (Wilcoxon matched pairs test: Z = 2.949; P = 0.0032) with R² medians of 0.9694 and 0.9055, respectively.

Further, we compared shapes with the best fit between forests with low (rank = 1) and severe disturbance impact (rank = 2; Table 2). In the first group, the most frequent shape was the RS shape followed by the NE and IQ shapes. The RS shape was also the most frequent in forests with severe disturbances, but, in contrast to the first group, the difference in frequency between this shape and other shapes was greater. The RS shape was followed by the UNI and NE shapes, while the IQ shape was much less frequent compared with less disturbed forests. For the chi-square test, shapes having lower frequency than five (UNI and CO) were merged into one group. The test confirmed dependence between shapes and the severity of old-growth forest disturbance (chi-square = 11.370, P = 0.0099). On the other hand, the dependence between d.b.h. shapes and year intervals (<1980, ≥1980) was not confirmed (chi-square = 0.241, P = 0.9707; Table 4).

**Table 3:** Overview of the methods for data collection in 15 old-growth forests and years of measurements

| Stand key | d.b.h distributions, N*, growing stock | Regeneration | Reference |
|-----------|----------------------------------------|--------------|-----------|
| RR        | 7 × full calliperling: 1892†, 1957, 1967, 1976, 1985, 1995, 2007 | 2 × systematic sampling: 1984, 2008 | Diaci et al. (2010) |
| PE        | 7 × full calliperling: 1892†, 1953, 1963†, 1973, 1982, 1994, 2003 | 3 × systematic sampling: 1988, 1994, 2007 | Nagel and Diaci (2006) |
| KR        | 4 × full calliperling: 1961, 1984, 1995, 2004 | n.a.† | Vrecl (1999) |
| ST        | 3 × full calliperling: 1984, 1994, 2004 | 1 × sampling in gaps: 2000 | Konecnik and Zaplotnik (2001) |
| BV        | 2 × full calliperling: 1983, 1998 | n.a. | Kovac (1999) |
| LB        | 2 × full calliperling: 1953†, 1963†; 2 × sampling: 1991, 2007 | n.a. | Firm et al. (2008) |
| SU        | 2 × permanent plot (0.9 ha): 1979, 1998 | n.a. | Vrecl (1999) |
| DT        | 2 × permanent plot (1 ha): 1972, 1978 | n.a. | Mikac (2010) |
| CU1       | 6 × permanent plot (1 ha): 1957, 1965, 1970, 1975, 1987, 2007 | n.a. | Mikac (2010) |
| CU2       | 3 × systematic sampling: 1977, 1985, 2007 | 1 × systematic sampling: 2007 | Mikac (2010) |
| IG        | 2 × permanent plot (1 ha): 1978, 1988 | n.a. | Ballian and Mikic (2003) |
| TR        | 4 × sampling: 1963†, 1972†, 1985†, 2001†; 2 × line transect: 2002, 2007 | 1 × line transect: 2007 | Ballian and Mikic (2003) |
| PL        | 1 × permanent plot (1 ha): 2008 | n.a. | Visnjic et al. (2009) |
| BA        | 6 × full calliperling: 1957†, 1970†, 1977, 1986, 1997, 2008 | 4 × systematic sampling: 1977, 1986, 1997, 2008; 3 × permanent plots: 1957, 1970, 1986 | Korpel (1995) |
| DO        | 4 × full calliperling: 1978, 1988, 1998, 2010; 3 × permanent plots: 1948†, 1958†, 1968† | 4 × systematic sampling: 1978, 1988, 1998, 2008 | Korpel (1995) |
| SA        | 4 × permanent plots (6 × 0.5 ha): 1971, 1981, 1991, 2001 | 4 × systematic sampling within permanent plots: 1971, 1981, 1991, 2001 | Korpel (1995) |

* Tree density.
† Only data for tree species proportions in relation to growing stock was available.
‡ Data was not available.
The comparison of cumulative and species-specific d.b.h. distributions from successive inventories of the same old-growth forests revealed that out of a total of 180 comparisons (i.e. 15 old-growth forests with two to six inventories, see Table 3), 81 were significantly different (45.7 per cent). When comparisons were divided into decades that had elapsed between the individual inventories, we discovered that after 10 years, 10 of the 69 (14.5 per cent) comparisons were significantly different; after 11–20 years, 34 of 57 (59.6 per cent) comparisons were significantly different and after more than 20 years, 37 of 51 (72.5 per cent) comparisons were significantly different.

When fitted species-specific shapes were observed visually, we discovered a recurring pattern of a more steeply declining slope for beech in the 55-cm and larger d.b.h. classes when compared with fir (compare Figure 2). The results of analysis of covariance confirmed a higher intercept of beech d.b.h. sections (see Methods) in all comparisons (Table 5). Slopes of beech d.b.h. sections were generally steeper; however, they were significantly different only for the large-diameter section (d.b.h. > 55 cm) and for the unsectioned data. In all analyses, the fitted regression lines explained less overall variability for fir than for beech. Visual inspection of figures revealed that this was mostly due to the higher variability of data.

Dynamics of stand parameters

The mean growing stock for all inventories was 723.5 (±16.3 SE) m³ ha⁻¹, with minimum and maximum values of 446.2 and 1010.0 m³ ha⁻¹, respectively (Figure 3a). On the lower end, there were forests on more extreme sites with steeper slopes and at higher altitudes, such as forests BV and KR, and on the upper end were forests where data was taken from smaller permanent research plots, which

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Table 4: Percentages of best-fitting shapes for cumulative (N = 49) and species-specific diameter distributions (N = 96) for 15 old-growth forests and several inventory years per shape

| Shapes | Cumulative | Per species | Disturbance | Period |
|--------|------------|-------------|-------------|--------|
|        | All        | All         | Fir         | Low    | Severe | <1980 | ≥1980 |
| RS     | 59.2       | 52.1        | 53.2        | 53.1   | 33.3   | 62.1  | 50.0  | 54.6  |
| UNI    | 10.2       | 11.2        | 6.4         | 16.3   | 6.7    | 13.6  | 10.0  | 12.1  |
| NE     | 12.2       | 17.4        | 23.4        | 12.2   | 26.7   | 13.6  | 20.0  | 16.7  |
| IQ     | 18.4       | 15.3        | 12.8        | 18.4   | 30.0   | 9.1   | 16.7  | 15.2  |
| CO     | 0.0        | 2.0         | 4.3         | 0.0    | 3.3    | 1.5   | 3.3   | 1.5   |

Note: RS, rotated sigmoid; UNI, unimodal; NE, negative exponential; IQ, increasing Q; CO, concave (after Janowiak et al., 2008).
were often selected in optimal and more productive parts of the stands (e.g. IG and CU1). However, the majority of old-growth forests had relatively stable growing stock. For example, the growing stock in forest RR varied by a range of only 56 m$^3$ ha$^{-1}$ over a 50-year period (1957–2006). Exceptions were forests that experienced large disturbances, especially windthrows. For example, forest PE experienced a 244 m$^3$ ha$^{-1}$ drop in growing stock during the same period.

The mean basal area was 44.8 m$^2$ ha$^{-1}$ (±0.89 SE), with minimum and maximum values of 33.6 and 59.0 m$^2$ ha$^{-1}$, respectively. All forests with extreme values were influenced by windthrow, but at different times. Forest DO was still recovering from a large-scale windthrow in 1931, forest PE had a substantial decrease in stand basal area after two successive windstorms (1983, 2004), and forest LB, with the highest basal area, had achieved a even-sized stand structure after a stand replacing event 150 years ago.

The proportion of fir in the growing stock decreased synchronously in almost all old-growth forests during the last 50 years (Figure 3c). Exceptions were forest IG in BiH, Figure 2. Representative examples of temporal changes in species-specific diameter distributions in (a) Slovenia (Rajhenavski Rog), (b) Slovakia (Badin), (c) Croatia (Corkova Uvala, Devcica Tavani) and (d) BiH (Igman, Trstionica). Curves and lines represent the best regression models. The third and fourth letter following the stand key are the species abbreviations (e.g. FI for silver fir), the next two numbers represent the year of measurement, while the last two letters denote the key for the shape, e.g. NE for negative exponential function.

Table 5: Analysis of covariance of pooled data from all reserves and measurements for comparing intercept and parallelism of the regression lines for log of tree density in dependence of d.b.h. class midpoints for silver fir and beech.

| d.b.h. (cm) | Fir | Beech | F-test |
|------------|-----|-------|--------|
| 10–30      |     |       |        |
|            | R$^2$ | a  | b  | N  | R$^2$ | a  | b  | N  | F  | Pa  | Pb  |
| 0.077      | 1.47 | -0.024 | 199 | 0.386 | 2.10 | -0.036 | 204 | 0.0000 | 0.0522 |
| 0.022      | 1.04 | -0.010 | 240 | 0.036 | 1.47 | -0.010 | 242 | 0.0000 | 0.9044 |
| >55        | 0.641 | 2.15 | -0.026 | 440 | 0.802 | 2.91 | -0.034 | 428 | 0.0205 | 0.0000 |
|            | 0.589 | 1.45 | -0.018 | 879 | 0.779 | 2.01 | -0.023 | 874 | 0.0000 | 0.0000 |

The first three rows show the results for the three sections of the curve along the d.b.h. classes, and the final row is for unsectioned data.
Note: N = sample size, R$^2$ = coefficient of determination, a = intercept, b = regression coefficient, Pa = F-test significance for intercept, Pb = F-test significance for slope.

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with a short-time interval of measurements and no recent
data, and the recent inventories of forests DO and BA in
Slovakia. The overall average change in fir in the growing
stock was –0.29 per cent per year. In Slovakia, Slovenia,
Croatia and BiH, it amounted to –0.45, –0.32, –0.15 and
0.02 per cent per year, respectively. The steepest declines
were recorded in forest PE during the 1990s (–2.33 per cent
per year), in forest BA during the 1970s (–1.70 per cent per
year) and in forest ST during the 1980s (–1.16 per cent per
year). In addition to air pollution, the fir decrease in forest
PE was influenced by the 1983 windrow. Fir decline in for-
est ST was probably influenced by the steep, exposed south
slope, while forest BA is at the lower altitude border of fir-
beech forests. The largest increases of fir were recorded in
forest RR during the first half of the 20th century (0.55 per
cent per year), in forest DO during the 2000s (0.39 per cent per
year) and in forest TR during the 1970s (0.37 per cent per
year). In addition to air pollution, the fir decrease in forest
PE was influenced by the 1883 windrow. Fir decline in forest
ST was probably influenced by the steep, exposed south
slope, while forest BA is at the lower altitude border of fir-
beech forests. The largest increases of fir were recorded in
forest RR during the first half of the 20th century (0.55 per
cent per year), in forest DO during the 2000s (0.39 per cent per
year) and in forest TR during the 1970s (0.37 per cent per
year). The oldest data for forests PE and RR revealed
that the proportion of fir was lower in the 1880s compared
with the maximum values that were reached after WWII,
before fir started to decrease again (Figure 3c).

The fir decrease was even more noticeable when calcul-
lated as the difference in fir density (trees per hectare per
year) between successive inventories for individual forests
(Figure 3d). In the period 1892–2010, only 7 of 40 differ-
cences were positive (16.7 per cent). Time intervals between
inventories varied from 5 to 65 years, but the most fre-
quent (62 per cent) was 10 years. The mean difference was
negative and amounted to –1.17 trees per hectare per year
(±0.36 SE). The largest decrease in fir density was recorded
in forest DT (–7.2 trees per hectare per year), followed by
forest ST (–6.3 trees per hectare per year), while the largest
increase was recorded in forest TR (4.9 trees per hectare
per year). The largest fir decrease was recorded during the
1980s (Figure 3d).

Natural regeneration

Data on regeneration was available for nine forests and
a total of 24 inventories. It was not normally distributed;
therefore, median values with lower and upper quartiles (in
parentheses) are presented. Median seedling, sapling and
small-diameter tree density (8–10 ≤ d.b.h. < 20 cm) per
hectare amounted to 13,395 (2,357, 29,302), 3,566 (1,752,
9,348) and 150 (115, 215), respectively. Comparisons of
regeneration between old-growth forests revealed signifi-
cant differences in fir density and proportion (Figure 4a
and b). In four forests, fir was totally absent from the
sapling class in all inventories (RR, PE, ST and DO). Very
low numbers of saplings were recorded in forest BA also,
especially when compared with its proportion in the grow-
ing stock. Seedling densities were less variable; they con-
formed fir establishment potential. However, in Slovenia,
the repeated inventories also revealed a decrease among
seedlings, while in Slovakia, the repeated inventories
showed a more stable proportion of fir among seedlings or
even an increase in the case of forest DO. In contrast, forest
SA and all three forests in Croatia (CU2) and BiH (PL, TR) exhibited more stable proportions of fir in the seedling and sapling classes (Figure 4b).

The proportion of fir in the total tree density was not constant in successive tree size classes (Figure 4a). Median values of fir proportions among seedlings, saplings, small trees, medium-diameter trees (20 ≤ d.b.h. < 80 cm) and large-diameter trees (d.b.h. ≥ 80 cm) amounted to 11.3, 0.7, 22.2, 25.9 and 49.3 per cent, respectively. Two extreme size classes could be distinguished: saplings, which had an extremely low proportion of fir, and large trees, which had a high proportion of fir. However, fir proportions were highly variable, not only between forests, but also between different developmental stages within forests. Again, two groups of forests with light (SA, CU2, TR, PL) and heavy (RR, PE, ST, DO, BA) ungulate impact could be distinguished (see Table 2). The three old-growth forests with the lowest deer densities (CU2, TR, PL) did not exhibit an increase in the proportion of fir with respect to successive size classes; only large trees showed a significant increase. This indicated that in the overbrowsed old-growth stands, browsing had already decreased the proportion of fir in the small tree class. To get an insight into the conditions before the heaviest impact of browsing, fir proportions in different size classes from less disturbed old-growth forests were analysed. For this, we used all data from Croatia and BiH (N = 16) as well as data from Slovenia and Slovakia from inventories before 1980 (N = 15). Data on seedling and sapling classes were not available for this analysis. Median values of the proportion of fir in small-diameter trees, medium-diameter trees and large-diameter trees amounted 32.8, 26.4 and 66.7 per cent, respectively.

Figure 4. (a) Proportion of silver fir in 15 old-growth forests according to tree classes: seedlings (h < 0.5 m), saplings (0.5 ≤ h < 3–4 m), small-diameter trees (8–10 ≤ d.b.h. < 20 cm), medium-diameter trees (20 ≤ d.b.h. < 80 cm) and large-diameter trees (d.b.h. ≥ 80 cm). (b) Proportion of silver fir in representative old-growth forests (stand key) from Slovenia, Slovakia, Croatia and BiH and year of inventory (numbers following the stand key) according to tree classes.

Discussion

D.b.h distribution shapes were influenced by disturbances

Comparison of cumulative and species-specific d.b.h. distributions in our study revealed that the RS distribution was the most frequent best fit. Goff and West (1975), who analysed hardwoods in North America, argued that the RS shape has a biological cause which has to do with the vigorous growth and low mortality of trees just entering the upper canopy when compared with younger or senescent trees. This has been confirmed by subsequent research (Goodburn and Lorimer, 1999; Janowiak et al., 2008) and validated by U-shaped mortality functions (Lorimer and Frelich, 1984; Lorimer et al., 2001). However, in our study, the frequency of the RS shape was also positively influenced by disturbance severity. More severe disturbances were characterized by UNI and CO shapes, which tended to change to the RS shape over time. Less disturbed old-growth forests had similar proportions of RS, NE and IQ shapes. The NE shape was often attributed to old-growth forests, while the RS shape was connected with past disturbance (Schmelz and Lindsey 1965; Leak, 1996). However, IQ shapes also indicate the absence of large-diameter trees, which is a feature of managed forests (Leibundgut, 1982; Leak, 1996; Janowiak et al., 2008) or old-growth forests damaged by windthrow.

Different disturbance types and intensities may cause different changes in d.b.h. distributions (Lorimer, 1980). In our analysis, long-term ungulate overbrowsing decreased the density of fir in the small d.b.h. classes. Shape changes in d.b.h. distributions over time in this study (Figure 2) and in a comparable study (Diaci et al., 2010) indicated that canopy dieback of fir lowered the distribution across the intermediate d.b.h classes. On the other hand, windthrow lowered the d.b.h. distribution among large-diameters since taller trees were more likely to be damaged (Nagel and Diaci, 2006). Different factors contribute to the shape of d.b.h. distributions, including the type of disturbance (Lorimer, 1980; Leak, 1996); natural mortality patterns (Goff and West, 1975); species-specific recruitment, growth and mortality rates (Shimano, 2000) and the size of the reserve and research plot (Janowiak et al., 2008). It seems the RS shape plays an important role in forests with shade tolerant fir and beech since U-shaped mortality functions could be anticipated. However, the NE shape also appears to be frequent in less anthropogenically or naturally disturbed forests.
Our results indicate that species-specific distributions differ slightly, with the RS shape being the most frequent for both species and the NE and IQ shapes being the second most frequent shapes for fir and beech, respectively. This could be biologically meaningful since a constant, decreasing rate of the NE shape would be more expected for fir, which is more shade-tolerant and attains larger sizes and often greater ages (Korpel, 1995), whereas the IQ shape, in which the mortality rate increases with increasing d.b.h. class, would be more expected for beech. Westphal et al. (2006) found, when comparing European beech old-growth forests, significant deviations from the NE shape towards the RS shape; the IQ shape was not included in the study. In our study, overall fitted shapes, more variance was explained in beech than in fir. This was most likely due to different anthropogenic disturbances, such as overbrowsing and pollution, than caused by some specific recruitment or mortality pattern. We also recorded significant variations in d.b.h. distributions between forests and within the same forest over time. After 21 years or more, ~75 per cent of the recorded distributions were already significantly different from the initial distribution of the same forests. This analysis also showed faster changes in fir compared with beech. Westphal et al. (2006) determined that only 11 per cent of d.b.h. distributions between nine beech old-growth forests were statistically similar.

Further, we discovered that beech had a more steeply sloped curve than fir in the d.b.h. range above 35 cm. This could indicate a lower mortality rate of fir compared with beech in larger diameters and is consistent with analyses of distribution shapes (more NE in fir) and proportions of fir across different size classes. Similar results were reported by Shimano (2000), who discovered that differences in intercepts and slopes could be used to distinguish between climax and pioneer species. The latter would have a high intercept and a steep slope. In our case, differences were relatively small since the ecology of fir and beech is more similar (Ellenberg, 1988). However, despite a possible biological meaning, the results for smaller diameters should be interpreted with caution because of overbrowsing in some reserves.

**Long-term stability of growing stock and variability of other parameters**

Despite disturbances, many old-growth forests retained a high and relatively stable growing stock and basal area over time. This is in agreement with previous studies of the same or comparable forests (Korpel, 1995). Other parameters fluctuated more, especially tree density and the proportion of fir in the growing stock. Differences in growing stock, basal area and tree density could be linked with disturbance history and site quality. Stand parameters were similar to those presented in Leibundgut (1982) and Korpel (1995). The proportion of fir in the growing stock decreased simultaneously in almost all old-growth forests during the last 50 years. The mean loss was about one tree per hectare per year, and it peaked in the 1980s at about two trees per hectare per year. However, it seems that silver fir decline was compensated by the intensified growth of remaining trees and by the accelerated recruitment of advance beech regeneration into the subcanopy. Thus, forest climate was largely sustained, and shade-intolerant species could not recruit into the canopy. The stability of stand parameters is a function of the disturbance patch, disturbance severity and the size of the reserve. Busing and White (1993) further suggested that biomass equilibrium in old-growth forest does not imply compositional equilibrium, which is usually achieved at larger spatial scales. Our study forests were relatively large in comparison with the prevalent natural disturbance patches. Canopy dieback of fir, which affected whole reserves, was a chronic, long-term, and relatively slow process that gave survivors and other species enough time to acquire free growing space and compensate for the loss of growing stock.

**Impact of chronic overbrowsing on regional regeneration**

Natural regeneration was generally abundant, but saplings were rare in Slovenia and Slovakia. This can be attributed to heavy impact by ungulates. While seedling densities indicated fir establishment potential, in Slovenia there were no firs in the sapling class in any of the inventories (N = 6). The same was true of forest DO in Slovakia. Moreover, very low values were also recorded in forest BA. The reported deer density in the regions surrounding old-growth forests was different in different countries, with the highest densities in Slovenia and Slovakia. For example, there were about one and seven individuals per square kilometre of roe (Capreolus capreolus L.) and red deer (Cervus elaphus L.), respectively, in the area of forest RR (Jerina, 2006) and one to and three and six individuals square kilometre of roe and red deer, respectively, in the area of forests BA and DO in Slovakia (M. Saniga, personal communication). Significantly lower densities were reported in Croatia and BiH, rarely amounting to more than one deer per square kilometre in total (Anonymous, 2007, 2010). All reported deer densities should be evaluated critically since they are difficult to estimate. Moreover, they were assessed for larger areas of managed forests surrounding old-growth forests. Thus, deer densities might be underestimated. Heavy deer browsing has been frequently reported in European (Korpel, 1995; Linder et al., 1997; Kenderes et al., 2008), North American (Nowacki and Abrams, 1994; Davis, 1996; Rooney, 2001; Long et al., 2007; Stroh et al., 2008) and Japanese old-growth forests (Abrams et al., 1999). Deer may be more common in old-growth forests since hunting is often prohibited and since they are less disturbed by logging, harvesting and traffic. Besides this, low light levels in old-growth forests result in fewer food resources for deer and in the slow growth of fir; therefore, the most palatable species remain vulnerable to browsing for long periods.

When forests less disturbed by ungulates were analysed, we discovered that the proportion of fir (in density) was not constant among different tree size classes. There was some evidence of a higher proportion among small-diameter trees compared with medium-diameter trees, which could
be explained by its greater shade tolerance in relation to beech. The increase in the proportion of fir among large-diameter trees could be a result of fir lower mortality in this size class; it attains larger diameters and heights than beech. Leibundgut (1982) and Korpel (1995) also reported this feature.

Evidence of overriding anthropogenic disturbances in mixed old-growth forests

The inquiry on disturbance history revealed a high frequency and intensity of natural and anthropogenic disturbances. The latter were more important, with humankind-induced ungulate overbrowsing being the most severe, followed by fir canopy dieback and felling. Results from disturbance inquiries were consistent with results from analyses of d.b.h. distributions, structural parameters and regeneration. Similar results regarding long-term anthropogenic influences in old-growth forests have been reported on different continents (Nowacki and Abrams, 1994; Abrams et al., 1999; Uotila et al., 2002; Aldrich et al., 2005; Oulehle et al., 2010).

One of the most intriguing phenomena of mixed forests was the canopy dieback of fir (Ficko et al., 2011). The first reports of local and regional fir canopy dieback in South-eastern Europe date from the end of the 1920s (Safar, 1951). It occurred along the borders of fir’s natural range, where it affected mostly sun exposed, rookier and drier slopes. It was probably triggered by harsh winters and hot dry summers (e.g. 1950). Acute fir canopy dieback was often accompanied by bark beetle calamities. The spread of fir canopy dieback occurred from the mid 1950s onward, when it also affected younger trees and extended to larger areas (Milnesk, 1964). Fir canopy dieback involved several factors (Krause et al., 1986); however, the acute fir dieback in the 1970s and 1980s was predominantly influenced by regional and temporal patterns of SO₂ air pollution coupled with climatic extremes (Elling et al., 2009). According to the information presented in Stern (2006), in the period from 1975 to 1993, Eastern Europe was the world’s largest emitter of sulphur. After 1993, Eastern Europe was surpassed by Asia. The SO₂ deposits in study area were not as high as in the northern Czech Republic, south-eastern Germany or southern Poland (Saltbones and Dovland, 1986). However, the forests of former Yugoslavia were also affected by SO₂ emissions from Western and Northern Europe (Komlenovic, 1989). The peak in emissions for regions under research took place at different times, but the overall peak probably occurred in the 1980s (Saltbones and Dovland, 1986; Oszlan, 1997; ARSO, 2010; Oulehle et al., 2010). The rank of countries according to actual SO₂ impact on forest ecosystems is likely Slovenia and Slovakia followed by BiH and Croatia. This rank is inversely related to the rank of overall forest health status based on the percentage of foliage loss (Pric, 1989; Oszlan, 1997). Our results from the disturbance survey as well as the analysis of the decrease in the proportion of fir also followed this rank. We did not study direct causal relations between fir canopy dieback and SO₂ emissions; however, many indirect indices suggested its strong impact on old-growth structure and composition, especially in countries with the highest emission (Slovenia, Slovakia). Fir canopy dieback in old-growth forests was often underestimated, probably due to the abundance of old and non-vital trees, although old-growth forests may be more sensitive to air pollution than younger managed forests. The significant influence of air pollution on old-growth forests was also reported in North America (Elliott et al., 2008). However, besides air pollution and overbrowsing, other disturbances may have also caused the decrease in fir. For example, taller fir trees are more susceptible to wind (Nagel and Diaci, 2006) and in large gaps caused by windthrow, beech regeneration has an advantage (Nagel et al., 2010). This may lead to a change in species composition after windthrow. Moreover, fir is susceptible to drought and bark beetle outbreaks.

In addition to air pollution and overbrowsing, felling was the third most frequent anthropogenic disturbance. However, it was mostly dispersed along the borders of the reserves, and it occurred before or shortly after WWII. Similar events were frequently reported in many old-growth forests in Europe and North America and should be considered more critically when discussing species coexistence and successional development (Nowacki and Abrams, 1994; McLachlan et al., 2000; Uotila et al., 2002; Aldrich et al., 2005). The most important natural disturbance was windthrow. In the majority of old-growth forests, broken trees or groups of broken trees resulting from windthrow were observed. Intermediate wind disturbance was documented in four old-growth forests: BA (1947), DO (1931, 1992–95; data for both forests is presented in Korpel, 1995), PE (1950s, 1983, 2004; Nagel et al., 2007) and LB (1880s; Firm et al., 2008).

Conclusions

It seems that old-growth forests in Eastern and South-eastern Europe have been influenced by natural and anthropogenic disturbances more than previously thought (Leibundgut, 1982). Our results suggest that when discussing old-growth structural dynamics, long-term disturbance history should be considered. Coexistence of fir and beech in mixed mountain forests is influenced by several factors, natural and anthropogenic, which operate at different spatial scales. Differences in autoecology, growth rates and tree architecture (Ellenberg, 1988; Stanciu and O’Hara, 2006) drive their neighbourhood interactions on a local scale. Different ungulate densities, silvicultural systems and air pollution influence the development of mixed forests on a regional scale, as does climate change on an even larger scale. However, it seems that in the last 50 years, the most important factors have been anthropogenic influences, especially air pollution and overbrowsing. Instead of asynchronous, patchy changes in species mixture (White and Pickett, 1985), we have experienced large-scale synchronous changes. Firstly, fir had been directly and indirectly anthropogenically favoured across the whole forest.
landscape until the second half of the 20th century, when anthropogenically influenced decline began. Even with the current radical decrease in SO₂ emissions in the region (Stern, 2006), recent trends in Slovenia, and to a certain extent in Slovakia, point to further fir decrease due to lack of regeneration. Our results suggest that the restoration of fir regeneration in old-growth forests would require a significant reduction in deer abundance, a cessation of feeding and the maintenance of low deer densities over extended periods of time. Because similar processes are found in old-growth and managed forests, the promotion of fir overall also requires the adaptation of silviculture to fir ecology, e.g. the maintenance of high growing stock, longer rotation and regeneration periods, larger target diameters and special modes of regeneration.

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