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A PROTECTED SILVER FIR (*Abies alba* Mill.) STAND IN SECONDARY SUCCESSION ON A FORMER PASTURE IN POLJANSKA DOLINA, SLOVENIA

ŠUMSKI REZERVAT JELE (*Abies alba* Mill.) U SEKUNDARNOJ SUKCESIJI NA OPUŠTENIM PAŠNJACIMA POLJANSKE DOLINE U SLOVENIJI

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Abstract:

Silver fir (*Abies alba* Mill.) is regarded as a typical climax species susceptible to environmental change. We analyzed a protected silver fir stand growing in an unusual combination of conditions: The stand is in secondary succession and is located at low elevation on limestone substrate. Stand history was revealed by an old military map and stand structure, the radial growth of dominant trees, and tree regeneration were sampled. In addition, five characteristic relevés were taken according to the standard Braun-Blanquet method.

The results confirmed that the stand originated from secondary succession; however, fir vitality and dominance as well as stand structure, including regeneration, suggested long-lasting stadia of almost pure silver fir (77 % of the growing stock). The growth pattern of dominant trees and large age variability of fir indicated that the stand did not originate from a completely open space. It is likely that fir gradually colonized the pioneer forest from neighboring stands. The stand was characterized by a high volume of live trees (773.6 m^3 ha^{-1}) and a low share of dead trees (4.1 %) in the growing stock. The most similar associations in terms of floristic composition are a secondary association Asperulo-Carpinetum betuli M. Wraber 1969 and a hornbeam-fir association (*Abio albae-Carpinetum betuli* Marinček 1994).

This study shows that fir can form almost pure stands during secondary succession of abandoned pastures on some sites and therefore expands the prevailing view that silver fir decline throughout human history has been due to anthropogenic influences. Due to the complex interactions between silver fir, its competitors, environmental factors, and human-induced disturbances, additional research is needed to support the conservative management of silver fir in decline.

KEY WORDS: total forest reserve, secondary succession, *Abies alba*, *Picea abies*, stem exclusion phase, silver fir decline and expansion

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Introduction
Uvod

Natural forests are extremely rare in Europe, especially if the European part of Russia is not taken into account (Parviainen et al. 2000). However, they are particularly important for the development of basic and applied natural sciences (Peterken 1996). The idea of the total forest reserves was initiated by foresters to ensure old-growth forests for the future and thus references for managed forests on different sites (Leibundgut 1957). At present, forest reserves are considered to be even more important due to the rising importance of ecosystem services, environmental monitoring, and nature protection (Parviainen et al. 2000). In the 1970s a network of forest reserves was established in Slovenia (Mlinšek et al. 1980). This network has been successfully maintained, although it was altered slightly due to the re-privatization of forests in the 1990s. Today there are 172 forest reserves in Slovenia covering 9,792 ha, which is less than 1 % of the total forest area in Slovenia (Diaci et al. 2006). A damaged, or artificially made forests for example plantations; areas damaged by fire and wind; and spontaneously developed forests on former agricultural land. One important goal for research in such reserves is to gain an understanding of secondary succession and recovery processes which have not experienced human intervention.

Succession refers to the sequence of changes in vegetation that occurs after a site is disturbed – a sequence of events that normally leads to the re-establishment of the vegetation that was initially removed. If the disturbance is minor, and the soil and propagules remain, as in the case of pasture land surrounded by woods, the recovery of the vegetation towards the forest is usually rapid; this is termed secondary succession (Keddy, 2007).

Forest sites on which silver fir dominates (*Abies Alba* Mill.; thereafter fir) are underrepresented in the Slovenian forest reserve network (Marinšek and Diaci 2011) since most of these ecosystems are very productive and yield high income. However, due to the overall importance of fir in Southeast Europe and the many insufficiently explained processes related to fir such as fir decline, overbrowsing, reciprocal replacement, coexistence with other species, and climate change (Šafar 1951, Matić et al. 2001, Tikvić 2008, Anić et al. 2009, Diaci et al. 2010, 2011), knowledge on developmental dynamics from reserves is a prerequisite for the improvement of fir conservation management.

The "Lipje" forest reserve is considered special for several reasons. Here, an almost pure fir stand grows in an unusual combination of site factors, i.e., very low altitude (370–380 m), carbonate parent material, and a geographic location in the southern part of Slovenia. Moreover, there is some indication that the stand originated from the spontaneous expansion of forest on former pastures, where fir may have played the role of the initial species in secondary succession. However, systematic research in the reserve has not yet been undertaken.

Fir is regarded as a late climax species that is very efficient in its overall resource use and thus extremely shade tolerant (Ellenberg 1988). In Slovenia most fir-dominated stands grow on deep, heavy, fresh neutrophilic or acidophilic soils of the submontane and montane vegetation belt (*Galio rotundifolii-Abietetum* M. Wraber 1959, *Bazzanio-Abietetum* M. Wraber 1958; Dakskobler and Marinšek 2009). However, there are also localized fir ecosystems that overgrow very rocky calcareous or silicate parent material (e.g. *Calamagrostio-Abietetum* Horvat (1950) 1962, *Paraleucobryo-Abietetum* Belec et al. ex Belec 2009, *Neckero-Abietetum* Tregubov 1962). In Croatia a forest association is reported (Vukelić et al. 2006) where fir grows on limestone at an elevation between 700–800 m a.s.l. in extremely thermophilic habitat (*Ostryo-Abietetum* (Fukarek 1963) Trinajstić 1983).

Fir is reported to be susceptible to human disturbances such as forest fires, heavy logging, and forest grazing (Kozakova

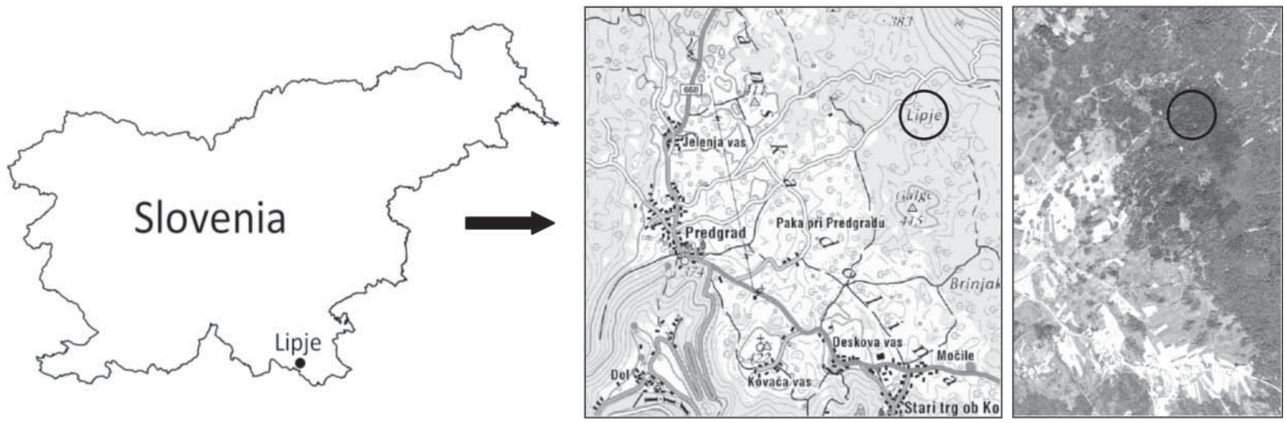

Figure 1 Location of the Lipje forest reserve within Slovenia, on the regional map and aerial photo (year 2006)
Slika 1. Položaj šumskog rezervata Lipje u Sloveniji, na topografskoj karti i na aerofoto snimci (2006. godina)

et al. 2011), thus there is numerous paleoecological evidence that its share has decreased substantially throughout the course of human history (Wick and Möhl 2006, Feurdean and Willis 2008). Fir is also extremely susceptible to polluted air, especially SO_X emissions, which resulted in an especially pronounced decline in the second half of the 20th century (Elling et al. 2009, Diaci et al. 2011). However, there are also local exceptions to the general trend of fir regression. For example, in the period from the mid-19th to the mid-20th century, the share of fir in the Dinaric Mountains increased due to its systematic promotion by silviculture and the extinction of large ungulates (Matić 1973, Klopcic et al. 2010). Another example of localized fir expansion, which is less documented, is its role in secondary succession on abandoned agricultural lands (Mlinšek 1968, Dolezal et al. 2004, Bartolome et al. 2008). In this study a combination of two rare characteristics for fir occurrence is presented, namely a special habitat (low elevation, south open valley, and carbonate parent material) and its relatively rare role as a pioneer in secondary succession.

The main objectives of this study were to (1) analyze the forest reserve history and verify if the stand originated from secondary succession, (2) examine the structure and development of the stand and determine the role of fir, and (3) compare the composition of ground vegetation in the reserve and indicated ecological factors with other fir associations in Slovenia.

Materials and methods
Materijali i metode

Stand and site characteristics – Karakteristike staništa i sastojine

The Lipje forest reserve is situated in Poljanska dolina in the foothills of Poljanska gora (45° 30' 54" N, 15° 04' 52" E). It belongs to the Poljanska dolina forest management unit, Section 103c, and covers 2.43 hectares (Figure 1). The elevation of the reserve ranges from 360 to 380 m a.s.l. The parent material is composed of limestone. Karstic phenomena, such as sinkholes and rocky outcrops, are common. The reserve lies on a flat plateau with a slight slope inclination of 5 %. Stoniness is about 10 %. The soil type is calcocambisol of variable depth. The nearest meteorological station is Kočevje (463 m a.s.l.), and the station for precipitation measurements is located in Predgrad (375 m n.m.v.). The long-term mean yearly temperature in Kočevje (1960–90) was 8.3 °C and mean July temperature was 17.8 °C. Due to the lower elevation of the research site and its openness towards the influence of the sub-Pannonian climate, the estimated mean yearly temperature was about 1 °C higher. Long-term average rainfall for the station in Predgrad was 1438 mm $year^{-1}$.

The entire forest reserve was protected in 1976 in an area of 5.0 ha. After denationalization a part of the reserve was returned to the village community. In the first management plan (Anon., 1961), a pure silver fir stand with an admixture of Norway spruce and broadleaves, especially hornbeam, was reported. It was also mentioned that this forest very likely developed very likely on a former pasture. Growing stock was estimated at 106 m^3/ha, and the ratio of coniferous and deciduous trees was 96 % versus 5 %, respectively. Selection felling was prescribed as a way of management. In subsequent forest management plans (Anon., 2010), the section was referred to as a forest reserve, but only the last management plan provided a reliable assessment of growing stock (819.8 m^3/ha, Bitterlich relascope method). In addition to sheep grazing on pastures in the vicinity of the reserve, there was also local production of lime, for which substantial quantities of firewood was needed. For this study, the forest site has been provisionally identified as a secondary association *Asperulo-Carpinetum betuli* M. Wraber 1969 var. *Abies alba* nom. prov. (Mlinšek et al. 1980) which occurs on potential beech or hornbeam forest sites as pioneer vegetation on former pastures and mostly sunny slopes in the colline and submontane vegetation belt. Due to its small size, the reserve is under the influence of management in adjacent stands. However, neighboring stands have only recently been excluded from the reserve. The entire forest area is also characterized by a low impact selection management regime. During the course of research we did not find signs of logging or other human intervention in the research area.

Recordings and analyses – Prikupljanje i obrada podataka

In 2010 we carried out a full inventory of all trees with dbh > 5cm in the reserve. We also measured the height of 30 fir and 30 spruce trees on a transect through the reserve. Additionally, a permanent 125 x 80 m research plot, oriented in the N-S direction, was set up in the reserve core. Species, dbh, and tree coordinates were assessed. Within the larger research plot, a N-S aligned grid (4 x 4 m) was laid out with a total of 26 permanent regeneration plots on the grid intersections. The size of the plots was 1.5 x 1.5 m. There were no distinct gaps in the forest reserve; therefore, all plots were under a dense, closed canopy. All plots were permanently marked with iron stakes in order to be located with a metal detector at the next inventory. We recorded species composition and percent cover of all vascular plants on the plots. Plant cover was estimated visually from above, to the nearest 10 % from 10 to 100 %, and to the nearest 1 % from 1 to 5 %, excluding mosses. Regeneration density was recorded per species in two height classes: small seedlings ≤ 20 cm (excluding one-year-old seedlings) and seedlings (20 cm < h ≤ 130 cm). All woody plants were scored for browsing

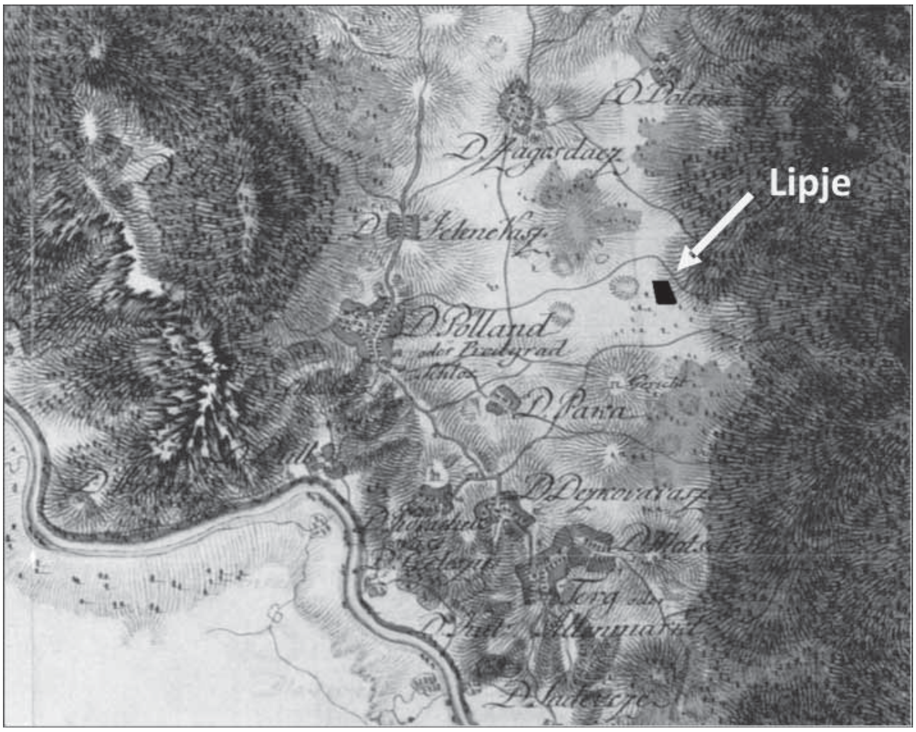

Figure 2 The Lipje forest reserve depicted as a black quadrilateral on an old military map, 1763–1787 (black: forest, dark gray: fields and vineyards, light gray: pastures)
Slika 2. Šumski rezervat Lipje prikazan je kao crni četverokut na staroj vojnoj karti 1763–1787 (crno obojeno: šuma, tamno siva: polja i vinogradi, svijetlo siva: pašnjaci)

damage. They were classified as lightly browsed if less than 10 % of lateral shoots were damaged. If more than 11 % and less than 50 % of lateral shoots were browsed, including terminal shoot, seedlings were classified as moderately browsed, while plants with even more damage were categorized as heavily browsed.

Five characteristic relevés according to the standard Braun -Blanquet method for vegetation sampling were taken (Braun-Blanquet 1964) across the entire area of the reserve. A comparison of vegetation samples from this study with samples from other fir, fir-beech, beech, and hornbeam sites in Slovenia sampled with the same method was done by Detrended correspondence analysis (DCA). Environmental data (altitude, inclination, and stoniness) and Ellenberg indicator values (EIV) for light, temperature, continentality, moisture, and soil reaction (Ellenberg 1988) were added on the ordination plot as a result of regression with ordination axes. Additionally, the nitrogen EIV and Shannon-Wiener diversity index were drawn as isolines onto the ordination plots. Differences in EIV between sites were tested with a one-way ANOVA and the Tukey HSD test.

The current shape of the forest reserve was transcribed onto an old military map, which was created between 1763 and 1787 (Rajšp 1997) and geocoded (Figure 2). In this way we were able to determine how the land in the area of the current reserve was used at the time the map was created. The large permanent research plot was divided into 10 smaller areas 25 x 40 m in size. In each area a dominant tree was identified according to its social status, dbh, height, developmental tendency, and vitality. All dominant trees were cored to the center at 1 m height and their dbh and height were recorded. For comparison we also drilled three dominant trees outside the forest reserve following the same methodology, hence the cumulative sample included 13 trees. The samples were prepared for analysis with established dendroecological procedures (Stokes and Smiley, 1968). The samples were digitized and ring widths were measured to the nearest 0.01 mm with WinDENDRO software. Age differences in dominant fir and spruce trees were analyzed with the Mann-Whitney U Test. Data was analyzed in Microsoft Excel Version 2003 and R Version 2.13.0 (R Development Core Team, 2011).

Results of research
Rezultati istraživanja

Forest history – Povijesne prilike

Analysis of the old military map (Figure 2) showed that the shape of today's reserve was at the border between pastures and forests at the time the map was created (1763–1787). At that time significantly more area was devoted to agricultural land (pastures, fields, vineyards) than today. Also, the age structure of the analyzed dominant trees showed fairly uniform structure. Mean age of dominant firs at 1 m height was 79.4 (±13.7) years and for dominant spruce trees 89.4 (±2.7) years. Minimum ages for fir and spruce were 58 and 86 years, respectively, and maximum ages were 100 and 92 years, respectively. There was a tendency towards greater mean height in spruce, but it was not statistically significant

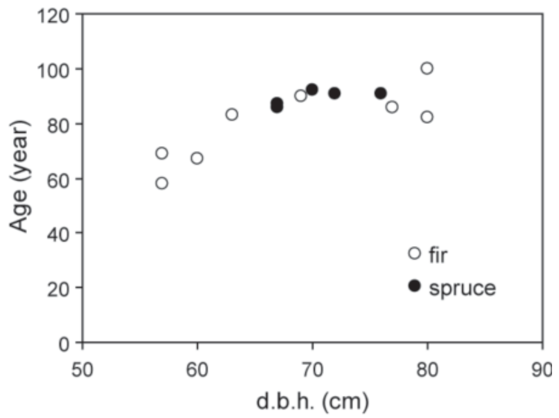

Figure 3 Scatter plot of dominant tree age by dbh, coded by tree species
Slika 3. Raspršeni grafikon starosti dominantnih stabala prema promjeru za smreku i jelu

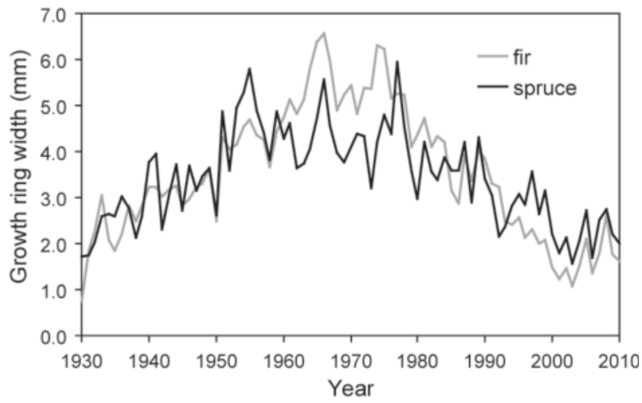

Figure 4 Radial growth of dominant silver fir and spruce trees in the Lipje forest reserve from 1930 to 2010
Slika 4. Debljinski prirast dominantnih stabala jele i smreke u šumskom rezervatu Lipje od 1930–2010.g.

($p = 0.0665$). The results suggested greater age variability for fir (Figure 3). Thus, fir may have invaded the site first and was also able to grow under the canopy of broadleaves and pioneer species. The maximum age spread of fir (42 years) suggests that the stand is not even-aged and that the colonization of pasture was gradual. Considering the growth pattern in the juvenile phase, we should add approximately 10 years to the age at 1 m. This would mean that succession of conifers had begun in about 1900–1910.

The growth pattern of dominant trees showed a negative parabolic pattern, with slow growth in the initial phase, accelerated growth in the intermediate period, and a reduction in the recent period (Figure 4). In the initial phase, growth performance of both species was similar; in the intermediate period, performance of fir was better; and during the last period, the diameter growth performance of spruce was better. Some of the poorest performances of both species were synchronized and probably caused by periods of drought (e.g. 1952/53, 1958, 1992/1993, 2003).

Composition of ground vegetation – Sastav prizemne vegetacije

In the Lipje forest reserve, five phytocenological relevés were made and 71 vascular plant species were inventoried, but bryophyte species were not identified. The composition of syntaxonomic groups shows a predominance of species from the *Aremonio-Fagion* (Ht.1938) Borhidi in Torok, Podani & Borhidi 1989 alliance, *Fagetalia sylvaticae* Pawł. in Pawł. & al. 1928 order and *Carpino-Fagetea* Passarge in Passarge & Hofmann 1968 class, which indicates potential beech or hornbeam habitat (Table 1). The larger proportion of *Vaccinio-Piceetea* Br.-Bl. 1939 emend. Zupančič (1976) 2000 species indicates some degree of acidification, probably resulting from coniferous litterfall or the chemical characteristics of the bedrock.

In the biological spectrum, hemicryptophytes and phanerophytes predominate with a two-thirds majority (Table 2). Among them, stem forms are the most numerous. They are followed by geophytes, mostly with rhizomes. The proportion of chamephytes is rather small since bryophytes and lichen species were not inventoried. Given the high proportion of phanerophytes and hemicryptophytes, it can be established that the forest, despite acidified soils, grows in quite favorable habitat conditions.

Ground vegetation composition was compared to the following related fir, fir-beech, beech, and hornbeam phytocenoses: *Galio rotundifolii-Abietetum* M. Wraber 1959 (G-A), *Galio rotundifolii-Abietetum* M. Wraber 1959 var.

Table 1 Synsystematic units in the Lipje forest reserve
Tablica 1. Sinsistematske jedinice u šumskom rezervatu Lipje

Synsystematic units – Sinsistematske jedinice	(%)
Aremonio-Fagion	9.9
Fagetalia sylvaticae	31.0
Carpino-Fagetea s.lat.	12.7
Vaccinio-Piceetea s.lat.	16.9
Quercetea pubescentis s.lat.	4.2
Rhamno-Prunetea s.lat.	4.2
Epilobietea angustifolii s.lat.	4.2
Mulgedio-Aconitetea s.lat.	2.8
Asplenietea trichomanis s.lat.	2.8
Quercetea roboris s.lat.	1.4
Erico-Pinetea s.lat.	1.4
Artemisietea s.lat.	1.4
Adenostyletalia s.lat.	1.4
Other species	5.6
Total	100

Table 2 Biological spectrum of flora in the Lipje forest reserve
Tablica 2. Biološki spektar flore šumskog rezervatu Lipje

Biological form – Biološka forma	%
PHANEROPHYTES (Phanerophyta)	32.8
stem phanerophytes (P. scap.)	17.9
tufted phanerophytes (P. caesp.)	6.0
nanophanerophytes (NP)	6.0
climbing phanerophytes (P. lian.)	3.0
CHAMAEPHYTES (Chamaephyta)	7.5
creeper chamaephytes (Ch. rept.)	7.5
TEROPHYTES (Terophyta)	0.0
HEMICRYPTOPHYTES (Hemicryptophyta)	35.8
stem hemicryptophytes (H. scap.)	17.9
rosette hemicryptophytes (H. ros.)	11.9
tufted hemicryptophytes (H. caesp.)	6.0
GEOPHYTES (Geophyta)	23.9
geophytes with rhizomes (G. rhiz.)	22.4
geophytes with tuber (G. bulb.)	1.5
TOTAL	100

Epimedium alpinum Marinček 1977 (G-A var. Ea), *Omphalodo-Fagetum* (Tregubov 1957) Marinček & al. 1993 var. geogr. *Calamintha grandiflora* Surina 2002 *neckeretosum crispae* Puncer 1980 (O-F neck.), *Omphalodo-Fagetum* (Tregubov 1957) Marinček & al. 1993 var. geogr. *Calamintha grandiflora* Surina 2002 *asaretosum* Puncer 1980 (O-F asar.), *Hacquetio-Fagetum* Košir 1962 var. geogr. *Ruscus hypoglossum* Košir 1979 (H-F), *Abio albae-Carpinetum betuli Marinček 1994* (Ab-C), *Asperulo-Carpinetum M. Wraber 1969* (As-C). Forest reserve relevés on the DCA (Detrended correspondence analysis, Figure 5) ordination plot were positioned in the middle, among fir, beech, and hornbeam phytocenoses. In relation to the compared fir relevés, they were the most distinguished by species *Euphorbia dulcis, Galeobdolon montanum, Hacquetia epipactis, Omphalodes verna, Cyclamen purpurascens* and *Primula vulgaris*, which are classified to the order of European beech forests on nutrient-rich soils (*Fagetalia sylvaticae*). In comparison with hornbeam and submontane beech forests on carbonate bedrock, the relevés in this study were mostly distinguished by species *Luzula luzuloides, Dryopteris dila-*

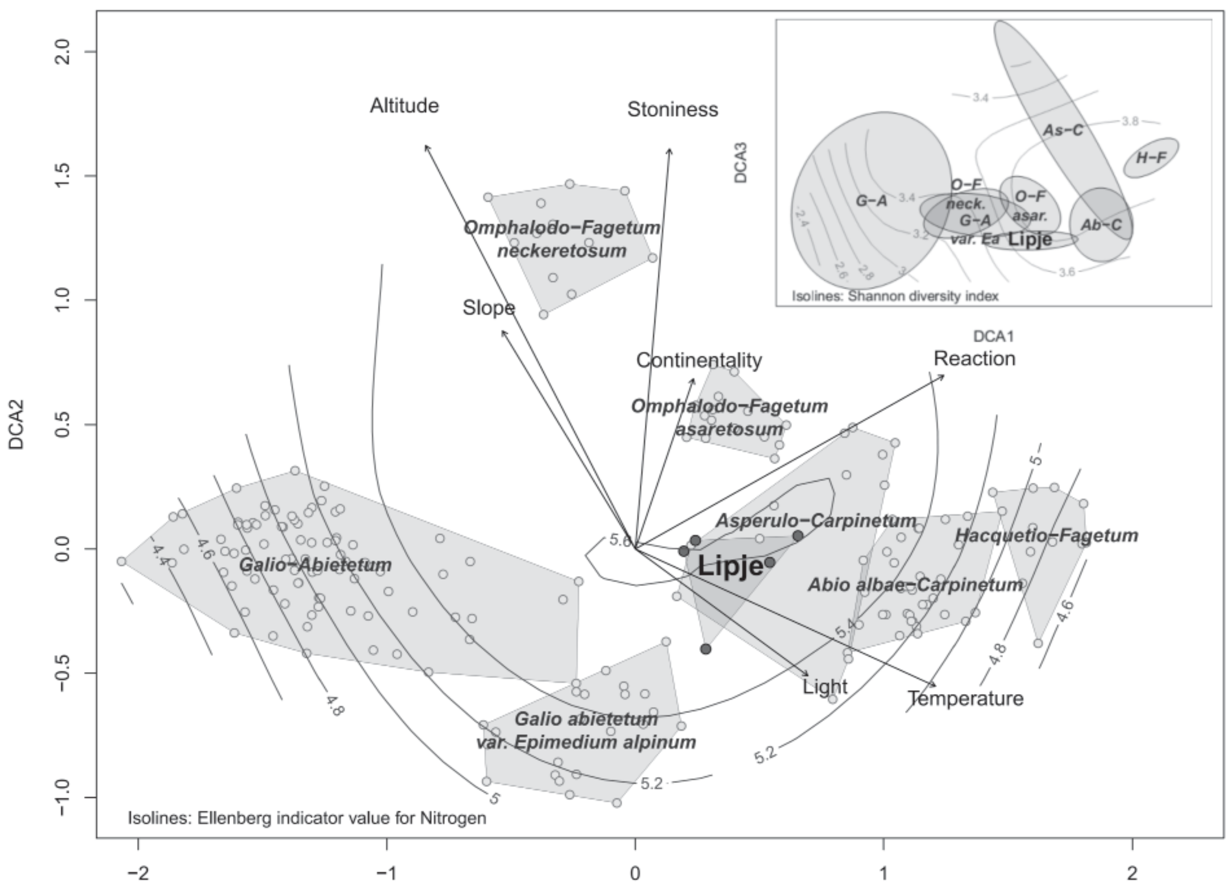

Figure 5 The ordination plot of the 1st and 2nd Detrended correspondence analysis (DCA) axes of vascular plant coverage in herbal layer in the Lipje forest reserve and similar associations. Arrows represent Ellenberg indicator values and some environmental variables. The Ellenberg nitrogen indicator value is represented with isolines. The DCA plot of the 1st and 3rd axes is shown in the smaller picture; isolines represent the Shannon diversity index value.

Slika 5. Ordinacijski dijagram prve i druge DCA osi pokrivenosti vaskularnih biljaka u prizemnom sloju u šumskom rezervatu Lipje i sličnim zajednicama. Strelice predstavljaju Ellenbergove indikacijske vrijednosti i druge ekološke varijable. Ellenbergova indikatorska vrijednost za dušik označena je s izolinijom. DCA dijagram prve i treće osi prikazan je na manjoj slici, izolinije predstavljaju vrijednosti Shannonovog indeksa diverziteta.

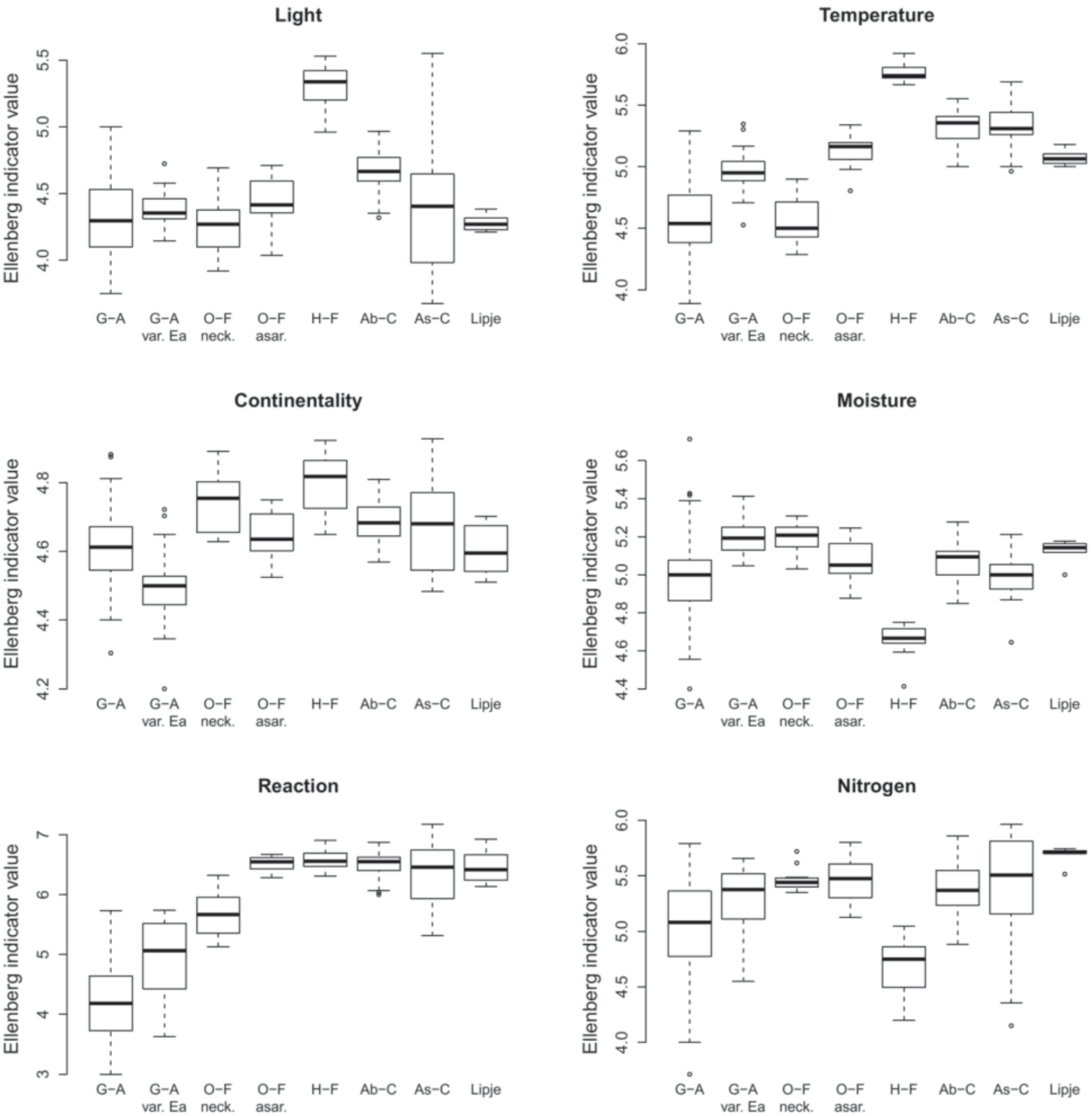

Figure 6 Comparison of distributions of Ellenberg indicator values between the Lipje forest reserve and similar syntaxes
Slika 6. Usporedba distribucije Ellenbergovih indikatorskih vrijednosti između vegetacije šumskog rezervata Lipje i sličnih sintaksona

tata, Blechnum spicant, Abies alba, Oxalis acetosella and *Phegopteris conectilis,* which belong to the class of holarctic coniferous forests (*Vaccinio-Piceetea*) and indicate a higher level of habitat acidity. The Lipje relevés were distinguished from the other fir-beech subassociations mainly by species *Epimedium alpinum, Carpinus betulus, Helleborus dumetorum, Quercus petraea, Hedera helix, Melica uniflora, Euonymus europaea, Galium album*, which can mainly be classified in the alliance of thermophilous Illirian oak-hornbeam woods (*Erythronio-Carpinion*) or class of termophillous oak forests of Submediterranean regions (*Quercetalia pubescentis*). The Lipje forest reserve seems to be most related to hornbeam and fir-beech phytocenoses of lower altitudes and carbonate bedrock in the surrounding region, particularly to the secondary hornbeam phytocenoses, classified as *Asperulo-Carpinetum*, which grow on abandoned agricultural areas or degraded, potential beech habitats.

Shannon-Wiener index values indicated a greater degree of diversity in the Lipje relevés compared to fir phytocenoses and a slightly lower degree compared to hornbeam and submontane beech forests (Figure 5 upper right corner).

Table 3 Tree density (N) and volume of live and dead trees per hectare and species from the full inventory of the Lipje forest reserve
Tablica 3. Gustina (N) i zapremina živih i mrtvih stabla prema vrstama drveća u šumskom rezervatu Lipje

Tree species Vrsta drveća	Live trees – živa stabala				Dead trees – mrtva stabala			
	N ha^{-1}	%	Volume (m^3 ha^{-1})	(%)	N ha^{-1}	(%)	Volume (m^3 ha^{-1})	(%)
Fir – jela	390,9	79,5	591,6	76,5	203,7	77,7	23,0	69,7
Spruce – smreka	52,7	10,7	172,4	22,3	7,0	2,7	3,2	9,8
Beech – bukva	2,1	0,4	1,3	0,2	/	/	/	/
Wild pear – divlja kruška	6,2	1,3	1,7	0,2	5,3	2,0	0,8	2,4
Hornbeam – grab	38,3	7,8	6,1	0,8	46,1	17,6	6,0	18,1
Lime – lipa	0,8	0,2	0,4	0,1	/	/	/	/
Ash – jasen	0,8	0,2	0,0	0,0	/	/	/	/
Total – ukupno	491,8	100,0	773,6	100,0	262,1	100,0	33,0	100,0

In terms of site conditions evaluated with Ellenberg indicator values (EIV), we found the greatest difference between the Lipje sites and submontane beech forests, but also between Lipje and fir forests. Light conditions in Lipje were significantly less favorable (Tukey HSD, $p < 0.05$) compared to *Hacquetio-Fagetum* as well as *Abio albae-Carpinetum betuli*. Temperature conditions were significantly worse in *Galio rotundifolii-Abietetum* and *Omphalodo-Fagetum neckeretosum*, but more favorable in *Hacquetio-Fagetum*, compared to Lipje sites. Vegetation on *Galio rotundifolii-Abietetum* sites reflected a significantly higher level of acidity (also in var. *Epimedium alpinum* and *Omphalodo-Fagetum neckeretosum*) and lower soil nitrogen levels in relation to Lipje sites. On the other side of the ordination space, vegetation on *Hacquetio-Fagetum* sites reflected significantly less favorable moisture conditions and soil nitrogen levels compared to Lipje sites.

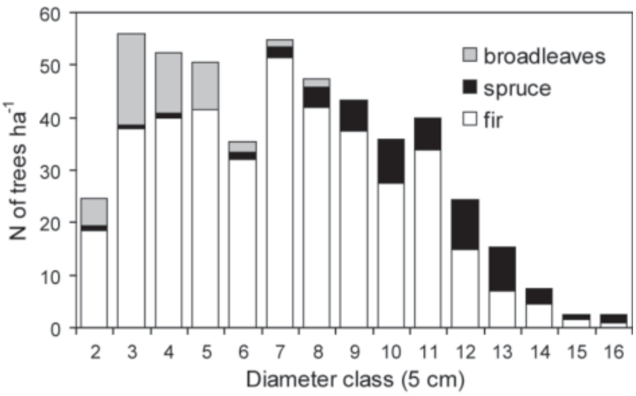

Figure 7 Diameter distribution of living trees by tree species
Slika 7. Distribucija promjera živih stabala po vrstama drveća

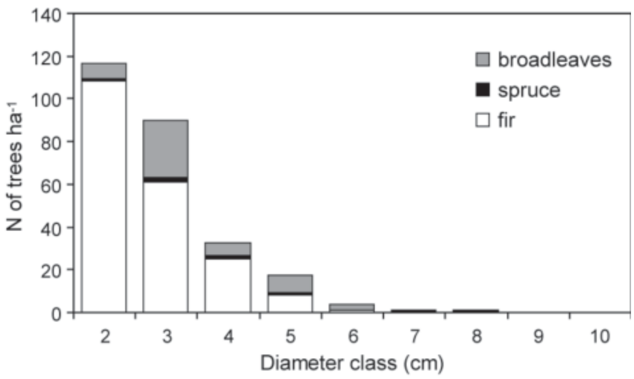

Figure 8 Diameter distribution of dead trees by tree species
Slika 8. Distribucija promjera mrtvih stabala po vrstama drveća

Stand structure – Struktura sastojine

The Lipje forest reserve was characterized by a high growing stock and basal area of live trees, with 773.6 m^3 ha^{-1} and 52.9 m^2 ha^{-1}, respectively. The dominant tree species in the forest reserve in number and density was fir, followed by spruce (Table 3). Other species such as beech, wild pear, hornbeam, lime, and ash were represented with less than 10 % in tree density and less than 2 % in stand growing stock. Dominant trees were exclusively conifers. Broadleaves were in the intermediate layer. Hornbeam was found in small clusters in the rockiest part of the reserve, while other broadleaves appeared individually throughout the reserve.

The cumulative frequency distribution of live trees showed three distinct modes, since it presented a sum of three different distributions of dominant species (Figure 7). The mode was in the 3^{rd} diameter class for broadleaves, in the 7^{th} diameter class for fir, and in 12^{th} diameter class for spruce. The largest fir and spruce had a dbh of 80 cm and 76 cm, respectively. All three dbh distributions were closer to a bell-shaped distribution than to thea reverse-J.

Dead trees were represented with 262 individuals per ha^{-1}, or 35 % of the total tree density in the reserve (Table 1). The

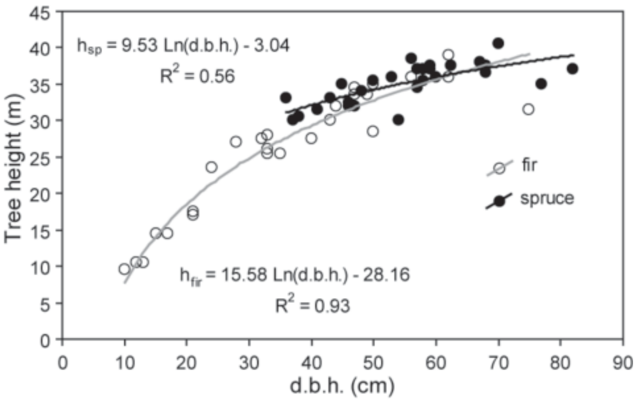

Figure 9 Height curves of fir and spruce in the Lipje forest reserve
Slika 9. Visinske krivulje jele i smreke u šumskom rezervatu Lipje

volume of dead trees was 33 m^3 ha^{-1}, or 4.1 % of the total growing stock. Wild pear and hornbeam had a higher percentage in density of dead trees than live trees, while conifers had lower percentages, spruce in particular. Almost 80 % of dead trees were in the 2nd and 3rd diameter classes (Figure 8). The frequency distribution of dead fir trees was similar to a reverse-J shaped distribution, with the mode in the 2nd diameter class. Large dead trees were almost completely absent, which is another sign of overall stand vitality and that the trees had not yet reached the terminal phase. However, some individual trees showed signs of ageing such as transparent crowns, heavy moss and lichen cover on the trunk, fruiting bodies of fungi, and a secondary crown. Almost all broadleaves were snags, followed by fir (80 %) and spruce (47 %).

The upper canopy layer was very dense and allowed only a small amount of light to reach the forest floor; therefore, the shrub layer, woody regeneration, and ground vegetation were poorly developed. Top heights of fir and spruce were 35.8 m and 37.4 m, respectively. Height curves of fir and spruce were comparable with indication of slightly taller spruce in the range of mean diameters (35–60 cm; Figure 9).

The stand structural parameters on the permanent research plot were similar to those recorded on the whole reserve area, with the exception of higher growing stock (881.7 m^3ha^{-1}) and basal area (60.3 m^2 ha^{-1}).

Regeneration plots were on average 28.0 % covered with stones and rocks, 7.6 % with woody debris, 50.6 % with ground vegetation, 1.3 % with spruce and fir regeneration, while the rest was litter, soil, or roots of adult trees. We recorded 10,944 fir and 171 spruce one-year-old seedlings ha^{-1}, respectively, and 10,260 fir and 2,394 spruce small seedlings ha^{-1}, respectively. Within small seedling density, fir prevailed with 80 %, which is a slightly higher percentage compared to its share in density of trees or growing stock. Due to small seedling size, no browsing damage was recorded.

Disscusion
Rasprava

This study presents indirect evidence suggesting that fir stands represent a successional stage in the course of spontaneous forest expansion on former pastures as suggested in the first management plan for the region (Anon. 1961). This was supported by the following: the reserve position on an old military map, the presence of early successional broadleaves in the medium layer and their reduced vitality (hornbeam, wild pear), the comparable age of the oldest dominant trees, and the pattern of radial increment and overlapping bell shaped diameter distributions of individual tree species. Mlinšek (1968) reported that in the submontane belt in nearby Kočevje, many climax trees species were involved in secondary succession on abandoned agricultural lands, especially spruce, fir, maple, lime, and hornbeam. The sequence of immigration differed greatly; it depended on sites and also on chance. The exception was fir, which abundantly regenerated under dense crowns of hazel and pioneer species.

The growth pattern of dominant trees with slow growth in the initial phase, low vitality of broadleaves in the medium layer, and great age variability in fir indicate that the stand did not originate from a completely open space. It is likely that pioneer species such as hazel were the first colonizers, followed by maple, lime, hornbeam, fir and spruce. Shade tolerant fir can colonize sites under pioneer species and overgrow them when they gradually start losing vitality (Motta and Garbarino 2003). At the time of the study, pioneer species were already decomposed, while other, more long-lived broadleaves were still present. The greater light demand of Norway spruce compared to fir was indicated by the absence of rejuvenation and linkage to the larger diameter classes, i.e. dominant canopy trees.

However, we cannot exclude the possibility that stands were at the forest border or even within forest limits, but still under the heavy influence of grazing and other human activities (collection of firewood for lime production). In particular, the age spread of dominant firs may indicate a continuity of forests or long lasting succession stadia. Yet, progression of vegetation was confirmed, namely broadleaved species were in regression, and spruce was also confined to the upper canopy layer only. There is substantial evidence of landscape changes due to socio-economic changes. Several waves of emigration were reported from Poljanska dolina, especially during the "Long" and "Great" depression which triggered spontaneous expansion of forests (Anon. 1961, Prelesnik 2011).

The stand was characterized by a high growing stock and basal area of live trees and a large number of dead trees which were restricted mainly to the 2nd, 3rd and 4th diameter classes, while large diameter dead trees were almost completely absent. All this indicates high competition among trees and is typical for the stem exclusion (aggradation) phase of the natural forest cycle (see Oliver and Larson 1990; Emborg 1998). In the stand, light in particular had become limiting and thus prevented further establishment of new plants. Top heights indicated an above average site index. The low volume of dead trees in comparison to old-growth forests was in line with similar findings in forest reserves in Europe and indicated past management and succession history (Christensen et al. 2005). Seedling coverage was low due to the dark understory; still, fir seedling densities where high compared to similar studies (Marinšek and Diaci 2011, Diaci and Firm 2011) and indicated great potential for fir regeneration. There was no indication of future colonization of the stand by broadleaves.

Analysis of ground vegetation reflects rather favorable site conditions in the Lipje forest reserve. This confirms the major proportion of species of the *Carpino-Fagetea* s. lat. classis. Compared to other communities of beech and hornbeam forests, there is somewhat more moderate acidophilic plant species of the *Vaccinio-Piceetea* classis. This is connected with partial site acidification as a result of litterfall from fir, which completely dominates the tree layer. Higher proportions of phanerophytes and geophytes also indicate potential beech or hornbeam forest habitat. Site conditions indicated by Ellenberg phytoindication values classify the fir forest in the Lipje reserve closer to hornbeam societies, which again shows that it is probably a secondary fir forest resulting from overgrowth. Further successional development of the above is likely to proceed in the direction of deciduous forest.

Our assumptions were confirmed by the DCA analysis, where the fir forest of the Lipje reserve is classified in the middle of the ordination space among the related phytocoenoses. Based on fir's predominance in the tree layer, which partially modifies acidity and light conditions in the stand, the results give the impression of potential hornbeam or beech habitat. The most similar associations in terms of floristic composition seem to be a secondary association *Asperulo-Carpinetum betuli* M. Wraber 1969 and hornbeam-fir association (*Abio albae-Carpinetum betuli* Marinček 1994). The first occurs as a degraded stadium following major logging or as the pioneer stadium of the overgrowing of agricultural land in more thermophilic beech forest habitats (*Hedero-Fagetum* (1962) Košir 1994, *Ostryo-Fagetum* M. Wraber ex Trinajstić 1972, *Hacquetio-Fagetum* Košir 1962, *Ornithogalo pyrenaici-Fagetum* Marinček, Papež, Dakskobler & Zupančič 1990). Also, Dakskobler and Marinšek (2009) report good fir vitality on such sites, where the origin of fir is not known. The second mentioned association, like the Lipje fir forest, is also found in the lowland and hilly belt (160 to 300 m asl.) of the Slovenian Predinaric region, on calcareous rocks or clastic sediments, but within it, fir is represented only sporadically and perhaps only subspontaneously (Marinček 2001).

Conclusions
Zaključci

This study analyzed a fir stand growing in an unlikely combination of conditions: it is in secondary succession on a special site (low elevation, limestone parent material). The high vitality of fir and its dominance, with no indication of future colonization by any other tree species, suggests a long-term fir stadium in a secondary succession or even a forest with an enduring fir potential. However, due to the complex interactions between fir and its competitors (e.g. reciprocal replacement) as well as climate change, it is extremely difficult to speak of potential vegetation. At the time of stand establishment, the average growing stock in Slovenian forests was tree times lower than that of today. Additionally, many activities resulting in forest degradation were taking place and have since largely been abandoned. From this point of view, the increase of late successional fir can be understood. On the other hand, there are many reports that fir is being replaced by beech in natural forests (Šafar 1952; Marinšek and Diaci 2011). This study, in showing that fir can locally colonize some new sites during secondary succession, expands the prevailing view that fir decline throughout human history has been due to anthropozoogenic influences. There may be more similar examples since the origin of many pure fir forests has not yet been explained. The overall regression of silver fir calls for additional research that would help unravel the complex interactions between fir and its competitors, environmental factors, and human-induced disturbances. Nevertheless, we can conclude that the presence and vitality of this fir stand at the very edge of its typical distribution raises optimism for fir's future despite the threat of climate change.

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Sažetak:

obična Jela (*Abies alba* Mill.) je kao klimatogena vrsta izrazito skiofilna i jako učinkovita što se tiče primanja hrane iz okoliša. U Sloveniji obično raste na dubokim, teškim, svježim, neutrofilnim do acidofilnim staništima, u submontanskom i montanskom pojasu (*Galio rotundifolii-Abietetum* M. Wraber 1959, *Bazzanio-Abietetum* M. Wraber 1958), mjestimično se pojavljuje u sastojinama i na kamnitim karbonatima ili silikatnima podlogama (*Calamagrostio-Abietetum* Horvat (1950) 1962, *Paraleucobryo-Abietetum* Belec et al. ex Belec 2009, *Neckero-Abietetum* Tregubov 1962). U članku smo predstavili istraživanje gotovo čiste sastojine obične jele (*Abies alba* Mill.) na za nju neuobičajnom staništu. Jelova sastojina u šumskom rezervatu Lipje u Poljanskoj dolini (Slovenija) uspijeva na prisojnom položaju, razmjerno niskoj nadmorskoj visini (370–380 m) i na karbonatnoj matičnoj podlozi. Sustavnih istraživanja u rezervatu do sada još nije bilo, ali se pretpostavlja da je sastojina nastala poslije sekundarne sukcesije na nekadašnjim pašnjacima. Svrha ovoga istraživanja je (1) analizirati povijest šumskog rezervata i jelove sastojine, (2) istražiti strukturne i razvojne karakteristike jelove sastojine, (3) usporediti florni sastav rezervata sa srodnim asociacijama fitocenoza. Povijest sukcesije sastojine utvrdili smo uz pomoć stare vojničke karte. U sastojini smo na većoj pokusnoj plohi napravili totalnu klupažu, na dominantnim stablima izmjerili visine i uzeli izvrtke. Na manjim plohama analizirali smo pomlađivanje i brst divljači. Dodatno je napravljeno pet fitocenoloških snimaka po standardnoj srednjeeuropskoj metodi.

Na vojničkoj karti iz godine 1763–1787. godine, područje današnjeg rezervata leži na prijelazu iz šume u pašnjake, koji su u tom razdoblju većih površina, što potvrđuje sumnje na sekundarnu sukcesiju. Dobna struktura sastojine ukazuje na početak sukcesije jele u godinama 1900–1910.godine. Prirastni uzorci dominantnog drveća jele i njihova umjerena starosna varijabilnost ukazuju da jela nije odjednom kolonizirala nešumsku površinu, nego se postepeno širila sjemenom u postojećoj pionirskoj sastojini. Vitalnost jele i njena dominacija u sastojini, kao i struktura i pomlađivanje, ukazuju da se vjerojatno radi o dugotrajnom stadiju pretežito čiste jelove sastojine (udio jele u drvnoj zalihi iznosi 76.5 %). Karakteristika sastojine je i visoka drvna zaliha (773.6 m^3 ha^{-1}) i malen udio mrtvog drveta (4.1 %). Analiza prizemne vegetacije ukazuje na povoljne stanišne prilike u šumskom rezervatu Lipje. To i potvrđuje veći udio vrsta razreda *Carpino-Fagetea* s. lat. U usporedbi s ostalim zajednicama šuma bukve i bijelog graba ima više umjereno acidofilnih vrsta razreda *Vaccinio-Piceetea*, što je povezano s djelomičnim zakiseljenjem staništa zbog jelovih iglica koja dominira u gornjem sloju. Veći udio fanerofita i geofita ukazuje na potencijalno stanište bukve ili bijelog graba. Indikacija stanišnih prilika s Ellenbergovima fitoindikacijskima vrijednostima svrstava šumu jele u rezervatu bliže staništima bijelog graba, što ukazuje da se tu vjerojatno radi o sekundarnoj šumi jele kao posljedici zarastanja te da će budući sukcesijski razvoj vjerojatno ići u smjeru bjelogorične šume. DCA analiza popisa iz Lipja i srodnih fitocenoza ukazuje na prijelazni karakter, između šuma jele (*Galio rotundifolii-Abietetum* M. Wraber 1959), šuma bukve i jele (*Omphalodo-Fagetum* (Tregubov 1957) Marinček & al. 1993), šuma bijelog graba (*Abio albae-Carpinetum betuli Marinček 1994, Asperulo-Carpinetum M. Wraber 1969*) i submontanskih šuma bukve (*Hacquetio-Fagetum* Košir 1962). S obzirom na prevladavajući udio jele u dominantnom sloju, koja inače djelomično mijenja kiselost i svjetlosne prilike u sastojini, rezultati ukazuju na potencijalno stanište bijelog graba ili bukve. U florističkom smislu stanište najviše sliči sekundarnoj asociaciji *Asperulo-Carpinetum betuli* i zajednici bijelog graba i jele (*Abio albae-Carpinetum betuli*).

Istraživanje je pokazalo da jela može kolonizirati nova staništa u procesu sekundarne sukcesije, nasuprot stajalištu koje zagovara izostanak jele zbog antropozoogenih utjecaja. Poznato je više sličnih staništa, gdje izvor dominacije jele nije poznat. Za objašnjenje uzroka općenitog propadanja jele potrebno je izvršiti istraživanja koja će osvijetliti zapletene međusobne odnose između jele i kompetitorskih vrsta, okolišnih prilika i antropogenog utjecaja. Možemo zaključiti da proučavana sastojina jele koja uspijeva na samom rubu ekološke niše jelovih šuma, ulijeva optimizam za budućnost jele.

KLJUČNE RIJEČI: šimski rezervat, sekundarna sukcesija, *Abies alba*, *Picea abies*, faza isključivanja stabala, propadanje i širenje obične jele