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Comparison of spontaneous regeneration in unmanaged oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) forests: implications for close-to-nature silviculture

Vergleich spontaner Regeneration in unbewirtschafteten Eichen- and Buchbeständen: Implikationen für die naturnähe Forstwirtschaft

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Key words: spontaneous forest dynamics, floodplain oak forests, submontaneous beech forests, gaps, Pannonian ecoregion, Ellenberg indicator values

Summary

Spontaneous dynamics of unmanaged floodplain oak and submontaneous Illyrian beech forests were compared in the Pannonian ecoregion (southern Hungary), with special respect to changes of abundance of species in the ground layer. Due to gap forming, light availability, estimated by Ellenberg indicator values, improved significantly in oak stands, in a smaller extent in beech stands. Oak regenerated very poorly in the unmanaged stands, but the diversity of tree seedlings increased. On the other hand, in beech forests the diversity of tree regeneration decreased notably, due to dominance of beech seedlings. No light-demanding specialist species appeared. Changes in share of shade-tolerant specialists were controversial. Serious conservational

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concerns regarding the spread of weeds and invasive species were not confirmed, as their share did not exceed 1.5% in the floodplain oak stands either. Our results draw attention to that experiences on close-to-nature silviculture gained in beech forests should be applied precautiously in other forest with quite different natural dynamics.

Zusammenfassung

Die Dynamik unbewirtschafteter Eichen-Auenwälder und submontaner illyrischer Buchenwälder in der pannonischen Ökoregion (Südungarn) wurde verglichen, unter besonderer Berücksichtigung von Abundanzveränderungen der Pflanzenarten der Waldbodenvegetation. Durch Lückenbildung erhöhte sich das verfügbare Licht, geschätzt durch die Lichtzahl nach Ellenberg in Stieleichenbestände signifikant, zu einem geringeren Ausmaß in Buchenbeständen. Die Naturverjüngung von Stieleichen war in unbehandelten Beständen sehr gering, aber die Diversität der Baumarten der Naturverjüngung erhöhte sich. Hingegen wurde in den Buchenbeständen Diversität der Baumarten der Naturverjüngung verringert war zurückgedrängt wegen der Dominanz der Buchenverjüngung. Keine lichtabhängigen Spezialisten erschienen. Pessimistische Vorhersagen über die Überwucherung von Unkräutern und Invasiven Arten wurden nicht bestätigt: ihre Anteil blieb auch in den Stieleichen-Auwäldern unter 1.5 %. Unsere Ergebnisse lenken die Aufmerksamkeit darauf, dass Erfahrungen aus der naturnahen Waldwirtschaft in Buchenbeständen nur mit größter Vorsicht auf Beständen ganz anderer natürlicher Dynamik übertragen warden dürfen.

1. Introduction

Dynamics of old-growth (semi)-natural forests is one of the knowledge gaps highlighted by Hüttl et al., 2000. Unmanaged forests are popular objects of research in themselves (Brang, 2005). They are regarded as best possible substitutes for virgin or natural forests, of outstanding conservational value (Wesolowski, 2005). Strict forest reserves are often biodiversity hotspots, important nature protection sites, considered consequently as conservation baselines (Schmidt 2005) and as sources of reference data for close-to-nature silviculture (Parviainen et al., 2000; Madsen and Hahn, 2008). Close-to-nature silviculture is often regarded as synonymous with the concept of continuous cover forestry (CCF, Pommering and Murphy, 2004), which is based on the assumption that the process of natural forest regeneration occurs in small-sized natural gaps, according to Watt's (1947) gap dynamics theory. This simplification disregards the fact that different forests may have different regeneration types (Bengtsson et al., 2000).

Vast amount of studies on gap dynamics had proven that gap regeneration occurs naturally in beech forests, both in natural and artificial gaps created by selective felling methods (see reviews e.g. Standovár and Kenderes, 2003; Wagner et al., 2010), consequently CCF is successful and more and more accepted way of their commercial management (Parvianinen, 2005). Main conclusions of gap studies are that gaps provide better light climate, detectable around the gaps too (Mihók et al., 2005, 2007; Aikens et al., 2007). However, in case of small gaps it amounts only to 6-8% relative light intensity, and small gaps close in some years (Madsen and Hahn, 2008). Better light availability enabled regeneration of tree species (Dzwonko, 2001; Mihók et al., 2005, 2007). Seedlings and small saplings appearing in the understorey represent the first step of the regeneration, providing a regeneration bank for the next forest generation, the "trees of future" (Oldeman, 1990). Their establishment and survival in the first some years may be considered as the first filters determining future composition and structure of forest. The turning point of competition, e.g. between *Acer campestre* and *Carpinus betulus* occurs in the advanced sapling state (Janik et al., 2011). Spontaneous regeneration may lead to diversification of tree species composition (Madsen and Hahn, 2008), but also may lead to homogenization due to the high competitiveness of *Fagus sylvatica* (Schmidt, 2005; Wagner et al., 2010). Light had been found to be important determinant of herb-layer diversity (e.g. Skov and Svenning, 2003; Borschenius et al., 2004; Härdtle et al., 2003; Standovár et al., 2006; Barbier et al., 2008; Wagner et al., 2010, 2011; Plue et al., 2013). Most typical forest herbs were well adapted to gaps and partly depended on them (Brunet et al., 1996; Böhling, 2007). Dark-tolerant specialist species may decrease in quantity or even disappear, reducing diversity. At the same time, light-demanding species may immigrate (Schmidt, 2005; Aikens et al., 2007).

Gap management is supposed to make forests more natural than those managed by common clear-cutting method (Gamborg and Larsen, 2003), as it imitates natural dynamics (at least in some types of forests, as noted by Bengtsson et al., 2000). Naturalness is often characterised by diversity (Onainda et al., 2004; Schmidt 2005; Standovár et al., 2006; Kern et al., 2013), although Schütz (1999) questions that close-to-nature silviculture leads to any increase of diversity. Diversity differences between managed and unmanaged forests had been intensively studied (see e.g. the review of Paillet et al., 2009). The diversity of the herb layer constitutes the largest fraction of the total plant diversity in temperate deciduous forests (Decocq, 2000; Gilliam, 2007), being about one magnitude higher than that of trees and shrubs. Furthermore, herb species are more sensitive indicators of environmental conditions and changes, due to their smaller size and shorter life cycles (Decocq, 2000); although Dzwonko (2001) noted that species with less colonization abilities may corroborate this relationship. Herbs are controlled strongly by canopy (Graae, 1997; Härdtle et al., 2003; two current reviews: Barbier et al., 2008; Wagner et al., 2011), so they provide valuable information on the whole forests, e.g. on its naturalness (Schmidt, 2005; Standovár et al., 2006; Naaf and Wulf, 2010) or on effects of different management practices (Skov and Svenning, 2003). An increase in share of light-demanding species may be predicted after opening of gaps (Schmidt, 2005), although very small single-tree gaps favour shade-tolerant species instead of light-demanding ones (Brang et al., 2014).

Possible conservational effects of gap opening, and also of forest abandonment may be manifold and often debated (Christensen and Emborg, 1996). Many case studies demonstrate the deleterious effects of certain forest management activities to rare or protected species, or report that protection from disturbances help to preserve their populations (e.g. Wesolowski, 2005); on the other hand, abandonment may lead to decrease of diversity (Brang, 2005; Schmidt, 2005; Miklin and Cisek, 2014), and insufficient regeneration (see e.g. examples of *Quercus robur*). Increase of light-demanding specialist and competitor species is preferable from conservational point of view, but the disturbance connected to gap opening may also provide opportunity to disturbance tolerant species, weeds and invasives among them (Brunet et al., 1996; Schmidt, 2005; Mölder and Schneider, 2011), suppressing shade-tolerant specialist species.

Gap regeneration studies usually had been executed in beech forests, which are the most widespread forests of Europe (Standovár and Kenderes, 2003), so their results are valid for large regions. Nevertheless, extrapolation of results should be made with caution, as different forest types may have different natural dynamics (Bengtsson et al., 2000).

Studies on spontaneous regeneration were carried out rather scarcely in *Quercus robur* forests. Some studies had been reported from *Fagus sylvatica – Quercus robur* stands. Barbier et al. (2008) listed *Quercus robur* stands always mixed with or dominated by *Fagus sylvatica* in their review of understory vegetation diversity for temperate and boreal forests. Competitive advantage of beech seedlings over oaks had been regarded as a serious problem of regeneration in mixed oak-beech stands (von Lüpke, 1998). Lack of spontaneous regeneration of *Quercus robur* had been proven in an ancient beech-oak forest in Denmark (Borschenius et al., 2004), contrasting to *Fagus sylvatica*. Nevertheless, results on dynamics of *Quercus*-stands may be misleading when originating from studies carried out in stands where *Quercus robur* dominance may be a consequence of human preference and selection for oaks, being more valuable for timber and wood pastures. Extensification or cessation of management in hornbeam-oak stands led towards more closed, poorly-lighted beech one, due to expansion of *Fagus sylvatica*, instead of improved light ability due to gap opening (Böhling, 2007; Plue et al., 2013).

In contrast to the above-mentioned studies, there are little information on edaphic mixed *Quercus robur* stands of higher, rarely flooded terraces of floodplains, although they may be of quite different natural dynamics (Schütz, 1999, Bengtsson et al., 2000). Unfortunately, floodplains of large rivers are mostly deprived of their original vegetation, as they are most adequate places for human civilization since millennia (Cater and Batic, 2006; Janik et al., 2008). Floodplain oak forests are under commercial management almost everywhere, being very productive and economically valuable; they are represented poorly in strict forest reserves network (Bücking, 2003). "Original-natural" (Peterken, 1996) floodplain oak forests do not exist any more, so their natural dynamics can be studied only in unmanaged stands with quite different history.

Studies on natural oak regeneration carried out almost exclusively from reforestation of formerly open areas: unmanaged wooded meadows, pastures and grazed forests with *Quercus robur*. These sites are characterized by similar environmental factors, but have been conditioned by basically different history than closed oak forests. The main process is not opening, but closure of the canopy, leading often to more mesophilous stands and to decrease of biodiversity (Schmidt, 2010; von Oheimb and Brunet, 2007). Miklin and Cizek (2014) presented a detailed case study of Pannonian alluvial woodlands and meadows from the March-Thaya region (Czeh-Slovak-Austrian border). An impressive amount of empirical evidence on the spontaneous regeneration of oaks in open or semi-open natural or anthropogenic landscapes, but not under closed stands have been published by F. Vera (2000), supporting the cyclic succession theory elaborated by him.

Spontaneous regeneration of *Quercus robur* in closed floodplain oak stands needs further investigation. Its very poor regeneration under closed canopy, and even is small gaps was mentioned as early as Watt (1919) and had been documented since then by many authors (e.g. Lorimer et al., 1994; Harmer et al., 2005; Rodriguez-Campos et al., 2009; Terwei et al., 2013). Janik et al. (2008) documented a continuous decrease of *Quercus robur* in thirty years in an unmanaged floodplain forest. Their results were confirmed by a model-based assessment of Simon and Machar (2014), who found that non-intervention management in floodplain oak forests resulted the total disapperence of oaks. *Quercus robur* regenerated very scarcely under closed canopy in northern Italy in floodplain stands mixed with *Carpinus betulus* and *Ulmus minor*, invaded by *Prunus serotina* and *Robinia pseudacacia* and unmanaged ten years ago. It needed larger-scale disturbances and preferred dryer sites (Terwei et al., 2013). Survival and growth of oak species (*Q. robur* and *Q. petraea*) were positively related to canopy openness in Sweden (Götmark, 2007). Few studies had proven the ability of *Q. robur* to establish and survive for 1-2 years in stands of very poor light availability (Welander and Ottoson, 1998). In Slovenia, *Q. robur* was able to regenerate successfully in gaps of 0.15 ha; the regeneration cycle might be possible even is smaller gaps if commercial quality of trees is of no concern (Diaci et al., 2008). In floodplain forests of Elbe river, oak seedlings had been found to be able to tolerate low light levels if sufficient soil moisture were available (Küssner, 2003). In line with these results, Sanchez-Gomez et al. (2006) experimentally proved that *Quercus robur* were more drought-sensitive under low irradiance. Water deficit had been one of the factors of decline of *Quercus robur* seedlings, as proven by field measurements in Slovenia (Cater and Batic, 2006). Commercial oak regeneration under permanent canopy cover is very problematic (von Lüpke 1998). Some authors considered shelterwood system and/or group felling as possible ways of natural regeneration for oak (Orsanic and

Drvodelic, 2007; Houskova et al., 2007; Dobrowolska, 2008). Clearcut sizes of 1-2 ha were suggested for safe regeneration by Hobza et al. (2007). No scientifically proven case had been found of *Quercus robur* regenerating spontaneously in stands opened by natural-like gaps in proportions high enough for economic forestry, although some studies had proven regeneration in smaller quantities (Welander and Ottoson, 1998; Diaci et al., 2008).

Comparative studies between beech and oak forests are not abundant. Trends in ten-years changes of oak and beech forests were similar to each other in southern Sweden: the main floristic gradient was related to acidity; management intensity promoted the establishment of ruderal species; species richness of typical forest flora was unaffected by (moderate) management; the majority of the typical forest plants were well adapted to gaps (Brunet et al., 1996). In a comparative study Härdtle et al. (2003) found different determinants of species richness in beech and oak forests: canopy structure and light conditions in acidophilous beech forests, and soil moisture in moist hardwood forests. No severe biotic impoverishment, just a general trend towards homogenization had been detected after 20 years in nortwestern Germany, in lowland Alno-Ulmion and Querco roboris-Carpinion stands, similar to our plots (Naaf and Wulf, 2010). Interestingly, they did not found remarkable differences had been found between the changes of generalist and specialist species (Naaf and Wulf, 2010).

Beyond the general purpose of providing new data on spontaneous dynamics of unmanaged mixed floodplain *Quercus robur* forests, our study aims to test four specific hypotheses in them and also in submontane beech stands. Comparing results obtained in the two forest types we look for differences which may help to understand the economically important question: why floodplain oak forests are unable to spontaneous regeneration in spite of natural gap formation; and so to direct practice-oriented studies on their close-to-nature silvicultural management.

Our hypotheses are:

H1 Light conditions in forest stands improve by opening of spontaneous gaps.

H2 Abundance (a) and diversity (b) of regeneration of tree species increases due to excess of light

H3 Abundance of light-demanding species, preferential from conservational point of view, increases due to improved light conditions (a). On the contrary, abundance of shade-tolerant specialist and competitor species decreases (b).

H4 Share of light-frequent natural disturbance tolerant (a), weed (b) and invasive species (c) increases

2. Study areas and methods

Study sites

Our research was carried out in the Pannonian ecoregion (southern Hungary), representing more continental-submediterranean conditions than the studies reported above. Floodplain oak forests were studied in the floodplain of Drava river (southwest border of Hungary), beech ones in the Mecsek Middle Mountains, about 40 kms north of it. Drava floodplain lies in elevation 90-110 m a.s.l. Its climate is moderately warm – moderately wet, with summer drought period occasionally up to two months. Soils are Histosols and Luvisols (FAO-UNESCO, 1997). Groundwater table is at 2-4 m (Dövényi, 2010). Depressions (former watercourse beds) are covered by water in springs up to three-six weeks. Dominant phytosociological associations are hornbeam-pedunculate oak forests (*Circaeo-Carpinetum* Borhidi 2003), and oak-ash-elm hardwood alluvial forests with *Quercus robur*, *Fraxinus angustifolia* and *Ulmus laevis* (*Carici brizoidis-Ulmetum* Kevey 2008), with a transitional zone between them (Ortmann-Ajkai, 2002). Both associations belong to natural habitats of European Community importance (NATURA 2000 habitats: 91L0, 91F0, accordingly). For a more detailed site description see also Ortmann-Ajkai (1998). Current even-aged stands originate from planting *Quercus robur* on clear-cut areas, intensively managed in the first years, then thinned in about ten years periods. Due to selection favouring oak, the canopy is dominated by *Quercus robur* (70-90%), mixed with Fraxinus angustifolia, and in the lower canopy, *Carpinus betulus*. The shrub layer is dense in the oak-ash, but may be missing in the oak-hornbeam stands. Most important herb species are: *Circaea lutetiana*, *Carex sylvatica*, *C.remota, Stachys sylvatica, Pulmonaria officinalis, Galium odoratum, Rubus fruticosus* and *R.caesius*. No viable spontaneous regeneration of *Quercus robur* can be observed, although seedlings are abundant.

Mecsek Middle Mountains is topographically and geologically diverse. Its area is cca 500 km², its average height is between 400-600 m a.s.l. The climate is influenced by mediterraneous, continental and atlantic effects. Soils are predominantly Luvisols. 70% of the area of Mecsek Hills is covered by forests, mainly of near-natural Illyrian oak-hornbeam (*Asperulo taurinae-Carpinetum* Soó and Borhidi 1962), submontaneous Illyrian beech (*Helleboro odori-Fagetum* Soó and Borhidi 1960) and Pannonian-Balcanic turkey oak-sessile oak forests (*Potentillo micranthae-Quercetum dalechampii* A. O. Horvát 1981), all of them are NATURA 2000 habitats (91K0, 91L0, 91M0, accordingly). Current even-aged stands originate mostly from natural regeneration under old stands, released by harvesting more hectares; then thinned in about ten years periods. *Fagus sylvatica* is monodominant in the canopy, shrub layer is usually missing. Characteristic elements of the herb layer are submediterranean ones, e.g. *Lonicera caprifolium, Ruscus aculeatus, Ruscus hypoglossum, Helleborus odorus, Lathyrus venetus, Asperula taurina*. Abundant spontaneous regeneration of *Fagus sylvatica* can be observed in more lighted patches under old stands. More details on study sites see in Table 1.

Sampling and data sources

Data on managed stands originated from classic phytosociological releves (Braun-Blanquet, 1928 cf. Whitaker, 1980) made and published formerly by two of the authors. For floodplain oak forests 25 releves had been used, from which nine was made in the immediate neighbourhood of the unmanaged area (Ortmann-Ajkai, 1998) and 16 more from similar stands from the whole Drava floodplain (Kevey, 2007a,b). For beech forests 20 releves of Kevey (2012, 2013) were selected from the Mecsek Hills, from stands on sites similar to the unmanaged ones (exposure, slope, bedrock). All releves were made in middle-aged or old (above 80 years), even-aged, but relatively undisturbed stands managed by clear-cutting method common in Hungary.

In unmanaged stands management had been stopped for about 20 years. Vegetation sampling was implemented according to the Hungarian Forest Reserve Protocol (Horváth et al., 2012). A systematic 50x50 m grid of sampling points had been marked permanently in the field. Three surveys have been carried out at each sampling points: of tree stand structure, of regeneration and shrub layer and of herb layer. Herb layer study, whose data are analysed in this study, was implemented in 30 circles of 0.5 m^2 each, positioned systematically inside a circle of 6 m radius around the centre of each sampling points. Cover of each herb species, and of woody species under 50 cm height were recorded on the Braun-Blanquet scale. Unmanaged oak forests were sampled in 2012 in the southern core area of Bükkhát Forest Reserve. Unmanaged beech forests were sampled in 2010 in Márévár unmanaged forest. More detailed site descriptions see: Ortmann-Ajkai, 1998, Ortmann-Ajkai et al., 2013, accordingly.

Classic phytosociological releves and the forest reserve protocol both are designed for characterizing stands (usually of some hectares) of the same forest type (phytosociological units), contrary to the difference in the size of the sampling units. Common attributes (percentage coverage of species under 0.5 m height) are documented by both of them. On the other hand, the unmanaged forest data originate in both cases from an area of cca. 15 ha, till phytosociological releves from more sites of a geographically homogenous microregion. For the sake of robustness of results, data of species under 0.1% abundance were omitted from analysis.

Table 1: Description of study stands

Tabelle 1: Beschreibung der Untersuchungsständen

	Floodplain oak stands	**Submontaneous beech stands**
micro-region	Drava floodplain	Mecsek Middle Mountains
coordinates	N45°52'; O18°00'	N46°10'; O18°17'
elevation (m)	90-110	400-600
mean annual temperature (°C)	10.4	9.5
mean annual precipitation (mm)	730-760	720-760
soils	Histosols and Luvisols	predominantly Luvisols
phytosociologic associations	*Circaeo-Carpinetum* Borhidi em. Kevey 2006 *Carici brizoidis-Ulmetum* Kevey 2008	*Helleboro odori-Fagetum* Soó and Borhidi 1960
NATURA 2000 categories and codes	Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris* (91F0)	Illyrian Fagus sylvatica forests (91K0)
Main tree species	*Quercus robur*	*Fagus sylvatica*
Age of stand (years)	120	140
Average D130 of the main species (cm)	54	45
Stand density of the main species (db/ha)	124	240
Basal area of main species (m^2/ha)	29	38
Growing stock volume (m^3/ha)	478	730
Average gap diameter (m)	20	20
Proportion of gap area (%)	8	1
Spontaneous regeneration of main tree species	near to zero	abundant
Management before abandonment	planting *Quercus robur* on clear-cut areas, intensively managed in the first years, then thinned in about ten-years periods	natural regeneration under old stands, released by harvesting more hectares; then thinned in about ten-years periods
Managed forest data	25 releves (Ortmann-Ajkai 1998, Kevey 2007a,b)	20 releves (Kevey 2012,2013)
Unmanaged forest data	54 sampling points	53 sampling points

Statistical analyses

Hypotheses were tested by comparing abundance-weighted means of species abundance data; relative light indicator values, (Ellenberg et al., 1992, Borhidi, 1995); abundance of species groups of specialists and disturbance indicators (Grime, 1977, Borhidi, 1995). Significance of differences were determined for datasets having normal distribution by t-test, otherwise by nonparametric Mann-Whitney U-tests, calculated in R.

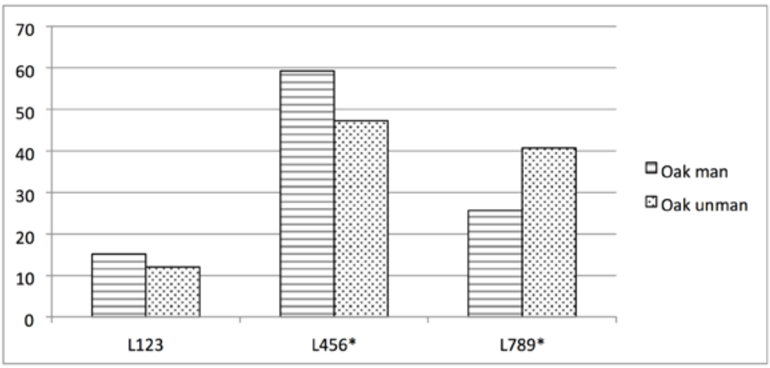
Diversity of tree regeneration elements was computed in R, according to the Shannon diversity formula. Diversity profiles, a more robust method of comparing diversities (Tothmeresz 1995) were created also by R, using the package "vegan" (Oksanen et al. 2013).

Results

Changes in light conditions

In oak forest abundance-weighted mean of light indicator values increased from 4.97 to 5.3, in beech forests from 3.68 to 3.91 (latter change is not significant at $p<0.05$).

According their light indicator values, species were grouped into shade-tolerant (L123), medium (L456) and light-demanding (L789) categories. (Figure 1). Managed oak forest, having relatively open canopy, were dominated by species with medium and high light demand; managed beech forests with closed canopy by shade-tolerant and medium-light-demand ones. Share of shade tolerant species decreased in both types, but not significantly. In oak forests there was a marked shift from medium to high-light-demand species. In beech forests both the medium and high-light categories increased in a small extent.



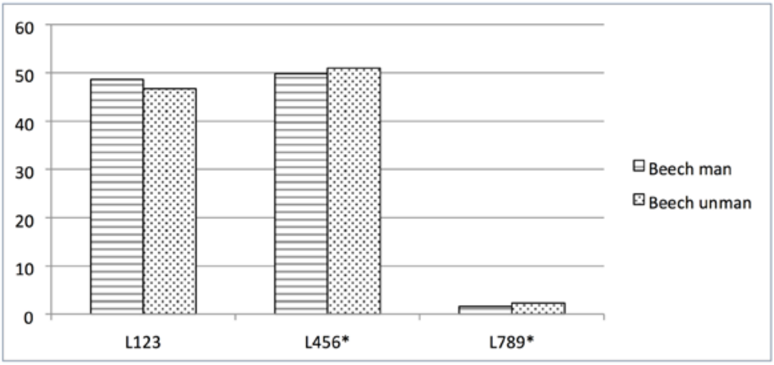


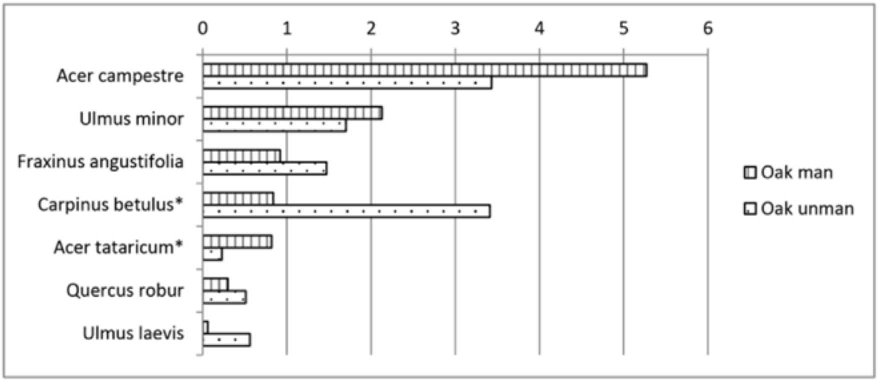
*Figure 1: Light indicator spectra for oak (a) and beech (b) forests. Significant differences (p<0.05) between managed and unmanaged stands are marked with **

Abbildung 1: Lichtzahlen-Spektren für Stieleichen- und Buchenbeständen. Signifikante Unterschieden (p<0.05) zwischen bewirtschafteten und unbewirtschafteten Beständen sind mit * markiert.

Spontaneous regeneration in unmanaged stands

In floodplain oak forests, there was a non-significant decrease of total cover of tree species in the herb layer (7.82 to 3.9%). The significant increase of *Carpinus betulus* was overwhelmed by the large simultaneous decrease of *Acer campestre* and *Ulmus minor*, two generalist species. Abundance of main species of floodplain oak forests – *Quercus robur*, *Fraxinus angustifolia* and *Ulmus laevis* – had not changed significantly (Figure 2a). Regarding the relative proportion of regenerating species, in managed stands two generalist species, *Acer campestre* and *Ulmus minor* added up to 78%; in unmanaged stands their proportion decreased to 44%. At the same time, the share of two competitor species (*Carpinus betulus, Fraxinus angustifolia*) increased to 43% (Figure 3b). *Ulmus laevis*, a specialist also showed notable proportional increase (1 to 6%). Regeneration in unmanaged forests was more diverse than in managed ones, according to Shannon diversity index (changes from 1.27 to 1.67). Diversity profiles (Figure 3c) also showed markedly higher diversity of unmanaged stands.

In beech forests gap creation induced a fourfold total increase of the cover of tree seedlings and small saplings (3.55% to 14.1%, Figure 2b). *Fagus sylvatica*'s cover increased to more than tenfold (0.43% to 5.59%). Majority of other species also showed significantly higher values, e.g. specialists as *Acer pseudoplatanus*. At the same time, the diversity of tree species decreased in unmanaged stands (Shannon diversity changed from 2.59 to 1.9, Figure 3b), due to the excessive mass of beech seedlings. Diversity profiles (Figure 3c, d), showed markedly higher diversity of managed beech stands contrary to oak ones.



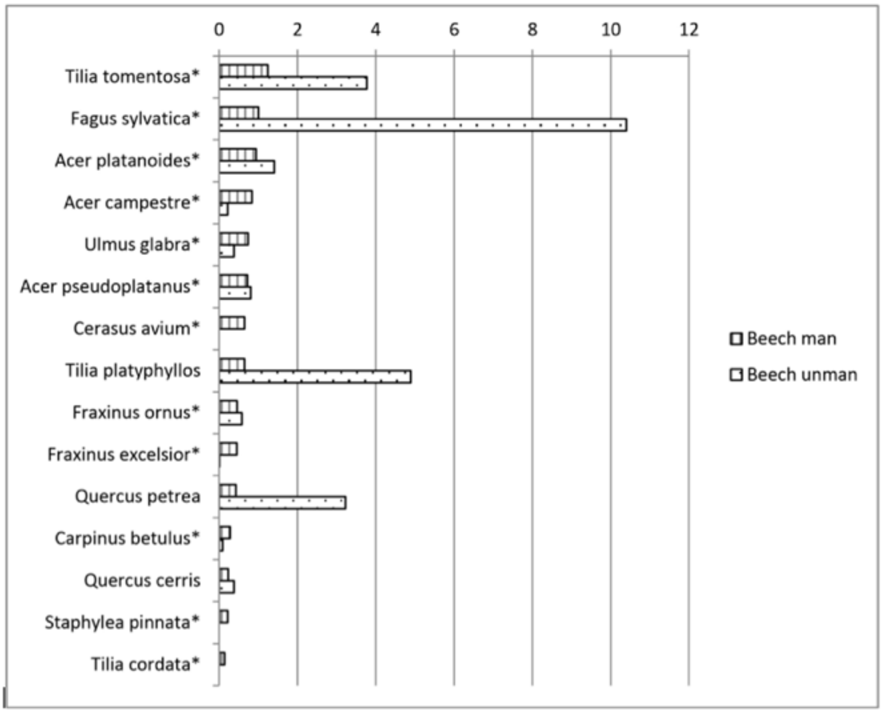


*Figure 2.: Cover of regeneration in the herb layer. (a) oak forests; (b) beech forests. Significant differences (p<0.05) are marked with *.*

Abbildung 2. Deckungsgrad der Naturverjüngung im Bodenvegetation. (a) Stieleichenbeständen; (b) Buchenbeständen. Signifikante Unterschieden (p<0.05) sind mit * markiert.

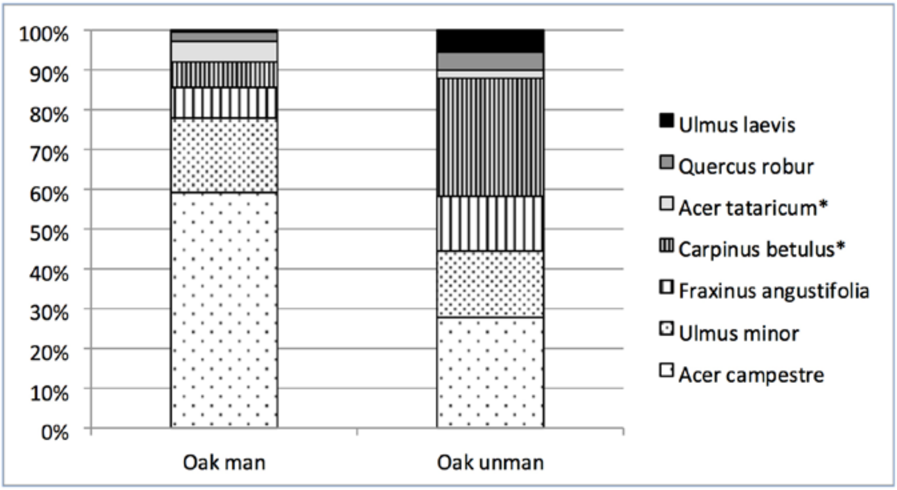


Fig. 3a.

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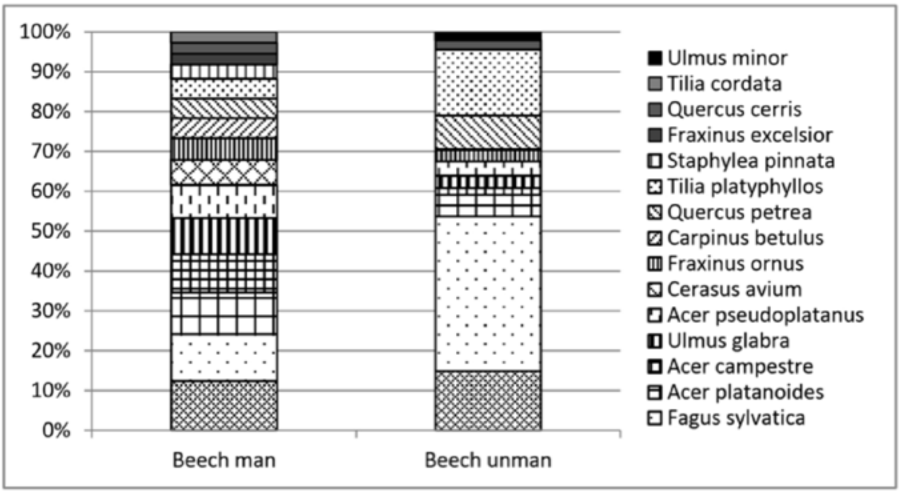

Fig. 3b.

Abb. 3b

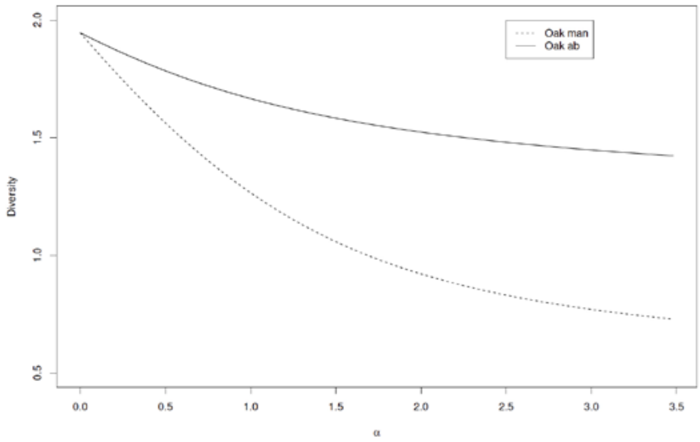

Fig. 3c

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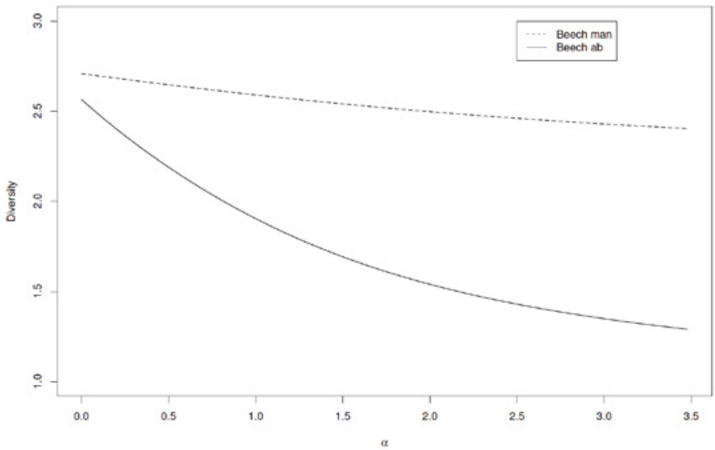


Fig. 3d

Abb. 3d

Figure 3. Diversity of tree regeneration. Relative proportions of tree species in the herb layer: (a) oak forests; (b) beech forests. Rényi diversity profiles for oak (c) and beech forests (d)

Abbildung 3. Diversität der Naturverjüngung: Relative Proportionen der Baumarten in Waldbodenvegetation: (a) Stieleichenbeständen; (b) Buchenbeständen; Rényi-Diverzitätsprofilen für (c) Stieleichenbeständen; (d) Buchenbeständen

Changes of specialist and competitor species

Light-demanding competitor or specialist species (L=7, 8 or 9) did not appear in neither types of forests, even in stands with gaps. In oak forests only one dark-tolerant competitor had been observed (above 0.1% cover), Galium odoratum, whose cover decreased (Table 2).

In beech forests six shade-tolerant competitor and one specialist species (Ruscus hypoglossum) have been found (Table 2). Their total cover has risen significantly (from 12.5 to 14.1%), but it was mainly due to increase of tree species (*Fagus sylvatica*, *Tilia platyphyllos*).

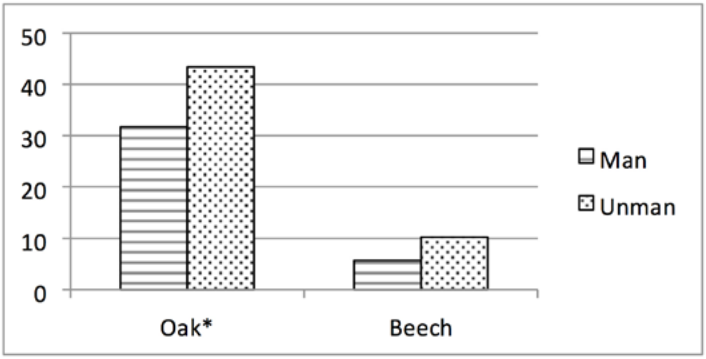
Table 2: Cover (%) of shade-tolerant competitor and specialist species (light indicator values: 1, 2, or 3) in the studied stands. Species with are considered as shade tolerants. Significant differences (p<0.05) are in bold and marked as s.

Tabelle 2: Deckungsgrad (%) schattentoleranter (Lichtzahlen 1,2 oder 3) Kompetitoren und Spezialisten. Signifikante Unterschiede (p<0.05) zwischen bewirtschafteten und unbewirtschafteten Beständen sind mit Fettdruck und s gekennzeichnet.

Species	**Oak managed**	**Oak unmanaged**	
Galium odoratum	4.49	2.55	ns
Species	**Beech managed**	**Beech unmanaged**	
Galium odoratum	5.05	4.32	ns
Oxalis acetosella	0.83	0.43	ns
Fagus sylvatica	**0.43**	**5.58**	**s**
Festuca drymeja	**4.6**	**0.24**	**s**
Mercurialis perennis	**0,65**	**1**	**s**
Tilia platyphyllos	0,18	2,23	ns
Ruscus hypoglossum	**0,5**	**0,25**	**s**
All shade tolerants	**12,5**	**14,1**	**s**

Changes of disturbance indicator species

For greater sensitivity, Grimes's (1977) "ruderal" group were divided into three groups (Borhidi, 1995): natural disturbance tolerants (DT), weeds (W) and invasives (Inv). Share of natural disturbance tolerant species was high in managed floodplain oak forests (31.7%) and increases with cca. 40% (to 43.4%, sign) after abandonment. In beech forests the increase is to two-fold, (ns) but even so far less (5.7/10.2%) than in the oak ones (Figure 4a). Share of weeds decreased in small, but significant extent in both stand types. Share of invasives has risen significantly in oak stands (but even so only up to 1.4%), but invasive species do not even appear in the unmanaged beech stands (Figure 4b).



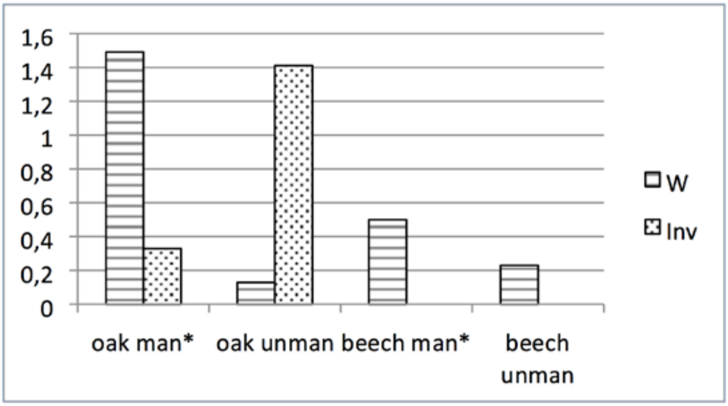


*Figure 4. Share of disturbance indicator species: (a) share of natural disturbance tolerants; (b) share of weeds and invasives. Significant differences (p<0.05) are marked with *.*

Abbildung 4. Proportionen der Disturbanzindikatoren: (a): Proportion von natürlichen Disturbanztoleranten; (b) Proportion von Unkräutern und Invasiven. Signifikante Unterschieden (p<0.05) sind mit * markiert.

Discussion

For comparing the spontaneous dynamics of unmanaged beech and floodplain oak forests, four hypothesis were tested in the Pannonian ecoregion. Results are summarized in Table 3.

Table 3: Summary of hypothesis testing (parenthesis: non-significant results; bold: differences between the oak and beech stands)

Tabelle 3: Zusammenfassung der Ergebnisse der Hypothesentests. (In Klammern: nicht signifikante Ergebnisse); Fettdruck: Differenz zwischen Stieleichen- und Buchenbeständen

HYPOTHESES	Floodplain oak forests	Submontane beech forest	Notes
H1 Light conditions of stands improve because of spontaneous gap forming	TRUE	(TRUE)	About 10% change, *sign* for oak, *ns* for beech. Shift towards more light-demanding categories in both cases
H2a Due to excess light, abundance of regeneration of tree species increases	**FALSE**	**TRUE**	***Quercus robur*: almost no regeneration even in gaps *Fagus sylvatica*: regeneration increased in gaps to more tenfold**
H2b: Due to excess light, diversity of regeneration of tree species increases	**TRUE**	**FALSE**	**Oak forests: dominance of generalists changed to co-dominance of competitor and specialists Beech forests: in gaps *Fagus sylvatica* overwhelmed all other species**
H3a Due to improved light conditions, abundance of conservationally prefereable light-demanding species increases	FALSE	FALSE	Light-demanding specialist and competitor species do not even appeared
H3b: Due to improved light conditions, abundance of shade-tolerant specialist and competitor species decreases	(TRUE)	FALSE	Oak forests: one species, *ns* rise Beech forests: Rise in dark tolerant species: under closed beech canopy even these are limited
H4a Share of light-frequent natural disturbance tolerant species increases	TRUE	(TRUE)	*sign* in oak, *ns* in beech
H4b Share of weeds increases	FALSE	FALSE	Lack of human interference
H4c Share of invasives increases	**TRUE**	**FALSE**	Beech forests: not appearing oak forests: degradation of landscape matrix

Light conditions and tree regeneration

Understory light conditions were assessed using Ellenberg's light indicator values (EIVs; Ellenberg 1992), adapted for Hungary by Borhidi (1995). Although the framework of applicability of EIVs is is widely discussed, they are considered as reliable if their limitations are considered (Diekmann, 2003). A detailed analysis on the reliability of each indicators were provided by Schaeffers and Sykora (2000). Frequency of certain tree and herb species could be linked to certain indicator values (Decocq, 2000). Barbier et al. (2008) reported on studies which demonstrated the effect of canopy on indicator values of the understorey. Mean EIVs were good predictors of environment in ancient, but far weaker ones in recent woodlands; this difference had been explained by the colonization ability of species (Dzwonko, 2001). Long-range edge-forest interior gradients were detected using EIVs for acidity, nitrogen, moisture, light and air temperature (Berges et al., 2013).

The generally accepted statement that in unmanaged forests gap opening leads to improved light conditions in the understory has been confirmed. Nevertheless, results obtained in beech forests in this context were not significant, because small natural gaps (size of 1-3 trees) make no considerable difference and close in some years (Madsen and Hahn, 2008). In our case, gap density of beech forests was far lower than in oak ones (Table 1), it also helps to explain lesser stand-level differences. Understory species composition shifts towards species of higher L values. In beech forests medium light-demanding species show a small, but significant rise (Figure 1b), indicating that light availability had been too sparse even for them, in line with Brang (2014).

Regarding the regeneration of main species, our results supports previous ones. The total cover of tree seedlings decreased in oak forests. However, this decrease was insignificant, in spite of significantly improved light availability. Other characteristic species of floodplain oak forests, Fraxinus angustifolia and *Ulmus laevis* did not show significant increase either, except *Carpinus betulus*, which is supposedly due to the drying site (Janik et al., 2011). The expected increase of tree species proportions was small because certain shrub or herb species (often *Rubus species* or *Pteridium aquilinium*) have a negative effect on tree seedling growth (Lorimer et al., 1994, Küssner 2003, Löf et al., 2004, Harmer et al., 2005, Harmer and Morgan, 2007, Koukoulas and Blackburn 2005, Wagner et al., 2010, Diaci et al., 2008, Mölder and Schneider, 2011, Kern et al., 2013). In our case *Rubus*-species (*R. fruticosus, R. caesius*) may play this role, as their total cover has changed from 12% to 17.1%. Growth release allowed abundant regeneration in beech forests (Figure 2b). Gap opening induced here a threefold increase of seedlings and small saplings (3.55% to 14.1%). Especially the share of *Fagus sylvatica* seedlings increased to tenfold (0.43% to 5.59%).

Diversity of regeneration did not increase according to species numbers, contrary e.g. to Bengtsson et al. (2000) and Brang et al. (2014). Nevertheless dominance structures have changed remarkably. In oak forests, Shannon diversity index and diversity profiles inevitably shows higher diversity (Figure 4.a, c), due to more balanced distribution of species. Similarly, the even distribution of tree species was reported by Janik et al., (2008). In beech forests the originally low and even distribution of seedlings of all species has changed differently after abandonment, presumably due to poor light conditions and forestry management: explosion of beech (published also by many authors, e.g. Schütz 1999, Brang 2005, Mihók et al., 2007) suppressed all other species. Diversity decreased (Figure 4.b, d) in line with Schmidt (2005).

Differences may be explained by various reasons. As for light demand, shade tolerance of beech is far the highest among European tree species (Schmidt 2005). Even so, it is not able to spontaneous regeneration under its own, closed, very shady stands, created by usual clear-cut management in the long run. However, due to advance regeneration, beech sapling are able to quick height grow (Brang, 2005) if getting extra light through natural or artificial gaps. Although oak forest canopy is more transmittant to light, even these conditions are not ideal for oak seedlings. *Quercus robur* is not so competitive, at least in young age and in the short run (e.g. Rodriguez-Campos et al., 2009; Terwei et al., 2013; Lorimer et al., 1994; Harmer et al., 2005). Comparing the two species, beech seedlings are able to survive and grow (very slowly) at 1% relative light intensity, till oak ones need at least 10% for it (von Lüpke, 1998; Diaci, 2008). Welander and Ottoson (1998) found that seedlings of both species are able to tolerate low light conditions in their first year of their life; but oak seedlings are sensitive to competition for light. On a macro-ecological scale, *Fagus sylvatica* in our study occurs under optimal mesoclimatic conditions, in a submontaneous position at the border of its climatic zone. On the contrary, floodplain oak forests are edaphic, depending on underground water supply, which may get scarce in the Pannonian steppe zone, especially due to climate change. Root competition is recognized as a potentially important factor of gap succession (Casper and Jackson, 2000), so different root competition abilities may also influence the regeneration success of beech and oak.

Conservational benefits and risks of abandonment

Numerous publications deal with changes of species with different light demand, however only few discuss conservationally preferable species with special emphasis. These two aspects are rarely considered together, although differentiation is necessary among species groups of differing conservational values (Standovár et al., 2006). The notion of "closed forest species" is used by some authors (e.g. Hermy, 1999; Schmidt et al., 2003). As there is no generally accepted "forest herb species" list in Hungary (except some local studies: Bölöni and Király, 2000; Kelemen et al., 2014) categorization of Borhidi (1995) on specialist and competitor species were used, excluding species of non-forest habitats (e.g. *Carex acutiformis, C. riparia* from oak forest analysis).

Decrease of abundance of shade-tolerant specialist and competitor species (hypothesis 3a) in oak forest was demonstrated: the only shade tolerant competitor, Galium odoratum slightly decreased (Table 2). There were more shade-tolerant specialist and competitor species in beech forests. *Fagus sylvatica* clearly increased, but other, mainly herbaceous ones decreased, or increased only insignificantly. Light-demanding specialist species occurred scarcely in oak forests and totally missed from beech stands, even from unmanaged ones with gaps (Hypothesis 3b). No light-demanding specialists appeared, because even the improved light conditions, lower than in closed oak forests, (Figure 1) are not satisfactory for their demand. Other authors also report different results. Resmerita, 1982 in Standovár and Kenderes, 2003) also found an extremely low percentage (1%) of light-demanding species in forest reserves of Roumania. On the other hand, light-demanding species disappeared from an unmanaged wood pasture, during the closing of the canopy (von Oheimb and Brunet, 2007). Differences between the behaviour of nemoral specialists and generalists had been found in forests of different disturbance regimes (Onainda et al., 2004). Generalist species were affected less or even positively by forestry disturbances, corrupted by N-oversupply (Borhidi 1995), while forest specialists may suffer (Bengtsson et al., 2000). Reduction of cover of shade-tolerant late-successional forest species were detected in mixed oak forests in New England after strong disturbances; the same species responded to minimal disturbance with vegetative expansion and becaming dominant in the plots, reducing immigration of more light-demanding ones (Aikens et al., 2007). No remarkable differences had been found in abundance changes of specialist and generalist species in lowland oak and ash forests during a 20-years long period, although different specialist groups (forest specialists, soil specialists) show slight differences (Naaf and Wulf, 2010). Increase of forest specialist, and decrease of generalist species had been found in an unmanaged oak forest in Southern Sweden, but presumably due to the closing canopy of the formerly grazed forest (von Oheimb and Brunet, 2007). Tree species, especially the highly shade-tolerant *Fagus sylvatica* may exclude other species (Schmidt, 2005; Slavikova, 1958 in Coomes and Grubb, 2000). These results contradict Borschenius et al. (2004), who found that environmental conditions (e.g. light) are more efficient predictors for woody species than for herbaceous ones. Dzwonko (2001) notes that changes in abundance of species with poor colonisation abilities need more time. Some shade tolerant species survive for some years in gaps (Resmerita, 1982 in Standovár and Kenderes, 2003). Spread of very shade-tolerant Allium ursinum had been recorded after weak thinning in southern Germany (Böhling, 2007). Small, one-tree gaps favour shade-tolerant species, and it is difficult to retain shade-intolerant species even in larger gaps created by group selection (Brang et al., 2014). Even closed-forest species may need recurrent light phases for their long-term survival (Plue et al., 2013).

Share of natural disturbance tolerant species were high in managed oak forests and increased cca. 50%, so in this case Hypothesis 4a was supported. In beech forests the increase is up to 10%, but even so remained less than in oak ones (Figure 4a). Floodplain oak forests are more disturbed by their nature, but even their measure has risen, presumably because of improved light conditions, being disturbance tolerants usually light-demanding. In their comparative study, Mölder and Schneider (2011) found that some fast-growing, competitive forbs (DTs and weeds, e.g. *Galium aparine, Rubus caesius, Urtica dioica, Glechoma hederacea*) became more abundant in more lighted stands of hardwood forests along the Danube; although they did not found an increase in diversity oh herb layer, using Shannon (H') and Shannon evennes (J') indices. They regarded it primarily a consequence of eutrophication, not of light abundance. Even the increased light availabilty is not appropiate for disturbance tolerant species, similarly to light-demanding competitors and specialists, in more shaded beech forests. Cover of native disturbance tolerant species, so-called "native invaders" increased in 20 years in lowland oak forests in northwestern Germany (Naaf and Wulf, 2010).

The good state of naturalness in our study sites was clearly indicated by the very low proportion of more dangerous indicators of degradation indicators: weeds and invasives (Figure 4b). Weeds had low cover in both forest types, conditioned probably by the lack of human interference, according to the explanation of Brunet et al. (1996). Weeds are remarkably more abundant in our floodplain oak forests, although their proportion is under 1.5%. Invasive species were not found in our beech stands at all; however, they showed a strong, significant increase from 0.33 to 1.41% in the oak forests. It may be a warning signal of the vulnerability of these stands, provoked by the surrounding degraded landscape environment. Schnitzler et al. (2007) estimated the proportion of exotic species in European oak-ash-elm forests 1.5% in a meta-analysis, noting that not all exotics are invasives. Naaf and Wulf (2010) reported a spread of only one invasive species (*Impatiens parviflora*) from a similar forest community. Invasives are missing from the studied beech forests, presumably because their stands are surrounded by near-natural forests of some thousand hectares.

Conclusion

The joint effect of the small differences demonstrated in our study between oak and beech stands may give some explanation for the different natural regeneration ability of the two forest types, although other factors, e.g. biotic interactions, root competition, game effect, site changes (drying) or historical or management factors may also play important role.

These differences highlight that our knowledge of spontaneous processes in unmanaged floodplain oak forests needs improvement. Results of studies from other forest types (especially from the well-studied beech forests) could and should not be extrapolated to them, or only with extreme precaution, because different natural forests are characterized by different types of natural dynamics (Schütz, 1999; Bengtsson et al., 2000, Yamamoto, 2000). Besides their scientific importance, further studies are justified also for practical reasons. Close-to-nature silviculture, often equalled with continuous cover management (Pommering and Murphy 2004, Brang et al., 2014), works well in beech forests, where spontaneous gap regeneration is proven, supported also by our results. On the other hand nature-based silviculture is less conducive to light-dependent and early-successional species, as Gamborg and Larsen (2003) notes. Spontaneous regeneration of closed stands of the less competitive pedunculate oak leads to more diverse forests with a very small proportion of this economically most important species, at least in the first two decades. If we consider spontaneous processes as “natural”, their conservational consequences may be regarded as beneficial. However, in cases of more or less anthropogenic habitats or communities, e.g. wood pastures or closed floodplain *Quercus robur*-forests, the issue of abandonment/management may be more difficult, even for conservational approach. In case when economic factors should be taken into consideration, the situation gets more intricate. Natural dynamics of floodplain oak forests differ basically from the well-studied gap theory, so decisions on their close-to-nature or conservational management need more scientific foundation.

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