Top-down segregated policies undermine the maintenance of traditional wooded landscapes: evidence from oaks at the European Union's eastern border

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Highlights

- traditional agricultural landscapes with trees maintain multiple ecosystem services
- maintenance of veteran-type oaks in agro-silvo-pastoral systems is a key challenge
- we compared four categories of oak tree development in three socio-economic contexts
- two distinct oak recruitment patterns – prolonged and short – were distinguished
- reconnecting rural economies and ecologies as a way forward for oakscape restoration

Abstract

Semi-open oak woods and solitary oaks commonly dominate the wooded fabric (i.e. the 'oakscape') of European traditional rural agricultural landscapes based on animal husbandry. However, modern land use systems fail to perpetuate oakscapes, posing a serious threat to biodiversity conservation and the associated diversity of ecosystem services. Reconstructing the dynamics of oakscape remnants can provide valuable insights concerning the maintenance of oakscapes. We used the socio-economic transitions at the European Union's eastern border as a natural experiment to explore the drivers for successful oak recruitment in 27 selected units representing 4 oakscape categories. Analyses of tree-ring data, historical maps, and orthophotos were used to reconstruct the oakscapes' establishment trajectories in relation to land use changes in the period 1790–2010. The oaks in cultural semi-open woods and wood-pastures differed substantially from those in closed canopy forests by more stocky shape and faster early age DBH annual increase. We found two distinct recruitment patterns: (1) FAST – recruitment usually completed within 2-3 decades, attributed to an unconstrained succession of abandoned agricultural land, and (2) SLOW – recruitment extending over several or more decades. In Ukraine, frequent illegal grass burning in marginal woods was the most successful mechanism perpetuating oak recruitment. Top-down policy encouraging specialized intensive farming, sustained yield forestry, and conservation efforts concentrated on the preservation of closed canopy forests compromise the future of traditional agro-silvo-pastoral systems. Maintenance of traditional integrated agro-silvo-pastoral management sustaining oakscapes needs to combine local traditional knowledge and landscape stewardship.

1. Introduction

Emerging in the Neolithic agricultural "revolution", traditional agro-silvo-pastoral systems have for long been determining the landscape development in Europe. Adapted to different natural conditions (e.g., geomorphology, hydrology, climate), the combination of agriculture and animal husbandry became a resilient foundation of the traditional village livelihood systems, which created multifunctional cultural landscapes (Angelstam & Elbakidze, 2017; Elbakidze & Angelstam, 2007; Vos & Meekes, 1999). Such traditional village systems proved to be efficient biodiversity 'time capsules' through the last millennium (Miklín, Sebek, Hauck, Konvicka, & Cizek, 2017). This is due to both the diversity of components including trees, other perennial plants and fine-grained land use (e.g., Angelstam, Boresjö-Bronge, Mikusinski, Sporrong, & Wästfelt, 2003), and processes such as roaming herds of livestock as an effective vector of species' dispersal as well as temporal abandonment (e.g., Bruun & Fritzbøger, 2002; Poschlod & Bonn, 1998).

A key feature of the once widespread traditional European cultural landscapes were solitary trees, semi-open woods and open wood pasture (Hartel, Réti, & Craioveanu, 2017; Moga, Samoilă, Öllerer, Băncilă, Réti, Craioveanu, Poszet, Rákosy, & Hartel, 2016; Plieninger, Hartel, Martín-Lopez, Beaufoy, Bergmeier, Kirby, Montero, Moreno, Oteros-Rozas, & Van Uytvanck, 2015; Rackham, 2006). Old, veteran-type trees provide a richer selection of crucial habitats for several specialised species, ranging from lichens and mosses to insects and birds, than trees developed in high forest habitats (e.g., Bergner, Sunnergren, Yeşilbudak, Erdem, & Jansson, 2016; Czarnota, Mayrhoffer, & Bobiec, 2018; Horak, Vodka, Kout, Halda, Bogusch, & Pech, 2014). This particularly pertains to oak species (Quercus spp.), the key-host trees to plethora of species in cultural landscapes in Mediterranean (Garrido, Elbakidze, Angelstam, Plieninger, Pulido, & Moreno, 2017a), temperate (Plieninger, T., Hartel, T., Martín-Lopez, B., Beaufoy, G., Bergmeier, E., Kirby, K., Montero, M. J., Moreno, G., Oteros-Rozas, E., & Van Uytvanck, 2015), and hemiboreal (Garrido, Elbakidze, & Angelstam, 2017b) ecoregions. Thus, open-grown and sun-exposed oaks form crucial habitats for species at the individual tree, patch and landscape scales, and provide a diversity of ecosystem services.

Neither forest management aimed at sustained yield wood production, nor benign neglect conservation favour the development of the high conservation value features of old oaks (i.e., ancient or veteran trees) (see Horak, Vodka, Kout, Halda, Bogusch, & Pech, 2014; Miklín, Sebek, Hauck, Konvicka, & Cizek, 2017; Mölder, Meyer, & Nagel, 2019).

Such trees have commonly occurred in landscapes shaped by various forms of agro-silvo-pastoralism (Moga, Samoilă, Öllerer, Băncilă, Réti, Craioveanu, Poszet, Rákosy, & Hartel,

2016; Vera, 2000). Sustaining semi-open woods and groves commonly involved livestock trampling and grazing (Öllerer, 2014). Bobiec, Reif, and Öllerer (2018) termed this type of land cover as the 'oakscape', referring to the wooded fabric of traditional cultural landscapes, important both for in situ biodiversity conservation and as reference for landscape restoration (Angelstam, Grodzynskyi, Andersson, Axelsson, Elbakidze, Khoroshev, Kruhlov, & Naumov, 2013).

However, the sustained existence of 'oakscapes' has been undermined by decoupling the human subsistence economic activity (such as pasturing, pannage, fodder making) from semi-open woods, which either left alone have undergone spontaneous succession, or have been intentionally transformed to dense timber stands (Hölzl, 2010; Rackham, 2006; Szabó, 2013; Vera, 2000). Thus, the traditional integrated wooded agricultural landscapes transitioned into segregated specialized systems focused either on agricultural or timber/fibre crops to satisfy growing urban needs. One of the most evident effects of this change is the decline of the "silvo"-component of traditional agricultural systems (Bergmeier, Petermann, & Schröder, 2010).

The abandonment of agricultural land is a phenomenon mostly driven by socio-economic factors, such as intensive agriculture powered by fossil fuel, and human migration to urban areas offering better economic opportunities (Benayas, Martins, Nicolau, & Schulz, 2007; Rotherham, 2011). From a traditional cultural landscape point-of-view, abandonment led to biodiversity loss, reduction of landscape diversity, and loss of cultural and/or aesthetic values (Assandri, Bogliani, Pedrinia, & Brambilla, 2018; Rotherham, 2011). De Souza, Tambosi, Romitelli, and Metzger (2013) concluded that a wide range of ecological characteristics influence landscape restoration outcomes and should be incorporated into programs and projects. Also, the social system context matters. Farmland abandonment is changing rural landscapes world-wide, and depending on the context it can be a threat to biodiversity, or an opportunity for habitat and landscape restoration (Levers, Schneider, Prishchepov, Estel, & Kuemmerle, 2018). In Europe, alteration, fragmentation and finally the loss of traditional agricultural systems with trees cause biodiversity decline, reduce the provision of multiple ecosystem services, and ultimately deteriorate human well-being (Elbakidze, Angelstam, Yamelynets, Dawson, Gebrehiwot, Stryamets, Johansson, Garrido, Naumov, Manton 2017. This requires approaches to active landscape restoration (Chazdon, 2008), which considers both ecological and social systems.

The objective of this study is to identify socio-economic contexts and trajectories that support long-term maintenance and restoration of the oakscape as a key component of agro-silvo-pastoral agricultural systems in the context of top-down vs. local traditional socio-

economic drivers. Unlike in Europe's West where land use became intensive earlier, in the East, agricultural systems based on multiple-purpose subsistence farming, involving the common pastoral use of woods still exist (Affek, 2015). Remnant pockets of such traditional agricultural system survived locally (Bomke, Wojcik, & Kutkowska, 1994), and can be best observed at the eastern border of the European Union (EU). These contrasting regions can thus be viewed as a true learning laboratory about landscape sustainability (e.g., Angelstam, Grodzynskyi, Andersson, Axelsson, Elbakidze, Khoroshev, Kruhlov, & Naumov, 2013).

In this study, we report on a comparative macroecological approach relying on 27 oakscape units of four types varying from open wood-pastures and semi-open silvo-pastoral woods to closed canopy stands, in three countries (Poland, Ukraine and Romania) located on both sides of the EU's eastern border to the former USSR. Using dendroecological reconstruction, the establishment of oak trees could be matched with the land use changes detected from the historical maps. Focusing on the maintenance of oak trees in traditional agro-silvo-pastoral systems, we discuss the negative effects of top-down driving forces vs. the need for maintaining traditional integrated agro-silvo-pastoral management systems. We conclude that maintenance of such systems needs to combine local traditional knowledge and bottom-up landscape stewardship.

2. Material and Methods

2.1. Comparative studies as a natural experiment

For logistic reasons it is not possible to design replicated experiments at landscape and regional level (Törnblom, Angelstam, Degerman, Henrikson, Edman, & Temnerud, 2011). We thus used the diversity of land use and landscape histories among local landscapes in different geopolitical units as a natural landscape-scale experiment (*sensu* Diamond, 1986). The European continent's fault lines between west and east (Huntington 1996) linked to different environmental histories, cultures and development trajectories during and after the end of the USSR, and the expansion of the European Union, is a useful example (see Bicik, Kupkova, Jelecek, Kabrda, Stych, Janousek, & Winklerova, 2015; Naumov, Manton, Elbakidze, Rendenieks, Priedniek, Uglyanets, Yamelynets, Zhivotov, & Angelstam, 2018). A particularly interesting gradient is formed by our study sites within the EU countries Poland and Romania, and post-Soviet Ukraine (see Törnblom, Angelstam, Degerman, Henrikson, Edman, & Temnerud, 2011), which are all located in the same continental biogeographic region (European Environment Agency, 2002) (Figs. 1, 2; Table 1).

Analyses of local oakscapes involved social and ecological system dimensions: (1) the socio-economic context as a proxy for the portfolios of land cover and land use trajectories (Poland and Romania representing the post-Soviet block and the eastern EU border; and Ukraine as a part of the former USSR and outside EU), and (2) four oakscape categories: Closed canopy forest with the Białowieża National Park as a model (F), Overgrown legacies of semi-open oak woods, including lapsed coppices (L), Semi-open oak marginal woods (M), and Open wood pastures (WP) (Fig. 2). Focusing on old oaks as the target species for biodiversity conservation in traditional cultural landscapes, a total of 27 oakscape units were selected for the study (Figs. 1, 2; Table 1). Each unit included an oak stand typical for the local landscape, ranging from 0.6 to 5.7 hectares in size (mean area 1.6 ha), and other land use categories identified within a 500-m radius buffer around the stand geometric centre (78.5 ha). This area extent satisfies the habitat patch requirements of herb layer mosaics (Bobiec, 1998), epiphytic lichens (Czarnota, P., Mayrhoffer, & Bobiec, 2018), saproxylic insects (Horak, Vodka, Kout, Halda, Bogusch, & Pech, 2014), and focal bird species, such as the middle spotted woodpecker (*Dendrocoptes medius*) (e.g., Angelstam et al., 2004). Field studies were performed in 2009–2016. A brief physiognomy description of the oak stands, including tree species composition in the canopy and percent tree cover of the studied stands, is provided in Table 1. Data on DBH at 1.3 m, tree heights, and crown lengths of all oaks was collected. For other species, only the canopy trees (here assumed DBH$\geq$20 cm) were measured (height and DBH), and their share in undergrowth was estimated (Table 2).

2.2. Dendroecological reconstruction of tree recruitment

The reconstruction of tree recruitment was based on the determination of the calendar years in which particular oaks reached the height of 1.3 m, i.e., the assumed baseline of saplings' recruitment into the population of trees. At least thirty randomly selected oaks were cored in each stand with a 5-mm Pressler's increment borer at breast height. In addition, wood discs were extracted from stumps of already cut trees located in the study sites, contributing to 29% of all wood samples. Due to Białowieża National Park restrictions, the sampling of F_{PL}1-4 stands was restricted to snags and logs at 1.3 m above the root neck, with the exempt for only a few core samples from living oaks for cross-dating.

The annual increment rings were measured with LINTAB-5, and all dead tree series were cross-dated with the chronology calculated from the local wood cores representing live trees series. The best matches were found with manual cross-dating and checked with the routine provided by TSAP-Win v. 4.65 software (Rinn, 2003). In the case of stump discs, the 1.3-m

'recruitment year' was assumed four years later than the original 0.2-m stump's 'pith year' (the median difference between 0.2 and 1.3 m, found in 59 oak saplings, Bobiec, unpubl.). When samples were missing the pith, a "pith-finder" was used to estimate the gap's length and to calculate the number of missing oldest rings (Rozas, 2003). Wood cores with more than 15 missing innermost rings were not included in the analyses.

2.3. Changes in landscape structure and dynamics

The long-term changes in oakscape units were assessed by comparison of four successive time periods. These were: (1) the First Military Survey maps of the Habsburg Empire (1763–1787) and the Map of the Brześć District (1796), (2) the Second Military Survey maps of the Habsburg Empire (1806–1869) and the Map of the Białowieża Forest (1830), (3) the map of the Military Geographical Institute (1919–1939) and the Military Survey of Hungary (1941 – the Romanian study sites belonged to Hungary at that time), and (4) the contemporary orthophoto imageries available in Google-Earth Pro software (Table SM1, SM – supplementary material). Because of cartographic inaccuracies of the historical maps and their relatively coarse scales, we did not appraise possible point-specific habitat development trajectories. Instead, as the representation of structural changes in a wider context, we investigated the changes in the ratio of land use categories within the entire 80-ha oakscape units. We distinguished five land cover types: Forest, Wooded grasslands, Grasslands (including both hay meadows and grazed tree-less pastures), Shrubland, and Ploughland. Buildings, covering not more than 2.1% of an oakscape unit, were excluded from the analyses. The land covers of the studied oakscape units were digitized separately for each time profile, using ArcGIS 10.0. software (SM: Fig. SM1). The land use structure during the oaks' recruitment periods was assessed by combining data from three historical maps and satellite imagery.

2.4. Statistical analyses

The mean increment ring widths in the first five decades of life after the recruitment year were used as a measure of oaks' response to underlying factors affecting the growth of trees. Series shorter than 30 years were not included in this analysis. Wood increment ring widths were compared using Kruskal-Wallis test with Dunn's non-parametric all-pairs comparison, and BH ranked data correction (Benjamini & Hochberg, 1995). To compare the dynamics of oak recruitment to the land cover dynamics of the oakscape units, we used the recruitment per-cent frequencies in 10-year wide intervals. All 27 recruitment series were standardized through replacing their medians with the value 0 (e.g., 0 instead of 1856 - $L_{PL}5$ or 1952 - $L_{UA}2$). Further

intervals were added to the right and to the left of the central one. The distributions were grouped with hierarchical cluster analysis (HCA, Ward's method, Euclidean distance). To test the null hypothesis of no differences among the clusters, we applied the analysis of similarities ANOSIM (Clarke, 1993). The ANOSIM significance R statistic, based on the difference of mean ranks between groups and within groups, was assessed by permuting the grouping vector to obtain the empirical distribution of R under null-model (999 permutations).

The oaks gross recruitment time slots, represented by the intervals between the 1st and the 9th percentiles of recruitment series, were referred to the dynamics of entire oakscape units. Changes in the share of four land use categories (Forest, Wooded grassland, Grassland, Shrubland, Ploughland) during the oak recruitment process were compared between three socio-economic systems represented by Poland, Romania and Ukraine (see Figure 2, horizontal dimension) with Friedman test (with Kendall's concordance coefficient). For computational operations we used the statistical software R in particular the vegan package (Oksanen, Blanchet, Friendly, Kindt, Legendre, McGlinn, Minchin, O'Hara, Simpson, Solymos, Stevens, Szoecs, & Wagner, 2017).

3. Results

3.1. Oak density

The density of the canopy oak stems varied from 10 ha^{-1} (wood-pasture in Romania) to 357 ha^{-1} (former coppice stand in Romania), and with the interquartile range (P$_{25}$-P$_{75}$) of 54–82 ha^{-1}. The overall basal area (BA) of the studied stands (excluding the four stands in Białowieża NP) varied from 5 to 28 m^{2}ha^{-1}, with a median of 12 m^{2}ha^{-1}, of which oaks made up 50-100% (see Tables 2, 3).

3.2. Dendroecological evidence

A total of 829 sampled oaks complied with the criterion of not exceeding 15 missing years estimated between the first measured ring and the pith (29% - with pith; 55% - 1-5 missing years; 12% - 6-10 missing years ; 3% - 11-15 missing years). The oldest cored tree was recruited in 1728 (F$_{PL}$3), and the youngest in 2013 (WP$_{RO}$2); the median recruitment year of sampled oaks was 1918. This corresponds to time since seed germination ranging from ca. 1720 to ca. 2005.

The comparison of the mean radial increments during the oaks' first decades of life revealed a conspicuous group of five oak assemblages (F$_{PL}$1-4 and F$_{RO}$4). These had substantially slower growth (medians of stems mean radial increment from 1.2 to 1.6 mm year^{-}

^{1}) than in other stands (from 2.2 to 4.2 mm year^{-1}), including the old stand in the Białowieża Forest margin M_{PL} (3.2 mm year^{-1}). Other noticeable differences occurred both between stands from different geographic regions (such as between $L_{PL}1$, 3.9 mm, and $WP_{RO}3$, 2.5 mm), and between stands within the same area (such as between $L_{PL}1$ and $L_{PL}7$, 2.2 mm), which suggests site-specific factors (e.g. the density-dependent competition vs. disturbances) being the most influential determinants of oak stems lateral increment (Fig. 3).

The medians of recruitment years of particular assemblages varied from 1846 in $F_{PL}2$ to 1988 in $L_{PL}3$ (mean of all medians was 1912). The inter-percentile P_{10-90} and P_{25-75} ranges of the recruitment series varied from 12 ($F_{RO}3$) and 4 years ($L_{PL}3$) to, respectively, 119 and 101 years, both in the Białowieża forest interfacing with long-used meadows M_{PL} (Fig. SM2). Although in 11 assemblages half of the sampled oaks recruited within 10-or-fewer years, 12 years (in $F_{RO}3$ lapsed coppice) was the shortest period in the same collection, necessary for the recruitment of 80% of trees constituting these oakscape units (mean(P_{10-90}) = 25 years) (Table 3).

In most oakscape units, regardless their median age of stands, the oak recruitment had been completed and ceased well before 2010, meaning that under the current land use regime there was no potential for further oak in-growth, except the very edge of the wooded areas. Among 11 units with the youngest oaks (recruited in 1975 and later: Table 3) there were six in Ukraine and one in Romania ($WP_{RO}2$) where tall oak saplings (>1.3 m) developed in the interior parts of oak stands (Table 1). Additionally, relatively numerous tall saplings were observed in Romanian dense woods $F_{RO}1$ and $F_{RO}4$, along with the paths regularly used by the passing herds of cattle (Table 1, Fig. SM3).

We identified two distinct groups of stand recruitment dynamics (Fig. 4): SLOW, with lower intensity but extended in time (inter-percentile ranges P_{10-90} = 63; P_{25-75} = 21) and FAST, with a short intensive recruitment wave (P_{10-90} = 26; P_{25-75} = 8). Both the overall cluster division and the differences between the clusters in the inter-percentile ranges were significant (ANOSIM difference: R = 0.733, P = 0.001; p = 0.0002 for P_{10-90}, p = 0.0006 for P_{25-75}, Mann-Whitney U test with continuity correction). Whilst the cluster SLOW is dominated by Białowieża Forest and Ukrainian oakscape units, the units with over-grown silvopastoral woods dominate the cluster FAST (Tables 1, 3; Fig. 4).

3.3. Oakscape units as dynamic components of traditional cultural landscapes

Except for the four stands in Białowieża NP ($F_{PL}1$-4), representing the 'forest' category throughout the entire 1790–2010 period, all other oakscape units were composed of at least two land use categories during this time. In the bulk of these units the dominating category was

Forest (average of 1790–2010 medians: 33%), followed by Ploughland (26%), Wooded grassland (15%), Grassland (12%), and Shrubland (<1%). However, considering the wider landscape context of the studied areas, the land use structure differed substantially between the geographic locations (e.g., the average 'Forest' proportion in Ukraine was 10% *vs*. 44% in Romania) and the oakscape units representing the same locations. The current land cover structure of the studied oakscape units differed from the past snapshots captured on the historic maps (Fig. 5). Considering the land use changes that accompanied the oak stands establishment (i.e. during the P_{10-90} periods), despite substantial stands age differences, Polish (without Białowieża NP, where Forest category covered 100% of units from 1790 to 2010) and Ukrainian oakscape units have undergone analogical structural changes, different from the Romanian units (Figs. 5, 6). Whereas in the two former regions the oakscape development corresponded with the increase of the Forest category at the expense of Wooded grassland and Ploughland, in Romania the recruitment of oaks was accompanied with a substantial increase of Wooded grasslands (Fig. 6).

4. Discussion

4.1. Regionally specific driving forces for oak recruitment in cultural landscapes

4.1.1. Poland: All oakscapes were subject to detailed mapping made in the mid-1800s. In particular, detailed estimates of land use metrics gave important insights into the historic landscape management. Substantial shares of fallows, coppice woods, and wooded grasslands, were commonplace (Table 1). In addition, most of the studied oakscapes were mixed with open fields or grasslands. Such a diverse landscape structure, unchanged during the last 150 years (Second Military Survey of the Habsburg Empire, ca. 1850, Timár, Molnár, Székely, Biszak, Varga, & Jankó, 2006; e.g., Fig. SM1), would have allowed regular access of livestock into the wooded areas, thus sustaining their semi-open character, conducive to oaks recruitment and high diversity of semi-open woods (Miklín, Sebek, Hauck, Konvicka, & Cizek, 2017). In parts of the studied oakscapes it is likely that the majority of recruitment cohorts were the progeny of the oldest sampled oaks, (e.g. if P_{25}-Min >30, as in $L_{PL}1$ and 4, or $M_{UA}1$ and $L_{UA}1$ - Table 2). However, 'parent-oaks' could also have disappeared (Fig. SM4). Establishment of younger oak stands corresponds with the dramatic socio-economic changes in the aftermath of World War II when much of the countryside along the Polish-Ukrainian border became depopulated and subject to afforestation and land acquisition by the state forest holding (Affek, 2015). Adopting the principles of sustained yield silviculture led to replacement of oakwoods with highly stocked beech-fir timber stands. This pattern was reflected by abundant stumps from cut oaks (Table 1). The best-preserved site, $L_{PL}1$, retained after the war as a communal property,

had not been subjected to this transition. The post-war steep decline of the human population in the region, causing the even sharper decline of the livestock, large-scale nationalization of land, ban on forest grazing, and timber-focused forestry (Affek, 2015), triggered the disappearance of semi-open oak woods. The only contemporary habitats with oak recruitment potential are fragments of abandoned grasslands in relatively short distance to cropping oaks, where tall oak saplings can be found. Usually, however, they are ephemeral because of systematic removal of shrubs and young trees - commonly motivated by the EU per-hectare payment to maintain permanent grasslands.

4.1.2. Romania: Similar to Poland, the recruitment of oak stands in traditional silvopastoral landscapes declined sharply. Transylvania in today's Romania employed the traditional model of silvopastoralism, including intentional care after young trees. However, this was disrupted by over 50 years of intensified land use during the communist rule (Öllerer, 2014). As in the Polish oak stands, the silvopastoral woods are currently being swiftly filled with dense undergrowth, mostly hornbeam (*Carpinus betulus*) (Table 2), which in turn prevents further oak recruitment. Additionally, cattle (WP$_{RO}$1) and sheep (WP$_{RO}$3) overgrazing prohibits oak recruitment. According to cattle owners and herders, this is encouraged by the per head payment scheme (Öllerer, 2014; M. Benedek, pers. comm.). The only exceptions are either open woods, where moderate grazing combined with intentional retention of oak saplings and scrub removal fosters successful recruitment (WP$_{RO}$2), or fragments of dense groves heavily disturbed by migrating herds, where numerous oak saplings emerge (F$_{RO}$1,4; Fig. SM3).

4.1.3. Ukraine: These oak stands were much younger than those in Poland and Romania, and had developed in the local context of conspicuous changes in land use structure after the end of the Soviet period. Overall, the Ukrainian oak woods had retained their semi-open character, resulting in relatively short tree stature and low set crowns (Table 1). Frequent grass burning in economically marginal area has led to unintended restoration. This was the most successful mechanism sustaining semi-open woods and perpetuating the wider oakscape in this study (Ziobro, Koziarz, Havryliuk, Korol, Ortyl, Wolański, & Bobiec, 2016).

4.2. Major patterns of recruitment dynamics

Oaks can be considered 'anthropophilic opportunists'. This is linked to oak species' life strategy and ecological adaptation to natural disturbance regimes such as fire (Dey, 2002), which are also satisfied by traditional multi-functional farming systems (Garrido, Elbakidze, & Angelstam, 2017; Garrido, Elbakidze, Angelstam, Plieninger, Pulido, & Moreno, 2017; Bobiec,

Reif, & Öllerer, 2018). Although the agricultural intensification and sustained yield forestry have led to major shifts in landscape structure and dynamics since the 1700s (Antrop, 2005; Rusch et al., 2016), there are regions where traditional village system of subsistence farming have been retained into present time (Affek, 2015). Although the World War II atrocities and the communist socio-economic 'experiments' broke the continuity of the family-based husbandry tradition, pockets of traditional village systems still endure and can sustain local livelihoods (Elbakidze & Angelstam, 2007). Therefore, the eastern EU borderland is a fascinating 'natural experiment' displaying the reaction of landscapes, habitats and species to shifting socio-economic drivers (e.g., Levers et al., 2018).

The reconstructed history of oak recruitment towards entire oakscapes in this study confirms that traditional cultural landscapes can sustain oak habitats. At least two decades is the time necessary to recruit saplings based on several subsequent oak mast years (Drobyshev, Niklasson, Mazerolle, & Bergeron, 2014). Once the canopy has been closed, either by growing oaks themselves, or by other accompanying trees or shrubs, the recruitment is stopped. More than half of the studied oakscape units developed following a relatively short recruitment wave, after release from suppressing factors (e.g., releasing wood/grassland from intensive grazing/browsing, field abandonment, or fast re-sprouting after the last coppicing). Apparently, the 'unconstrained' succession of woody vegetation was the most common process of oak woods establishment in the Polish Carpathian foothills and in Romanian Transylvania.

The longer disturbances hampered the development of woody species, the longer the oak recruitment lasted. Such conditions can be favoured by several kinds of land use. One was wood pasturing, which was observed in two Romanian sites, and in a recently abandoned grazed meadow at the edge of the Białowieża Forest. Another was early spring grass burning, as is habitually, though illegally, practised in Romania and Ukraine (Öllerer, 2014; Ziobro, Koziarz, Havryliuk, Korol, Ortyl, Wolański, & Bobiec, 2016). Interestingly, the four old-growth forest stands of the Białowieża NP belong to the same SLOW recruitment group as the Romanian wood-pastures and the Ukrainian fire-affected marginal woods. This corroborates the findings of earlier studies, according to which two of the Białowieża stands (FPL1,2) have developed in an area used in the 1800s for intensive bison feeding (Bobiec, 2012). Two other stands (FPL3,4) emerged in the part of the Białowieża forest where frequent ground fires by the early 19th century had secured an almost complete dominance of pine. The beginning of oak recruitment there coincides with the ban on burning that was imposed ca. 1830 (Bobiec, 2012) (Fig. SM2). Although the Białowieża Forest stands revealed a similar recruitment pattern to that of wood-

pastures or semi-open marginal oak woods, they substantially differed in their tree growth dynamics.

In Poland, as in most of the European countries, farming intensification and sustained yield forestry led to a divided landscape with dense forests and non-forest land cover (Angelstam et al. 2003; Skarpaas et al., 2017). Forestry aimed at oak wood production, as well as the conservation of oaks in protected forests, is dependent on silvicultural operations and treatments (e.g., Götmark, 2007). Oak species' natural reproduction involving zoochoric seed dispersal, usually targeting grasslands with scattered shrubs and trees, has thus become inefficient due to systematic removal of emerging undesired woody enclaves in permanent grasslands (Bobiec, Reif, & Öllerer, 2018). Since Poland entered the EU in 2004, this process has often been driven by EU agri-environmental payments.

Similarly, such payments became the most popular type of subsidy in Romanian cultural landscapes. This has led to substantial increase in herds of domestic grazing animals and has resulted in overgrazing of pastures (Roellig et al., 2018). Unlike in the traditional wood-pasture system, in which livestock owners had to safeguard a desirable level of tree regeneration, the over-grazed wood-pasture contemporary legacies lack the continuity of oakscape renewal, except in wood patches not affected by passing herds, or steep sites and ravines unsuitable for grazing.

As the fate of the studied oakscapes show, contemporary management regimes driven by top-down strict national or EU regulations and powerful economic mechanisms (e.g., mandatory swift reforestation of forest gaps, ban of forest grazing, CAP direct payments or EU agri-environmental incentives, promoting permanent treeless grasslands) secure neither the cultural landscape structures nor the dynamics necessary to sustain the oakscape.

The best example of the positive effect of local land use was the Ukrainian marginal oak woods. According to local inhabitants, most of today's oakscape woods were even much more open, managed as wooded meadows until the late 1970s (M. Korol, personal communication). Despite declining livestock, Ukrainian oak woods are still being occasionally grazed, which remains legal, unlike in many European countries. Perhaps the most conspicuous phenomenon observed in the Ukrainian oakscape units was the effect of (illegal) early spring grass burning. With the abandonment of ploughlands in the early 1990s, after the collapse of USSR, the emerging grasslands are intentionally burned to promote grassland development (M. Korol, personal communication, July 10, 2017). Such fires commonly spread into neighbouring woods (Ziobro et al., 2016). There is indeed strong evidence of the positive effect of grass burning on white oaks regeneration also in NE American woods (Hanberry, Dey, & He, 2014. Unlike less

tolerant locally present woody species, oak saplings survive, even after being partly burned (Fig. SM5). Although fire scars are commonly found in the wood discs extracted from young oaks (5-30 years at ground level) they are missing in the inner wood of older stumps - whether in Ukraine, Poland or in Romania (Bobiec, unpubl.). This is in accordance with the testimony of local inhabitants who emphasize the grass burning is a new trend (M. Korol, personal communication, July 10, 2017).

4.3. Driving forces – towards a synthesis

Our study shows that, as long as local multi-functional land uses were maintained, local oakscapes have thrived for a long time as a key component of the traditional agro-silvo-pastoral systems in rural landscapes. Thus, the spatio-temporal scale and dynamics of anthropogenic or natural disturbances were able to maintain oakscape habitats and species in such landscapes. This was driven by forces strongly embedded in and interconnected with the local social-ecological system, e.g., basic human needs, inheritable land ownership, traditional culture and local institutions for landscape stewardship (Angelstam & Elbakidze 2017). The human responses to processes occurring on the landscape level were driven by the direct interest in nature's benefits (Fischer, Hartel, & Kuemmerle, 2012; Rotherham, 2011), and the habitats maintained were sufficiently compatible with what is required to maintain biodiversity. As a result, resilient bio-cultural landscapes developed, occasionally affected or even destroyed by external pressures and impacts, such as outbreaks of lethal plague or wars (Rotherham, 2011). Thus, we suggest using living and perpetuating oakscapes as an important indicator of a sustainable local social-ecological agricultural system that is able to deliver high bio-cultural values.

However, pervasive socio-economic changes have led to a remarkable shift in the driving forces away from this local system level. Economic globalization, focus on monetary values, fossil-fueled agronomic intensification, as well as national and super-national policies, have disempowered locally-based socio-economic institutions and mechanisms, decoupling the human direct interest from locally conditioned natural incentives (e.g., Plieninger et al., 2015; Rotherham, 2011). The disappearance of oakscapes is the outcome of such 'cultural severance' or disconnecting ecosystems from 'social systems' (Fischer, Hartel, & Kuemmerle 2012; Rotherham, 2011). Thus, specialized intensive farming, sustained yield forestry, and conservation efforts concentrated on closed forest canopy preservation, instead of encouraging a cultural landscape dynamic approach, endanger the European oakscape. Hence, the agro-silvo-pastoral systems, besides being an important source of livelihoods and food, can provide

a plethora of immaterial benefits such as biodiversity conservation and cultural heritage (Hartel, Réti, & Craioveanu, 2017; Horrillo, Escribano, Mesias, Elghannam, & Gaspar, 2016). The restoration and conservation of such integrated wooded agricultural systems could be achieved through use of local traditions, complemented with state-of-the-art knowledge co-production and learning. This requires involvement of actors at multiple levels bottom-up (Angelstam and Elbakidze, 2017), drawing upon traditional management of cultural landscapes, experiences of landscape restoration (Antrop, 2005), and high nature value farming (Bignal & McCracken, 2000).

5. Conclusions

We identified two alternative oak recruitment processes: one unconstrained, and one prolonged being constrained by natural or anthropogenic disturbances (e.g., cattle grazing, undergrowth burning). In Romania, where free-range cattle grazing has been maintained, the erosion of the local traditional care for tree regeneration on pasture land hampers recruitment. In the Polish Carpathian foothills, most of the present oak woods emerged in times of grazing pressure on forest margins. After the mid-1900s, however, they have either been excluded by spontaneously developed dense woody undergrowth, or undergone systematic silvicultural replacement by beech and fir stands. The future of oak woods looks most promising in Ukraine, where widespread spring grass burning, though illegal, proved to be a successful surrogate of the historic management and use of wooded meadows. However, contemporary segregated land management systems, involving top-down policies, do not benefit the maintenance of the 'oakscape' components as a characteristic feature of European traditional integrated agricultural systems. As recommended in the *Rzeszów-Eger Resolution on traditional rural landscapes of the Carpathian region* (Bobiec and Mázsa, 2017), new policies are needed, "allowing and encouraging the rural communities to develop their economies in harmony of their traditions and in accordance with natural knowledge, complemented with state-of-the art scientific and technological assets." Reconnecting local rural economies, cultures and ecologies, could help restore and sustain the European 'oakscape'. Development of such systems needs to combine local traditional knowledge and maintenance of landscape stewardship.

Acknowledgements

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Table 1. Description of oakscape units stands: coordinates mark stand centroid position (altitude [m]); flat/NSWE - (slope) exposure; ABAL – *Abies alba*, ACCA – *Acer campestre*, ACPS – *A. pseudoplatanus*, BEPE – *Betula pendula*, CABE – *Carpinus betulus*, CEAV – *Cerasus avium*, COAV – *Corylus avellana*, COSA – *Cornus sanguinea*, CRMO – *Crataegus monogyna*, FASY – *Fagus sylvatica*, FREX – *Fraxinus excelsior*, PIAB – *Picea abies*, PISY – *Pinus sylvestris*, POTR – *Populus tremula*, PRSP – *Prunus spinosa*, PYSP – *Pyrus* sp., QUPE – *Quercus petraea*, QURO – *Q. robur*, ROSP – *Rosa* sp., TICO – *Tilia cordata*; BF - Białowieża Forest; + scarce; +++ abundant; > more abundant; = equally abundant; symbols of oakscape units are explained in Fig. 2.

Oakscape unit	Location (altitude a.s.l.); area; slope/ aspect	Tree layer; Canopy cover (Cc) and species composition	Undergrowth (ug), herb layer (hb), oak regeneration (q)	Remarks
$F_{PL}1$	N52.74°/E23.84° (165); 1.33 ha; flat	Cc 100%: CABE> QURO = PIAB> TICO	ug+ COAV; hb+	BF, mosaic of mesic and humid sites of rich *Tilio-Carpinetum*
$F_{PL}2$	N52.74°/E23.84° (165); 5.67 ha; flat	Like $F_{PL}1$	like $F_{PL}1$	like $F_{PL}1$
$F_{PL}3$	N52.75°/E23.90° (175); 1.61 ha; flat	Cc <50%: QURO = PISY = PIAB> BEPE	hb+++ *Calamagrostis arundinacea, Rubus idaeus* and *Pteridium aquilinum*; q+++	BF, formerly spruce-dominated, in 1990s canopy disrupted by spruce bark beetle outbreak
$F_{PL}4$	N52.75°/E23.90° (175); 3.50 ha; flat	like $F_{PL}3$	like $F_{PL}3$	like $F_{PL}3$
$F_{PL}5$	N49.68°/E22.64° (405); 1.63 ha; flat	Cc 70% QURO> ABAL	ug+++ CABE> ABAL (planted); hb+	Trees: two cohorts: from 1800s and early 1900s
$F_{RO}1$	N46.13°/E25.41° (560); 1.00 ha; flat	Cc 80% QUPE> QURO	ug++ CABE; hb++; q+	
$F_{RO}2$	N46.13°/E25.42° (600); 1.00 ha; undulated	like $F_{RO}1$	like $F_{RO}1$	
$F_{RO}3$	N46.22°/E25.43° (715); 0.66 ha; flat	Cc 100% QUPE	ug q+; hb++	
$F_{RO}4$	N46.13°/E25.41° (550); 0.56 ha; flat	Cc 80% QURO> QUPE	ug++ CABE; q++	Most of oaks double-, or triple-stemmed - lapsed coppice wood
$L_{PL}1$	N49.62°/E22.72° (407); 1.37 ha; NEE	Cc 60%: QURO> ABAL> CEAV = ACPS> ACCA	ug+++ COAV; hb+ (+++ after COAV removal); q+ only at the edge of stand	In 2013-2015 COAV coppiced in part of the stand
$L_{PL}2$	N49.61°/E22.71° (470); 1.00 ha; S-SE	Cc 100%: QURO = QUPE> ABAL> CEAV	ug++ COAV; hb+; q+ only at the edge of stand	
$L_{PL}3$	N49.61°/E22.71° (470); 0.57 ha; E	Cc 50% QURO = QUPE> CEAV> FREX	ug++ COAV; hb+; q+ only at the edge of stand	

$L_{PL}4$	N49.62490°/E22.69984° (400); 1.51 ha; (W) flat	Cc 60%: QURO> FASY> CABE	ug+++ FASY = CABE; hb+; q+	In 1990s 50% of oaks felled
$L_{PL}5$	N49.63°/E22.70° (395); 0.89 ha; SW	Cc 30% QURO> FASY> ABAL> ACCA	ug+++ COAV = CABE> FASY = ACCA = COSA; hb++; outside q++	in 1990s 80% QURO felled
$L_{PL}6$	N49.67438°/E22.66647° (375); 0.83 ha; flat	Cc 100% QURO> CABE> POTR = CABE	ug++ COAV; hb++	Most of oaks double-, or triple-stemmed - lapsed coppice wood
$L_{PL}7$	N49.66°/E22.73° (326); 1.00 ha; undulated	Cc 100% QUPE > FASY> PISY	ug+; hb+	
$L_{PL}8$	N49.62°/E22.70° (400); 0.93 ha; (W)	Cc 80% QURO> FASY> CABE> FASY> FREX > BEPE	ug++ CABE = FASY; hb++	
$L_{UA}1$	N48.98°/E24.12° (425); 1.00 ha; flat	Cc 70% QURO> CEAV	ug++ BEPE = POTR; hb+++; q+++	Frequent spring grass burning
$L_{UA}2$	N48.92°/E24.11° (413); 1.00 ha; flat	Cc 40% QURO> ALGL> BEPE = POTR	ug+++ COAV; hb+; q+	
M_{PL}	N52.82°/E23.78° (148); 1.03 ha; flat	Cc 60%: QURO> PISY > PIAB+	ug+ COAV, hb++; q+ at the edge	northern edge of BF; PISY with fire scares
$M_{UA}1$	N48.98°/E24.12° (425); 1.00 ha; flat	Cc 60% QURO	ug++ COAV; hb+++; q++	Occasional grass burning
$M_{UA}2$	N48.92°/E24.12° (420), 1.00 ha; flat	Cc 60%; otherwise like $M_{UA}1$	like $M_{UA}1$	
$M_{UA}3$	N48.89°/E24.09° (482); 1.00 ha; flat	like $M_{UA}1$	like $M_{UA}1$	
$M_{UA}4$	N48.89°/E24.10° (475); 1.00 ha; flat	like $M_{UA}1$	like $M_{UA}1$	like $M_{UA}1$
$WP_{RO}1$	N46.13°/E25.42° (540); 5.71 ha; W	Cc 5% QUPE> FASY> PYSP	hb+++	Heavily cattle-grazed
$WP_{RO}2$	N46.17°/E25.41°; 1.65 ha (595); NW	Cc 35% QUPE> PYSP> BEPE	ug++ PRSP = CRMO> COSA = ROSP; q+++	Moderately cattle-grazed;
$WP_{RO}3$	N46.22°/E25.42° (695); 2.42 ha; flat	Cc 30% QUPE>> PYSP	hb+++	sheep-grazed

Table 2. Key variables and parameter values of studied stands; Nha^{-1} - number of oak stems (including cut stumps), %Stp – percent of cut stumps in N, BA – basal area [m^{2}ha^{-1}], DBH - median of stem diameter at 1.3 m above ground [cm], QUSP – *Quercus* sp., other - other tree species, H - median of tree height (for QUSP: total tree H/length of branchless trunks) [m], P – significance level; for description of stands see Table 1.

Stand	Nha^{-1}	%Stp	BA		DBH			H		
			Stand	Oak share	QUSP	other	P	QUSP	other	P
F$_{PL}$(3+4)	n.d.	n.d.	n.d.	0.20^{FI}	51	n.d.	-	28/16	n.d.	-
F$_{PL}$(1+2)	n.d.	n.d.	n.d.	0.40^{FI}	62	n.d.	-	30/15	n.d.	-
M$_{PL}$	69	30	39.2	0.85	78	41	***	27/7	25	
L$_{PL}$1	42	14	23.2	0.75	73	36	***	22/6	19	**
L$_{PL}$2	140	19	29.9	0.48	35	38		21/10	21	
L$_{PL}$3	92	7	15.5	0.64	35	40		19/7	21	
L$_{PL}$4	33	42	24.2	0.49	81	41	***	25/10	22	*
L$_{PL}$5	72	80	14.5	0.58	90	41	***	22/7	20	
F$_{PL}$5	75	27	17.1	0.94	54	50		25/8	26	
L$_{PL}$6	36	10	15.0	0.65	60	31	***	23/7	17	***
L$_{PL}$7	154	46	21.8	0.62	43	38	**	22/11	22	
L$_{PL}$8	57	37	21.1	0.70	70	37	***	26/8	22	*
WP$_{RO}$1	10	34	7.0	0.80	78	53	*	18/4	10	**
F$_{RO}$1	177	40	14.9	0.93	47	30		19/8	16	
F$_{RO}$2	153	34	14.2	0.81	39	29	**	17/5	15	**
WP$_{RO}$2	18	10	6.4	0.84	64	36	***	15/2	8	***
F$_{RO}$3	357	1	29.5	0.97	31	0		20/7	0	
F$_{RO}$4	190	7	3.3	1.00	36	0		21/7	0	
WP$_{RO}$3	53	7	10.5	0.95	47	33	*	19/3	8	***
M$_{UA}$1	96	27	19.7	0.97	57	26	***	20/5	13	***
L$_{UA}$1	61	36	12.8	0.94	62	25	***	19/6	15	***
L$_{UA}$2	116	5	10.7	0.95	42	34		18/4	19	
M$_{UA}$2	143	14	15.8	0.83	38	23	***	18/6	16	**
M$_{UA}$3	82	0	5.9	0.83	33	26	*	14/4	14	
M$_{UA}$4	82	4	12.4	0.87	47	27	***	19/5	14	***

* <0.05, ** <0.001, *** <0.0001; Mann-Whitney U test; ^{FI} from forest inventory data

Table 3. Basic statistical parameters of the oak recruitment dynamics in studied stands and landscape units. Recruitment calendar years – years, in which saplings reach the height of 1.3 m. N – number of series representing stands, Cluster – refers to either of two clusters of Fig. 4. See Tables 1 and 2 for the description of stands.

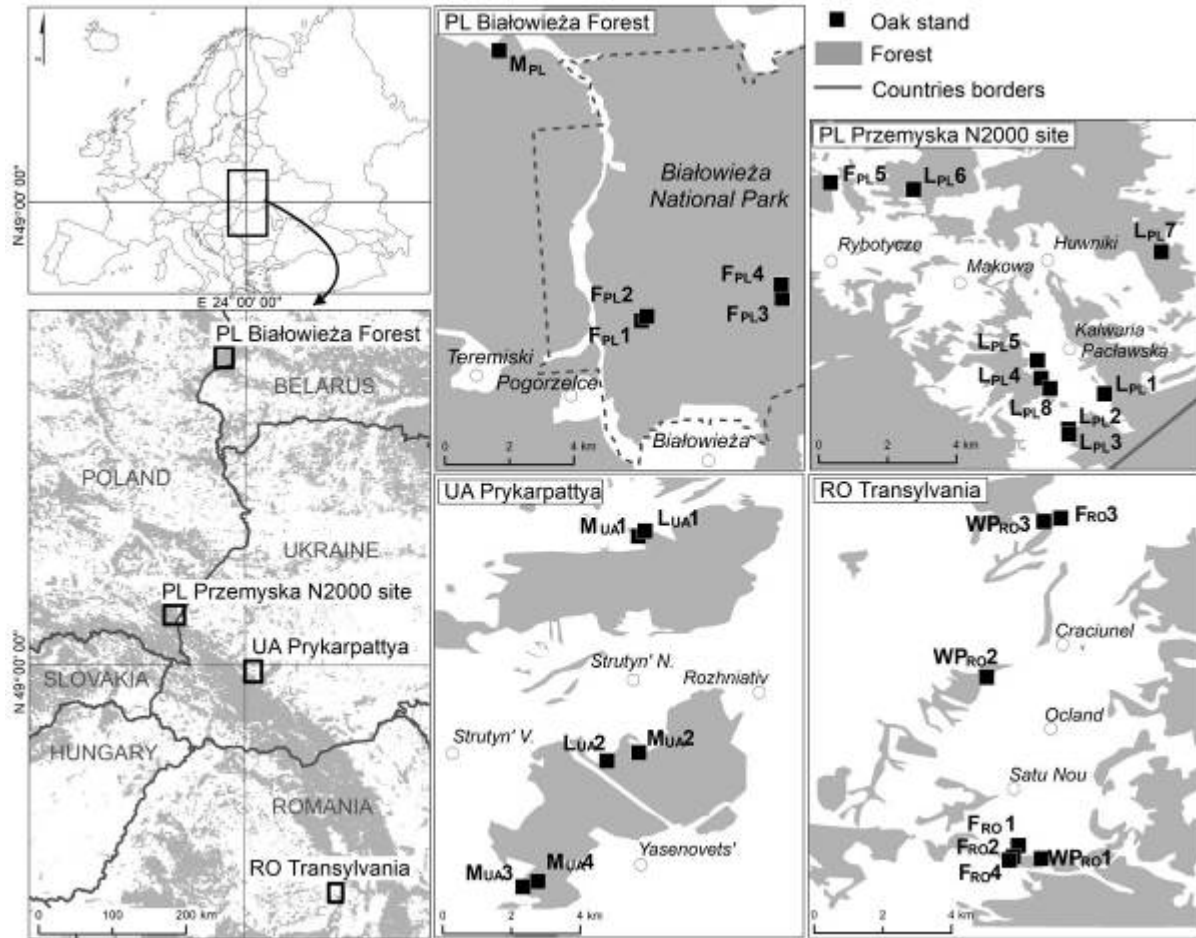| Stand	Cluster	N	Min	P_{10}	P_{25}	P_{50}	P_{75}	P_{90}	Max
$F_{PL}1$	SLOW	27	1728	1808	1836	1850	1857	1863	1917
$F_{PL}2$	SLOW	22	1748	1805	1827	1846	1854	1895	1945
$F_{PL}3$	SLOW	19	1842	1844	1857	1860	1876	1942	1948
$F_{PL}4$	SLOW	17	1819	1833	1846	1854	1867	1885	1909
$F_{PL}5$	SLOW	41	1839	1846	1854	1863	1870	1916	1918
$F_{RO}1$	FAST	20	1903	1908	1912	1916	1919	1930	1932
$F_{RO}2$	FAST	26	1905	1907	1914	1918	1921	1924	1935
$F_{RO}3$	FAST	39	1906	1926	1927	1930	1934	1938	1940
$F_{RO}4$	FAST	33	1904	1909	1910	1914	1919	1928	1948
$L_{PL}1$	FAST	57	1856	1905	1906	1913	1918	1944	1977
$L_{PL}2$	FAST	29	1929	1938	1941	1943	1948	1965	1990
$L_{PL}3$	FAST	35	1963	1968	1985	1988	1989	1994	2005
$L_{PL}4$	FAST	26	1809	1856	1860	1862	1883	1886	1903
$L_{PL}5$	FAST	47	1847	1855	1873	1877	1883	1903	1928
$L_{PL}6$	FAST	29	1931	1936	1939	1941	1946	1955	1982
$L_{PL}7$	FAST	34	1846	1887	1891	1895	1896	1900	1907
$L_{PL}8$	FAST	23	1840	1843	1846	1850	1876	1878	1904
$L_{UA}1$	SLOW	30	1889	1896	1926	1941	1949	1962	1975
$L_{UA}2$	FAST	27	1927	1938	1947	1952	1956	1970	1992
M_{PL}	SLOW	25	1813	1831	1839	1930	1940	1950	1956
$M_{UA}1$	SLOW	37	1858	1896	1900	1925	1944	1948	1976
$M_{UA}2$	SLOW	34	1919	1936	1947	1954	1965	1973	1981
$M_{UA}3$	SLOW	34	1953	1969	1975	1984	1990	1993	2000
$M_{UA}4$	SLOW	40	1917	1926	1933	1944	1962	1989	2005
$WP_{RO}1$	SLOW	25	1768	1894	1898	1911	1917	1929	1932
$WP_{RO}2$	SLOW	22	1901	1908	1921	1928	1943	2012	2013
$WP_{RO}3$	FAST	31	1886	1890	1921	1926	1930	1933	1946

Fig. 1. Location of the 27 oakscape units in Poland, Romania and Ukraine, representing gradients in socio-economic transition and from closed canopy forest to cultural oakscapes (see Fig. 2)

	Poland (EU)	Romania (EU)	Ukraine (former USSR)
Closed canopy forest (F)	F_{PL}1-5 5SLOW	F_{RO}1-4 3FAST	N.A.-
Overgrown legacies of semi-open oak woods, including lapsed coppices (L)	L_{PL}1-8 8FAST 1SLOW	N.A.	L_{UA}1-2 1FAST 1SLOW
Semi-open oak marginal woods (M)	M_{PL} 1SLOW	N.A.	M_{UA}1-4 4SLOW
Open wood-pasture (WP)	N.A.	WP_{RO}1-3 1FAST 2SLOW	N.A.

Gradient 2: Oak stand category

Fig. 2. Sampling design to study factors affecting the recruitment of oaks in two gradients: (1) socio-economic context and (2) oakscape category. Gradient 1 (columns) represents the current socio-economic gradient in transition away from rural livelihood farming, which is strongest in Poland and weakest in Ukraine. Gradient 2 (rows) represents the gradient from high forest to increasingly active cultural landscape management.
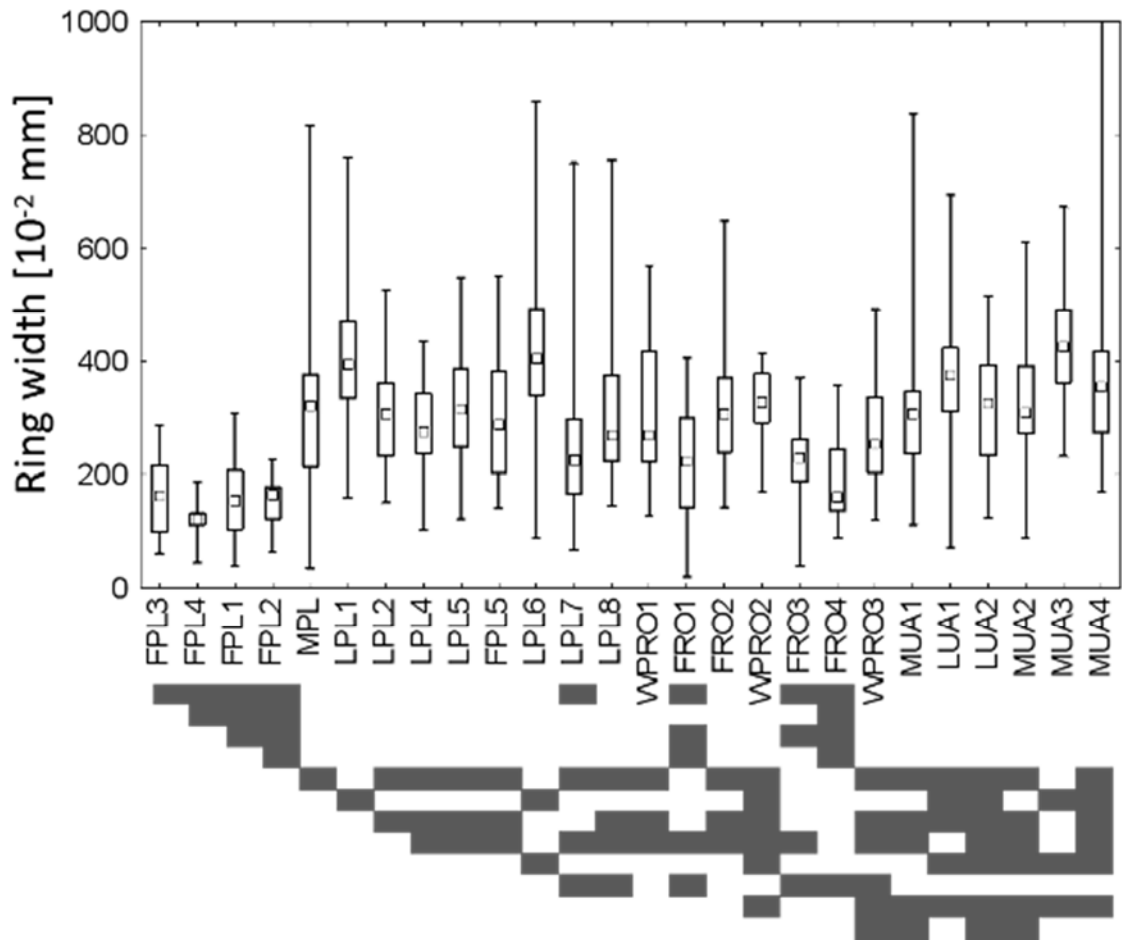F_{PL}1 etc. – oakscape units, see Table 1 for description

Fig. 3. Average tree ring width during the first 30-50 years of oaks life after recruitment; squares – medians; boxes – inter-quartile ranges; whiskers – absolute ranges; dark strips underneath – homogenous groups of stands according to Dunn's non-parametric all-pairs comparison test for Kruskal-type, p <0.05. $L_{PL}3$ with only three series ≥30 years was not considered.

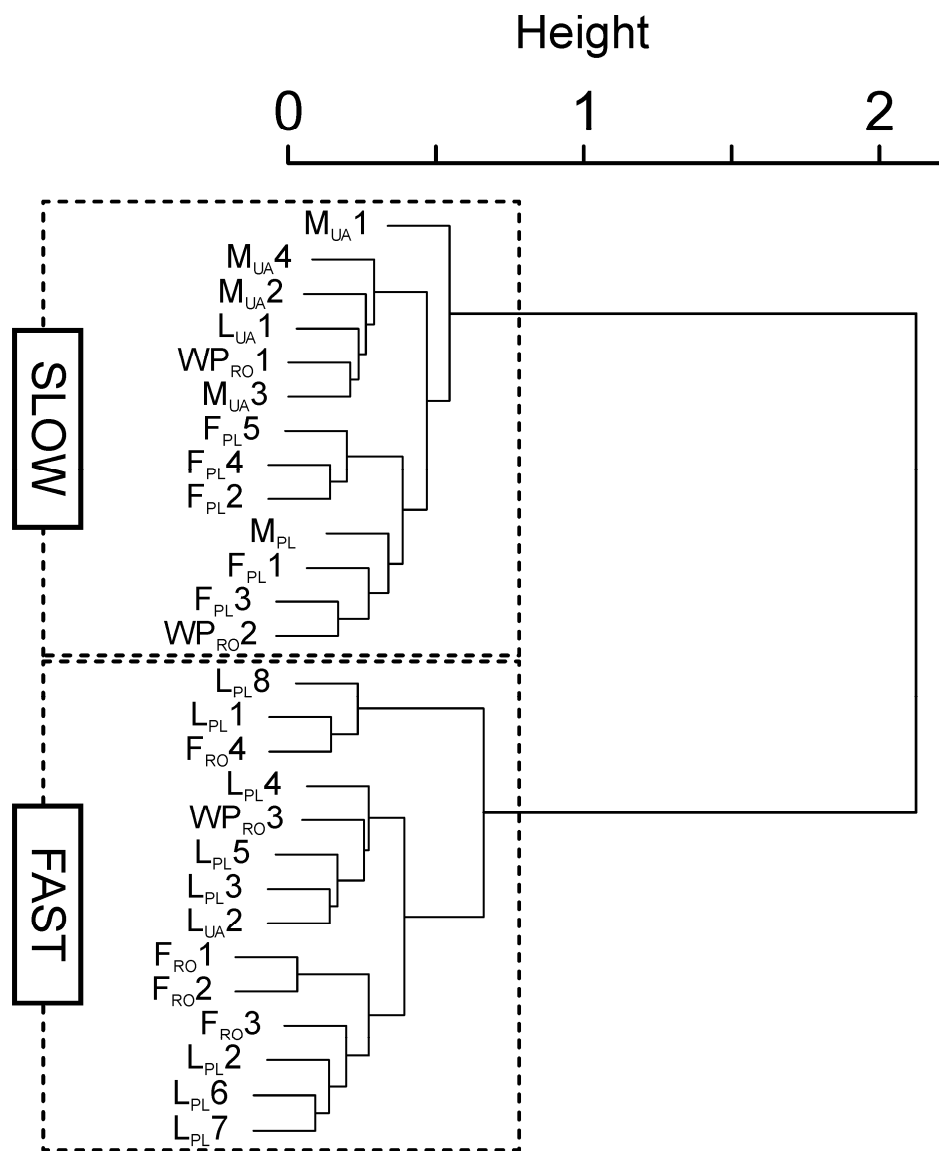$F_{PL}3$ etc.: oakscape units

Fig. 4. Hierarchical cluster analysis (HCA) of oak recruitment dynamics of the 27 investigated stands. These were grouped into two clusters, representing two major patterns of recruitment dynamic (SLOW and FAST).
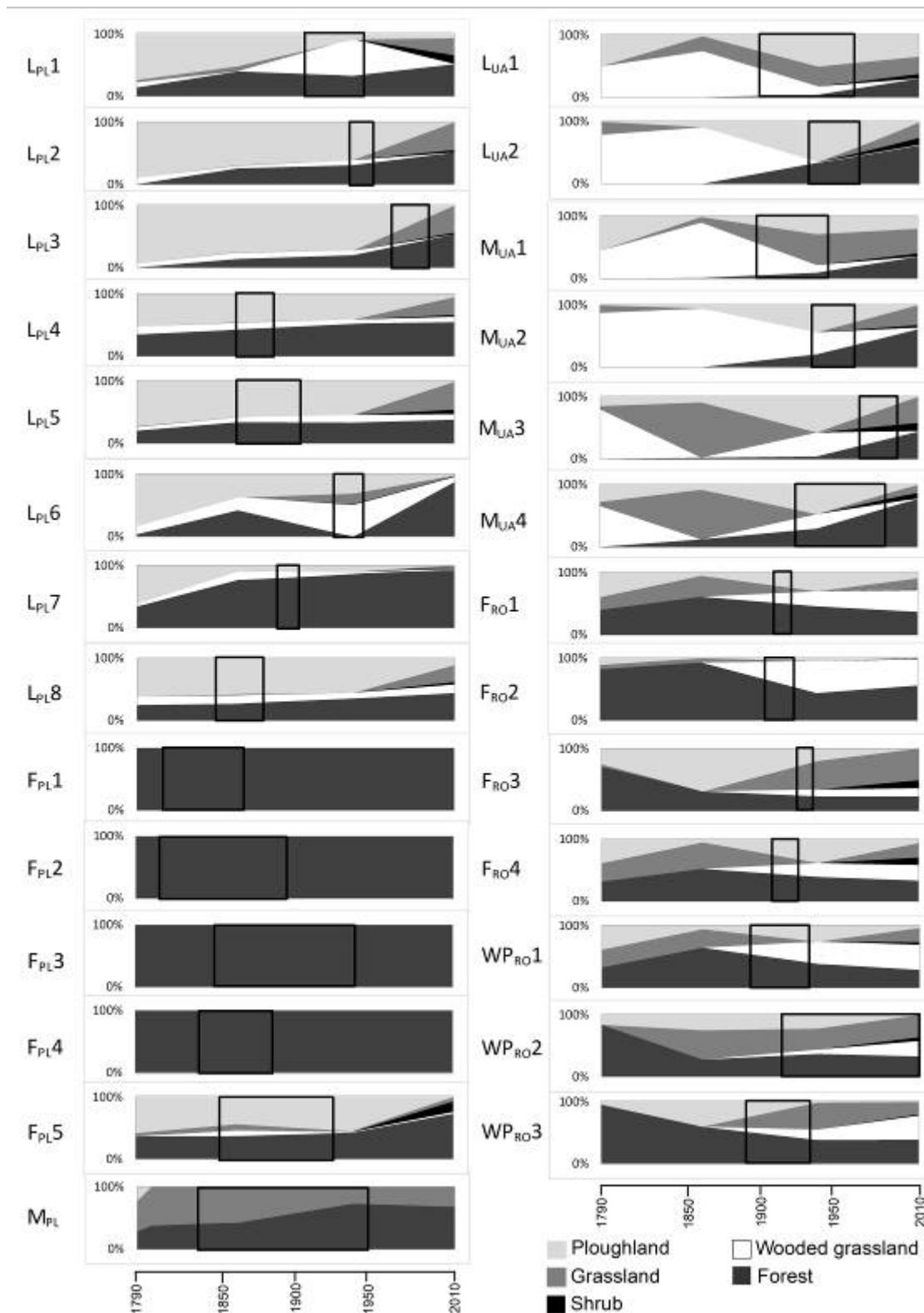
Fig. 5. Landscape structure dynamics in 500-m-radius buffers around the centroids of studied oak stands; black frames represent the intervals between P_{10} and P_{90} percentiles of oaks recruitment. For stands' description see Tables 1, 2
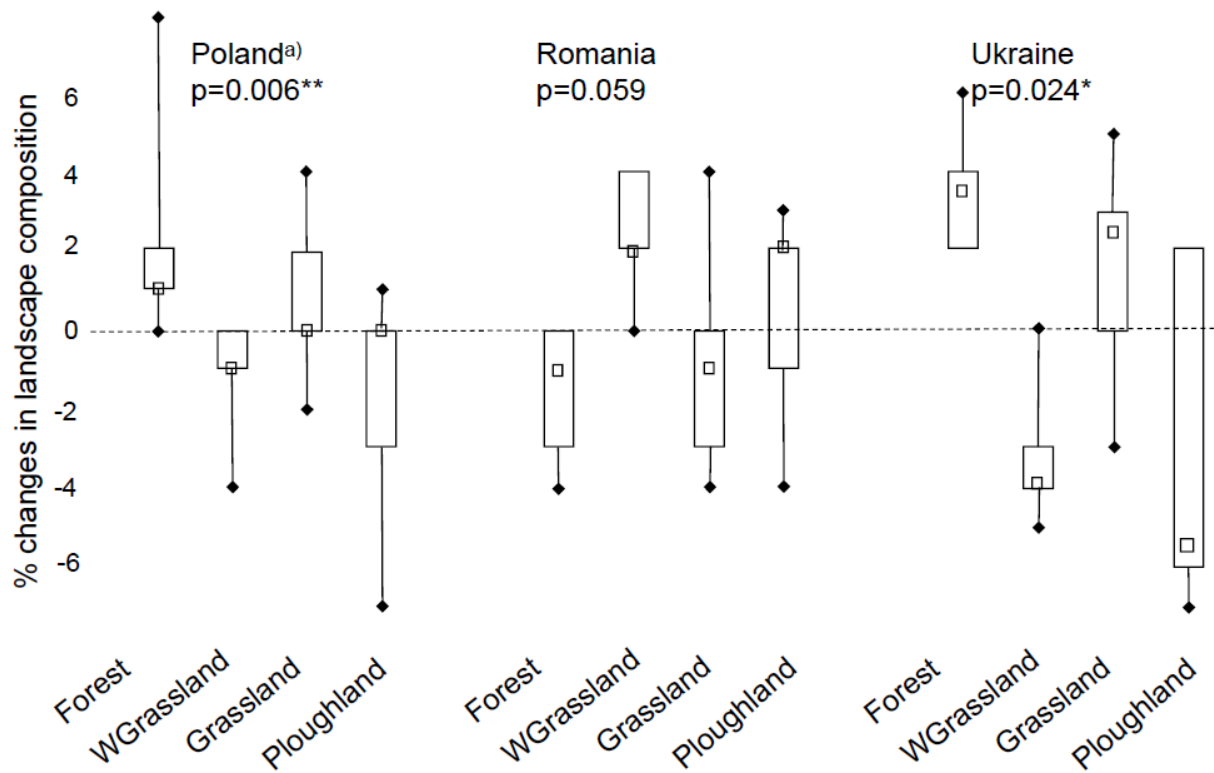
Fig. 6. Changes in % share of four land use categories within oakscape units, which occurred between the 1st and 9th oaks' recruitment percentiles (see Table 1 for details); [a] four entirely forest (no other land use category present between 1790 and 2010) units in Białowieża NP were not included in the analysis; p – significance in the Friedman ANOVA test; WGrassland – wooded grassland; neither buildings nor shrubs were considered due to their very low general share.

Supplementary materials

Table SM1. Characteristics of the cartographic sources used in the study

No	Name	Source	The scale and format
1.	First Military Survey maps of the Habsburg Empire [Josephinische Landesaufnahme] (1763–1787)	The Historical Map Portal www.mapire.eu (accessed 2018.04.17)	Scale 1:28 800, georeferenced
2.	Map of Brześć District, around 1796	Central Archives of Historical Records, Cartographic collection 68-3.	Approximate scale: 1:200 000, scanned (TIF)
3.	Second Military Survey maps of the Habsburg Empire [Franziszeische Landesaufnahme] (1806–1869)	The Historical Map Portal www.mapire.eu (accessed 2018.04.17)	Scale 1:28 800, georeferenced
4.	Map of Białowieża Forest [Plan des Waldes von Bialowesha]	Eichwald 1830	Approximate scale: 1:150 000, scanned (TIF)
5.	Map of Military Geographical Institute [Wojskowy Instytut Geograficzny] 1919-1939, the sheets: P37 S37 Narew P37 S38 Hajnówka P38 S37 Dobrowola P38 S38 Białowieża P50 S35 Dobromil P53 S38 Dolina	Archiwum Map Wojskowego Instytutu Geograficznego 1919-1939, www.mapywig.org (accessed 2018.04.17)	Scale: 1:100 000, scanned (TIF)
6.	Military Survey of Hungary (1941)	The Historical Map Portal www.mapire.eu (accessed 2018.04.17)	Scale1:100 000, georeferenced
7.	Ortho-photo images (2014–2017)	Google Earth Pro (Version 7.3.1.4507): Google Inc. (2018).	georeferenced

Table SM2. Land use structure of four communities according to the 1850's "Ausweis über die Benutzung des Bodens" (the acreage has been re-calculated from the original land register forms deposited in the National Archive in Przemyśl). In grey: such land use categories, which might have fostered oak woods development. Sopotnik - location of PL2,3; Kalwaria / Pacław - PL4,5,9; Sólca - PL8; Kopysno - PL6; grey rows refer to historical land use categories apparently beneficial for oak regeneration, almost absent in the contemporary landscape

Land use		Sopotnik		Kalwaria / Pacław		Sólca		Kopysno	
Category	Subcategory	ha	%	ha	%	ha	%	ha	%
Cultivated area	Crop-field	266.9	5	520.8	8	1514.4	20	984.9	16
	Crop/grass rotation	0	0	520.8	8	0	0	0	0
	Grassland	774.5	16	756.3	11	389.4	5	194	3
Grassland	Grassland with fruit trees	7.4	0	85.9	1	13	0	1378.9	22
	Grassland with timber trees	10.3	0	10.4	0	0	0	574.3	9
	Vege gardens	0.7	0	18.5	0	26	0	0	0
Gardens	Fruit orchards	866.5	18	202	3	11	0	284	5
	Ornamental gardens	0	0	339.8	5	0	0	0	0
	(Wood) pasture	50.5	1	267.7	4	82.2	1	494	8
Pastureland	Pasture with fruit trees	48.7	1	393.1	6	0	0	0	0
	Pasture with timber trees / pollards	268.3	5	0	0	896.2	12	55.1	1
	High deciduous forest	141.9	3	219.8	3	0	0	732	12
	High coniferous forest	709.3	14	0	0	0	0	0	0
Woodland	High mixed forest	362.7	7	825.7	12	1242.2	16	0	0
	Coppice wood	106.6	2	263.6	4	1270.4	17	615.6	10
	Thicket, scrubland	9.4	0	0	0	0	0	0	0
Ponds and swamps with reed vegetation		0	0	55.3	1	0	0	0	0
	Swamps without reed	94.7	2	0	0	0	0	9	0
	Gravel, sand and clay pits	0	0	51.4	1	0	0	372.7	6
Unproductive land	Fallows	245.4	5	455.8	7	186.5	2	0	0
	Bare rock	0	0	0	0	0	0	367.6	6
	Rivers and streams	343.8	7	907.6	14	0	0	0	0
	Paths	378.4	8	51.3	1	1071.3	14	64.5	1
Build-up area		234.2	5	676.1	10	919	12	20.4	0

Fig. SM1. Exemplary digitization of the landscape R=500 m buffer around the centroid of PL5 stand, based on three historic maps and contemporary imagery

Fig. SM2. 'High forest' oaks, forced to allocate their biomass in the fast stem vertical build-up (such as those in the Białowieża National Park, BNP) vs. oaks grown on the verge of the Białowieża forest, where oaks are growing on the ecotone between the floodplain grassland and high forest develop wide crowns with much lower basis; see Tables 1, SM1 for stands sites characteristics

Fig. SM3. Regularly migrating cattle sustains canopy gaps and stimulates oak recruitment - RO6, Transylvania

Fig. SM4. Exemplary open-grown dead oak 'swallowed' by the young stand that encroached on the abandoned field - an alleged parent tree to part of PL2 oaks
(see Tables 1, Table SM1 for PL2 description)

Fig. SM5. Regularly early spring grass burning in young UA5 oak stand (left) may eventually lead to a park-like grove, similar to UA1 (right)