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Open oakwoods facing modern threats: Will they survive the next fifty years?

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ABSTRACT

Open oakwoods are ancient but currently vanishing plant communities of high conservation value. We studied the vegetation of Eurasian steppic oakwoods in the Czech Republic where they are at the westernmost outcrop of their potential distribution to understand ecosystem changes and their drivers in the period of modern environmental change. In 2012, we resampled a set of semi-permanent plots established in 1965. Long-term compositional shifts and biotic homogenization were linked mainly to eutrophication and canopy closure. Ecological groups of nitrophytes and neophytes increased, while assemblages of species characteristic for open woodlands declined. This process can be attributed to several factors including changes in forest management, the rise of the native woody species *Tilia cordata*, airborne nitrogen input to generally nutrient-poor substrates and subsequent increase of invasive plant species, and finally to increased wildboar density. The decline of the unique communities of open steppic oakwoods will likely continue under the current management, increased nitrogen availability and canopy closure. Although reintroducing the wide range of historical forest uses is not realistic, the removal of *Tilia* individuals, reduction of the wild boar population and the promotion of *Quercus* to maintain the open-canopy structure may moderate the shift towards novel communities and help to restore open oakwoods.

1. Introduction

Increasing anthropogenic impact alters the global environment and causes changes in biotic communities at various spatial and temporal scales (Vitousek et al., 1997, McGill et al., 2015). This change is doubtless far from being a simple process. Driving factors are multiple and scale-dependent, and they interact with natural conditions and the legacies of past land-use (Bernhardt-Römermann et al., 2015, Jepsen et al., 2015, Perring et al., 2016). The resulting patterns challenge our ability to grasp the underlying mechanisms and provide accurate guidelines for ecosystem restoration (Perring et al., 2015).

Temperate broadleaf forests, one of the world's main biomes, have been shaped by interactions with humans for millennia. In Europe, forests have been more or less regularly managed since prehistory (Hermy, 2015). Canopy was thinned or clear-cut, woody and non-woody biomass exported; in other words, competition asymmetry by woody species was moderated, enabling the coexistence of a wide range of largely light-demanding species in the herbaceous layer (e.g., Buckley, 1992). The abandonment of traditional management and conversion to high forest systems in the 20th century has led to a historically unprecedented shift towards old-aged, closed-canopy forests (Müllerová et al., 2014). Analogous patterns of open-forest 'densification' and convergence to closed-canopy forests were documented in North American landscapes as well (Amatangelo et al., 2011, Hanberry et al., 2014). The resulting biomass and nutrient accumulation have been further enhanced with airborne nitrogen, entailing a shift towards nutrient-rich, shady conditions. Oligotrophic forest ecosystems in particular are undergoing massive compositional and biodiversity changes due to nitrogen input (Ewald et al., 2013, Verstraeten et al., 2013, Reinecke et al., 2014, Naaf and Kolk, 2016). Due to the shifts in environmental conditions, populations of open woodland specialists shrink and eventually suffer extinction, giving way to nutrient-demanding competitors. Related biotic and functional homogenization of plant communities poses a serious threat to the future existence of open, i.e. thermophilous and light-demanding woodland communities (Hülber et al., 2008, Naaf and Wulf, 2010, Kopecký et al., 2013).

Our study aims to elucidate contemporary biodiversity changes in

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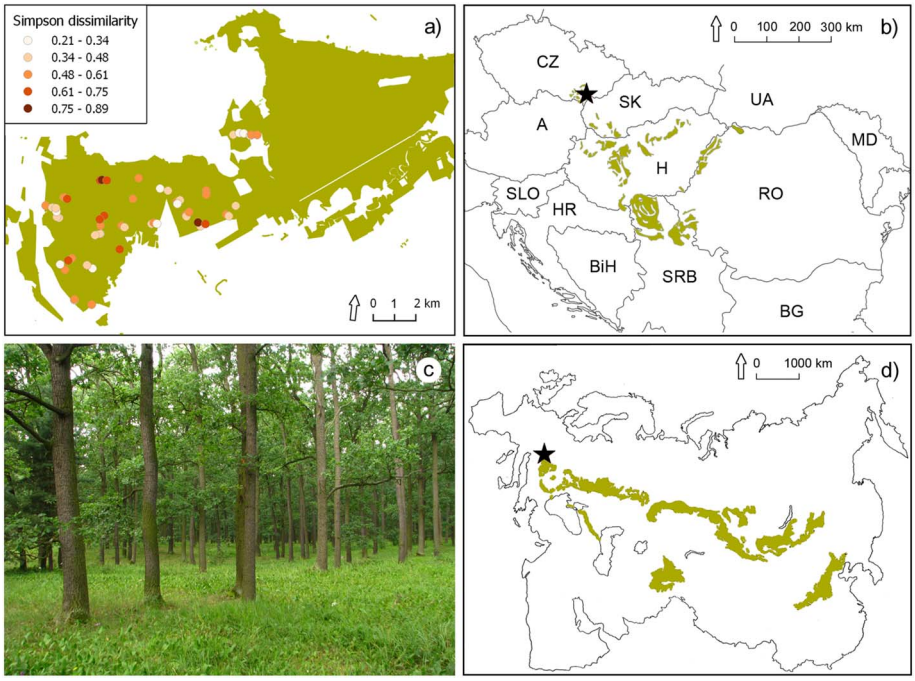

Fig. 1. Open oakwoods at four different scales. Species-rich vegetation of open oakwoods is concentrated in the western part of the Dúbrava Wood, our study site (a, c). 56 plots were resampled between 1965 and 2012 showing compositional change using Simpson dissimilarity index. They form part of the communities of 'Pannonian lowland mixed pedunculate oak forests' whose potential distribution was mapped by Bohn et al., 2000 (b), and in a broader sense, of the Eurasian forest-steppes (d; map adapted from Molnár and Kun, 2000). The study site is at the westernmost outcrop of the distribution range (marked by asterisk).

open oakwoods. These communities are especially threatened because of a lack of oak regeneration. Oaks are being gradually replaced by shade-tolerant species including lime, maple and ash (e.g., Abrams, 2003, Reif and Gärtner, 2007, Nowacki and Abrams, 2008). To better understand contemporary vegetation change in open oakwoods, we chose to study Eurasian steppic oakwoods in the Pannonian Basin (*Aceri tatarici-Quercion* Zólyomi, 1957), where the steppes and open woodlands of Eurasia reach their westernmost potential distribution (Bohn et al., 2000, Molnár and Kun, 2000, Fig. 1). Open steppic oakwoods in Pannonia were intensively researched in the past, and their origins, historical development, natural dynamics and prerequisites of high biodiversity are relatively well-known (e.g. Zólyomi, 1957, Horvat et al., 1974, Hédl et al., 2010, Magyari et al., 2010, Molnár et al., 2012, Jamrichová et al., 2013, Kuneš et al., 2015). Recently, these unique ecosystems experience the full range of what Rackham (2008) called 'modern threats'. Abandonment of traditional forest uses and their replacement with homogenizing timber-oriented forestry, pollution and eutrophication, excessive shade and overabundant ungulates are among the most important threats. Considering on-site management, open steppic oakwoods are subject to conflicting strategies of commercial forestry and nature conservation. Molnár et al. (2012) argued that these woodland ecosystems would disappear from Hungary in the upcoming decades.

Owing to their biotic values, steppic oakwoods are listed as a priority habitat under the European Union Habitats Directive, 91I0 'Euro-Siberian steppic woods with *Quercus* spp.' (Molnár and Kun, 2000, European Commission, 2013). It is therefore of the highest importance for EU conservation policy to understand long-term processes and their drivers in this priority habitat (Molnár et al., 2012). Despite this, long-term studies dealing with anthropogenic changes in forest vegetation at the continental level originated from relatively species-poor mesic forest types, while species-rich thermophilous forests in subcontinental climates remain undersampled (e.g., Verheyen et al., 2012, Bernhardt-Römermann et al., 2015). Our study is one of the few existing quantifications (cf. Molnár et al., 2012) of long-term environmental changes within the vast territory of open steppic oakwoods (Fig. 1).

In this paper, we resurveyed a set of quasi-permanent plots established five decades ago in Dúbrava Wood, one of the largest and best preserved steppic oakwoods in Central Europe. We used an approach increasingly applied in studies of long-term ecosystem dynamics, the resampling of not exactly located historical vegetation plots (Kapfer et al., 2017, Verheyen et al., 2017). We examined temporal shifts in plant community heterogeneity, changes in composition of species assemblages, and changes in dominance of selected species groups. Increase in small-leaved lime (*Tilia cordata* Mill.) was the most pronounced change in tree species observed during the resampling of plots. We therefore regarded it as one of the potential explanations for the observed changes in the herbaceous understory. Our ultimate goal was to assess our findings in the light of long-term management changes and the increase of small-leaved lime. We aim to test hypotheses assuming: 1. a shift to shadier, more nutrient-rich conditions, 2. a relative loss of species typical for open oakwoods and a reciprocal gain of nitrophilous, possibly newly arriving species, and 3. resulting taxonomic homogenization.

2. Materials and methods

2.1. Study site: nature, history and conservation

The research was carried out at the westernmost point of the range of the Eurasian steppic oakwoods, in one of the largest extant open oakwood in the Pannonian Basin. Dúbrava Wood is a compact forest over 20 km across. Coordinates are 48.8864° N, 17.1220° E (WGS 84), elevation ranges between 170 and 215 m above sea level. Species-rich vegetation of open-canopy oakwoods is concentrated in its western part (Fig. 1). Plant communities are ranked within the alliance *Aceri tatarici-Quercion*, distributed in eastern-central Europe (Horvat et al., 1974). Climate is temperate, with warm summers and no dry season (Köppen classification Cfb); the mean annual temperature is about 10 °C and the mean annual precipitation about 500 mm (http://www.chmi.cz). The forested area covers wind-blown sandy deposits, moderately acidic and