Acta Oecologica 85 (2017) 1–8

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Trade-off between light availability and soil fertility determine refugial conditions for the relict light-demanding species in lowland forests

Marcin Kiedrzyński [a, *], Józef Krzysztof Kurowski [a], Edyta Kiedrzyńska [b, c]

[a] Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Łódź, ul Banacha 12/16, 90-237 Łódź, Poland
[b] European Regional Centre for Ecohydrology of the Polish Academy of Sciences, ul Tylna 3, 90-364 Łódź, Poland
[c] Department of Applied Ecology, Faculty of Biology and Environmental Protection, University of Łódź, ul. Banacha 12/16, 90-237 Łódź, Poland

ARTICLE INFO

Article history:
Received 27 February 2017
Received in revised form
5 September 2017
Accepted 5 September 2017

Keywords:
Habitat suitability
Habitat factors interaction
Relict populations
Continental species

ABSTRACT

Identifying potential refugial habitats in the face of rapid environmental change is a challenge faced by scientists and nature conservation managers. Relict populations and refugial habitats are the model objects in those studies. Based on the example of *Actaea europaea* from Central Poland, we analyse the habitat factors influencing relict populations of continental, light-demanding species in lowland forests and examine which habitats of studied species corresponding most closely to ancient vegetation. Our results indicate that the current refugial habitats of *Actaea europaea* include not only communities which are very similar to ancient open forest but also forests with a closed canopy. Although the populations are influenced by nitrogen and light availability, the co-occurrence of these two factors in forest communities is limited by dense canopy formation by hornbeam and beech trees on fertile soils and in more humid conditions. Our findings indicate that the future survival of relict, light-demanding communities in lowland forests requires low-intensity disturbances to be performed in tree-stands, according to techniques, which imitate traditional forests management.

1. Introduction

The identification of places or habitats suitable for biodiversity protection during rapid environmental change is a challenge faced by scientists and nature conservation managers (Ashcroft, 2010; Keppel et al., 2012). One such area of scientific importance whose significance has greatly increased over recent decades is that of refugial sites: habitats which could harbour populations in the region under unsuitable environmental conditions (Keppel et al., 2015; Kiedrzyński et al., 2017). In the light of current climate change, relicts and communities associated with them are unique natural laboratories and model systems for observation (Hampe and Jump, 2011; Woolbright et al., 2014).

It is well known that topographical complexity generates more possibilities for the formation of numerous *in situ* refugial habitats under climate change (Keppel et al., 2012), while plain areas tend to encourage shifts in species range to follow suitable conditions (Moritz and Agudo, 2013). While a species exposed to climate change may survive in a rugged landscape with significantly varied abiotic conditions, biotic interactions mostly drive the formation of refugial habitats for populations in plain landscapes, especially in lowland areas (Hampe and Jump, 2011). Examples of habitats for relict populations of mountain plants in the European lowland areas have been given previously (Grzyl et al., 2014; Kiedrzyński et al., 2015; Zielińska et al., 2016). The aim of the present paper is to analyse the conditions which drive the existence of continental light-demanding plant in the area of the closed-canopy forests – zonal vegetation in the Central European lowlands.

One of the patterns described for the glacial/interglacial cycles is species migration along the oceanic-continental gradient (Stewart et al. 2010). 'Oceanic' adaptation implies a more humid, less seasonably variable climate, and 'continental' adaptation a drier climate with greater seasonal variation (Ellenberg, 1988). In Central Europe, such long-term vegetation dynamics along the oceanic-continental gradient are mostly in a longitudinal direction (Stewart et al. 2010). During glacial periods, continental species from the Eastern Europe have been widely dispersed to the west, according to the distribution of the steppe-like vegetation or hemi-

* Corresponding author.
E-mail address: marcin.kiedrzynski@biol.uni.lodz.pl (M. Kiedrzyński).

http://dx.doi.org/10.1016/j.actao.2017.09.004
1146-609X/

boreal forests (van Andel and Tzedakis, 1996; Birks and Willis, 2008). During interglacial periods, including the Holocene, continental light-demanding species have been in decline in Central Europe, when the transition from late-glacial cold steppe and open woodlands to the mixed and closed forests occurred (Puhe and Ulrich, 2001; Chytrý et al., 2010). As a result, some continental species already exist only as isolated populations in the region, and their relict status has been revealed recently by phylogeographic studies (Stewart et al. 2010; Kajtoch et al. 2016 and cited literature). Moreover, future patterns associated with climate change in Central Europe provide an eastward shift of conditions suitable for oceanic plants (Theurillat and Guisan, 2001; Bakkenes et al., 2002; Skov and Svenning, 2004; Thuiller et al., 2005). Hence, this projected future trends follow the long-term west-east shifts of species associated with the previous glacial and interglacial climate oscillations in the region (Stewart et al., 2010).

Of the continental plants, strictly steppic species are currently found in Central Europe mostly in extrazonal xeric grasslands, and many aspects concerning their ecology, phylogeography and conservation have been studied (Kajtoch et al., 2016). Less is known of the light-demanding continental species which exist mainly in forest or shrub communities. They are regarded today as climate relicts of late-glacial open woods (Ellenberg, 1988), and maybe more importantly, as biotic relicts which have lost their sites as a result of the Holocene expansion of mesophilic trees (Ralska-Jasiewiczowa et al., 2003). Subsequent invasions by elm, maple, lime, hornbeam and beech since the mid-Holocene reduced light availability below the canopy, resulting in a dramatic decline in the numbers of light-demanding species from forest communities (Chytrý et al., 2010). Some continental species, adapted to existence in nutrient-poor soils (e.g. *Pulsatilla patens, Arenaria graminifolia*), could benefit from the relatively higher light availability in that habitats, structured by coniferous or mixed stands. In fertile habitats, the shading pressure from broadleaved trees is stronger, and the balance between soil fertility and light availability drives the existence of light-demanding plants. They forced then to occur in sub-optimal habitats and play the “habitat trade-off game”: they are forced to continually choose between light availability and other habitat resources needed for their effective growth and reproduction. Such species include for example *Adenophora liliifolia* and *Lathyrus pisiformis*: indicators of thermophilous forest hotspots which are currently disappearing from the region (Kiedrzyński and Jakubowska-Gabara, 2014). Our study examines the pattern described above, using the example of another subcontinental plant, *Actaea europaea* (Schipcz.) J. Compton (Ranununculaceae), a survivor of early-Holocene open forest (Roleček, 2007) which grows on rather fertile soils.

Actaea europaea is the only taxon in Europe from the section *Cimicifuga* (Compton and Hedderson, 1997), and is closely related to *A. cimicifuga* from Siberia, despite being separated by a distance of 4000 km. This disjunction is probably a result of the Pleistocene extinction of the ancestor of *A. europaea* (Compton et al., 1998), implying that its current range could be recognized as a relict distribution on a broad Euro-Asiatic scale. In addition, the European-scale relict character is indicated by its current diffuse distribution (Fig. 1a). Hence, considering the historic and biogeographic aspects, the species is recognized as a relict in Central Europe. The predicted distribution of suitable conditions for *A. europaea* suggest that within the next few decades, the suitable climatic conditions of the species will shift north-east with climate change (Skov and Svenning, 2004). Unfortunately, with the long-term restriction of suitable habitats for continental species observed since the mid-Holocene and the projected unfavourable perspectives in Central Europe, the future of *A. europaea* in the region is rather pessimistic.

Populations of *A. europaea* on the western border of the temperate continental bioclimate in plain landscape of Central Poland were chosen for this study (Fig. 1a), as such border localities in lowlands are under particular threat from projected climate change. In the study area, *A. europaea* have been noted in various forest habitats on mesic and eutrophic soils (Kiedrzyński and Andrzejewski, 2012). Surviving populations can be found in open oak forests, but also in hornbeam and beech stands, which are rather closed by their nature. To determine which factors play a crucial role in the actual well-being of populations, our study goes on to examine various aspects of the current habitats of *A. europaea,* including soil parameters and community compositions.

It could be hypothesized that none of the current habitats of *A. europaea* in Central Poland exactly recreate the ancient conditions of the species. However, our analysis also examines which current habitat of *A. europaea* corresponds most closely to the ancient habitats suitable for a light-demanding continental species. Hence, the forest communities with *A. europaea* from Central Poland have been compared to southern Ural forest communities, which are regarded as being analogous to early- and mid-Holocene Central European forest communities (Chytrý et al., 2010). Modern analogues of ancient Central European forests occur in the region which are currently outside the geographical ranges of beech and hornbeam and where the current continental climate resembles the early Holocene climate of Central Europe (Davis et al., 2003). The analysis includes open woodlands of coniferous and small-leaved deciduous trees, which are considered as analogues to early-Holocene vegetation, as well as broad-leaved deciduous forests and closed-canopy forests, which are analogues to mid-Holocene vegetation in Central Europe (Willis and van Andel, 2004; Birks and Willis, 2008). Our analysis, therefore, allows the refugial habitats of *A. europaea* in Central Poland to be compared with habitats equivalent to the temporal sequence of the post-glacial habitats.

The main aims of the study were:

1) to detect the basic habitat parameters influencing the current populations of subcontinental species *A. europaea* in Central Poland;
2) to analyse possible opposed interactions between environmental parameters in the current lowland refugial habitats of *A. europaea*;
3) to indicate the similarity of the present plant communities with *A. europaea* with potential late-glacial vegetation by analogy with the southern Ural forests.

2. Materials and methods

2.1. Study area

The study area includes the central part of the Polish section of the western border of the geographical range of *A. europaea* in Europe (Fig. 1a). The average annual temperature in the region ranges from 7.4 to 7.8 °C and the average annual precipitation from 565 to 625 mm (data from period 1982–2012, Climate-Data.org, 2016). The main geological units on the surface are Pleistocene clays, sands and gravels from the Odranian and the Wartanian glaciations (corresponding to the Saale glaciation; 300 to 130 Kya) (Marks et al., 2006). However, Mesozoic rocks (limestones, sandstones) have a visible share in the southern and the south-eastern parts of the region (Marks et al., 2006).

The populations of *Actaea europaea* are thought to be disappearing from the region, and the species was included to the regional red book (Kiedrzyński and Andrzejewski, 2012), with only