Agriculture, Ecosystems and Environment 182 (2014) 137–143

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Weak evidence of long-term extinction debt in Pannonian dry sand grasslands☆

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ARTICLE INFO

Article history:
Received 2 January 2013
Received in revised form 19 July 2013
Accepted 22 July 2013
Available online 24 August 2013

Keywords:
Calcareous sand
Primary grassland
Land use change
Historical map
Habitat continuity

ABSTRACT

Habitat loss is one of the major drivers of the reduction in biological diversity worldwide. European dry grasslands are particularly endangered. However, the persistence of populations can temporarily mitigate species loss – a process referred to as 'extinction debt'. We test this hypothesis using historical and present day habitat maps and current plant biodiversity data collected in the forest-steppe zone of Europe. In 16 5 km × 5 km study sites, representing the landscape heterogeneity of the Kiskunság region (Hungary), 86 20 m × 20 m vegetation plots were surveyed in open and closed calcareous sand grasslands. Grassland diversity was measured as the number of specialist species, defined by statistical fidelity measures using primary and secondary grassland plots. Landscape context was quantified using the areal extent of semi-natural forest-steppe vegetation in a 300 m neighborhood of the plots, based on recent and historical maps (1783, 1860, 1950s, 1987–1989 and 2005). The number of specialist species was estimated with Poisson generalized linear models using the present landscape context, climatic conditions, and a proxy of soil type as covariates. To test for the effect of historical legacies, Pearson residuals from the present models were tested for significant relationships between the residuals and the historical landscape contexts using linear models.

We found that the present landscape context had no significant relationship with the specialist species richness of the primary grassland fragments. However, we found a significant relationship between the historical landscape context of the 19th century and the residuals of the present model. Even though the extent of natural vegetation in the 20th century showed more drastic changes, the landscape context in 1950s and 1987–1989 exhibited no significant statistical relationship with the residuals. This delay of species loss is consistent with the extinction debt hypothesis.

1. Introduction

Loss and fragmentation of natural and semi-natural habitats are among the main reasons for the erosion of biological diversity experienced worldwide (Foley et al., 2005). In Europe, dry grasslands are particularly endangered by habitat loss and fragmentation; therefore, they are a major focus of nature conservation. Large areas of dry grasslands were ploughed prior to the 20th century (Drobnik et al., 2011; Török et al., 2011; Molnár et al., 2012), and the loss of dry grasslands continues to the present day due to afforestation and urbanization. The residual fragments are often degraded by inappropriate management (e.g. over- or undergrazing, lack of mowing). However, these remnants maintain significant plant biodiversity (Ruprecht et al., 2009; Wilson et al., 2012). Long term habitat continuity of semi-natural grasslands increases the proportion of grazing-dependent and/or moving-dependent species without significantly changing total species richness (Johansson et al., 2008).

Habitat loss and fragmentation result in a decline of species diversity due to both increased extinction risk and reduced colonization rate (Cristofoli et al., 2010; Cousins and Vanhoenacker, 2011). Species diversity reduction can happen immediately following habitat destruction but usually occurs after a species specific time lag or 'relaxation time' (Diamond, 1972). The number of species extinctions expected to occur in the future is termed 'extinction debt' (Tilman et al., 1994), which is offset when the community reaches its new equilibrium species diversity corresponding to the altered landscape configuration (Jackson and Sax, 2010). Revealing the magnitude and time scale of this delay is

☆ Nomenclature: Simon (2000) for vascular plants.

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http://dx.doi.org/10.1016/j.agee.2013.07.016

important to estimate the conservation potential of a given habitat (Kuussaari et al., 2009).

Although extinction debt may be common in many natural communities worldwide (Kuussaari et al., 2009), our knowledge on the occurrence and magnitude of this phenomenon across ecosystems and taxa is highly incomplete (Krauss et al., 2010). Several studies found evidence of plant species extinction debt in semi-natural grasslands in north-western Europe (Lindborg and Eriksson, 2004; Helm et al., 2006; Piessens and Hermy, 2006; Ellis and Coppins, 2007; Cousins, 2009; Cousins and Vanhoenacker, 2011). Other studies did not detect the presence of extinction debt (Adriaens et al., 2006; Cousins et al., 2007).

However, knowledge of the presence of extinction debt in grasslands of the Central and Eastern European forest steppe zone is lacking, and there is a clear need for more studies from different parts of the world (Cousins, 2009; Kuussaari et al., 2009).

Plant species differ significantly in their likelihood of showing an extinction debt (Vellend et al., 2006; Kuussaari et al., 2009; Piqueray et al., 2011a). When populations come close to their extinction threshold, time delay to their extinction can last for particularly long periods (Kareiva and Wennegren, 1995; Hanski and Ovaskainen, 2002). Relaxation time can be long in cases of long-lived species (Helm et al., 2006), species with persistent seed bank (Piessens and Hermy, 2006; Cristofoli et al., 2010), species showing long-distance dispersal potential by wind and animals (Purschke et al., 2012), and species able to spread clonally (Purschke et al., 2012). Species with a high degree of habitat specialization are expected to exhibit greater sensitivity to habitat changes than generalist species (Kuussaari et al., 2009); therefore, they are expected to have a smaller extinction debt than generalists (Cousins and Vanhoenacker, 2011). Despite this trend, several studies demonstrated extinction debt of habitat specialists (Ellis and Coppins, 2007; Cristofoli et al., 2010; Cousins and Vanhoenacker, 2011). As the effects of habitat change can be masked with the arrival of new species, the number of habitat specialists can be a better indicator of extinction debt than total species richness (Kuussaari et al., 2009). In the study by Helm et al. (2006), habitat specialists showed an extinction debt in Estonian alvar grasslands after 70 years, while past landscape structure did not have any significant effect on total species richness.

Kuussaari et al. (2009) describes several approaches to evaluate extinction debt. As long-term data on species occurrences are rarely available, most studies assess extinction debt by comparing current species richness in currently stable and unstable fragmented landscapes (Hanski and Ovaskainen, 2002; Helm et al., 2006; Piqueray et al., 2011a, 2011b) or by assessing if current species richness can be better interpreted by past rather than present landscape variables (Adriaens et al., 2006; Ellis and Coppins, 2007; Sang et al., 2010).

Piqueray et al. (2011a) compared these two methods in calcareous grasslands in Belgium and found that the two methods resulted in the same conclusions. As the determination of stable and unstable fragmented landscapes is rather arbitrary, we use the second approach in our study.

We used historical and present day habitat maps and current plant biodiversity data collected in the European forest-steppe zone to examine the effect of the past and present surrounding landscape on the species richness of primary sandy grasslands.

In this paper, we address the following questions:

1. What is the magnitude of natural habitat loss in the surroundings of the Pannonian primary sand grasslands?
2. Is the number of specialists in primary grasslands related to either the current or historical extent of adjacent semi-natural forest steppe habitats?
3. Can extinction debt be observed in the vascular flora of primary sand grasslands in the European forest steppe zone?

2. Materials and methods

2.1. Study area

Our study area, the Kiskunság, is an inland sand dune area in the center of the Pannonian biogeographic region with an extent of 7500 km^2. The climate of the region is continental with sub-mediterranean influence. The mean annual temperature is 10 °C with monthly means ranging from −1 °C in January to 22 °C in July. Mean annual precipitation is 500–550 mm, with a peak in June, and a second, minor peak in November with a gradual decrease from North to South and from West to East (Borhidi, 1993; Kovács-Láng et al., 2000). The dominant substrate is calcareous sand, on which various sand soil types developed with high sand (over 90%) and low humus content (below 3%) (AGROTOPO, 1994; Csecserits et al., 2011). The elevation is between 110 and 160 m a.s.l. in the entire region. The natural vegetation mosaic consists of sand forest steppe with wetlands in lower elevation areas (Zólyomi, 1974). The major components of the forest-steppe complex have continuously persisted in a significant extent during the Holocene (Zólyomi and Fekete, 1994; Fekete et al., 2010; Magyari et al., 2010). Most of the endemic plant species in the region are dry grassland specialists (e.g. *Festuca vaginata, Festuca × wagneri, Colchicum arenarium, Dianthus diutinus, Dianthus serotinus, Iris arenaria*), which is also indirect evidence for the long-term persistence of dry grasslands in the region (Zólyomi and Fekete, 1994; Magyari et al., 2010). The species pool of sand forest steppe gets impoverished by loosing several elements of Central-European grasslands with decreasing precipitation eastwards and southwards in the Kiskunság region (Kovács-Láng et al., 2000; Fekete et al., 2010).

At present, this region is dominated by agricultural fields, including both annual and perennial crops, as well as vast timber plantations consisting of native and non-native tree species. Nevertheless, the remnants of sand forest steppe vegetation also constitute a substantial component of the present land cover. Sand forest steppe vegetation is a fine scale mosaic of dry and semi-dry grasslands, *Juniperus communis-Populus alba* shrublands and open steppic *Quercus robur-Quercus pubescens* forests with small extents of closed *Quercus robur* and *Populus × canescens* forests at the lowest elevations. The ratio of grasslands to woodlands varies with the climatic gradient (Kovács-Láng et al., 2000). This ratio has also changed over centuries because of drastic alterations in land use and fire regime. Most of the grassland specialist plant species can also colonize and survive in the forested parts of the landscape, which means that the whole landscape is permeable for these species. According to archive maps, most of the grasslands were never ploughed. Hereafter, we refer to this never ploughed grassland components of the natural forest steppe vegetation complex as ‘primary grasslands’.

Until the 18th century, extensive grazing was the dominant land-use in the region. In the 19th century, a significant increase in human population and agricultural activities led to fragmentation of semi-natural vegetation. The maximum of agricultural activity in the region occurred after the Second World War in the 1950s. This was followed by a process of land abandonment due to socio-economic changes, as well as a significant decrease in the groundwater table (Biró, 2003; Biró et al., 2008; Molnár et al., 2012). Former studies have found that the dry grassland vegetation of this region has a relatively good regeneration potential on abandoned agricultural fields (Csecserits & Rédei, 2001; Csecserits et al., 2011). Henceforth, we refer to the regenerating grasslands of former agricultural areas as ‘secondary grasslands’. Land abandonment, which