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The contribution of successional grasslands to the conservation of semi-natural grasslands species – A landscape perspective

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ABSTRACT

Many species that are typical of calcareous, semi-natural grasslands ("typical grassland species") are declining in Europe as a result of habitat-loss and -fragmentation. Whereas populations of these species are expected to be largest in old semi-natural grasslands, these species may also occur in successional grasslands on previously arable fields. We used a space-for-time approach to analyse changes in the frequencies of typical grassland species, and changes in soil properties, over a 280-year arable-to-grassland succession within a Swedish landscape. Our study revealed that a number of typical grassland species had higher frequencies in mid-successional (50–279 years) than in old (≥280 years) grasslands. Mid-successional grasslands also contained many of the typical grassland species that were present in old grasslands, but at lower frequencies, and had soil conditions similar to those of old grasslands. Early-successional (5–14 and 15–49 years) grasslands contained few typical grassland species. In highly fragmented landscapes, mid-successional grasslands provide additional habitat for many typical grassland species, and can function as temporary refugia ("substitute habitat") for these species until old grasslands are "restored". The overall population sizes of some typical grassland species and red-listed species are likely to be substantially increased by the presence of mid-successional grasslands within the landscape. Our study suggests that, rather than focussing solely on old grassland fragments, conservation strategies for typical grassland species should adopt a dynamic, landscape-based perspective that recognizes the role of successional grasslands. Ensuring a continuous development of mid-successional grasslands is expected to be beneficial for populations of many typical grassland species.

1. Introduction

In Europe, the area of semi-natural grassland has declined strongly over the last two centuries (Johansson et al., 2008; Bullock et al., 2011), and this type of habitat is now the focus of many conservation initiatives at both national and European levels (e.g. Council Directive 92/43/EEC, 1992; Naturvårdsverket, 2011). Semi-natural grasslands are defined as grasslands that have not been "improved" by fertilization, ploughing or reseeding (Bullock et al., 2011). Grazed semi-natural grasslands on neutral to base-rich soils contain species that are adapted to nutrient-poor conditions, as well as to disturbance such as grazing, trampling and mowing (Bernes, 2011) and are often characterised by high levels of fine-scale species richness (van der Maarel & Sykes, 1993; Reitalu et al., 2008). The present-day species composition of semi-natural grasslands is influenced by past and present levels of connectivity between habitat fragments (which determine the ability of species to disperse within a landscape), edaphic conditions and management regimes (Bullock et al., 2011; Poschlod, 2015). Semi-natural grasslands usually have an anthropogenic origin and may develop under long-term grazing management on previously arable sites (Poschlod & Wallis de Vries, 2002; Poschlod, 2015).

The process of succession, after disturbance, involves changes in species-composition, the frequencies of individual species and the overall community structure (McCook, 1994). The development of semi-natural grasslands on previously arable fields represents a special case of succession, in which continuous grazing management "truncates" the succession and prevents the development of woody vegetation (cf. Young et al., 2001). Recent studies of long-term grassland succession on previously arable fields have investigated changes in species richness, plant traits and beta diversity (e.g. Purschke et al., 2013), as well as the effects of management and edaphic factors on the course of succession (e.g. Prach et al., 2014). During the progress of arable-to-grassland succession, the number of "typical grassland species" (species characteristic of old semi-natural grasslands with long continuity of grazing management) is generally expected to increase with grassland

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age, and typical grassland species are also expected to have their highest frequencies in late successional plant communities (e.g. Redhead et al., 2014). However, a number of studies reveal that some typical grassland species may, in fact, have their highest frequency in younger grasslands on previously arable fields (e.g. Prentice et al., 2007), suggesting that successional grasslands may make an important contribution to the overall population sizes of these species within landscapes. If this is the case, the younger grasslands may play a valuable role in the maintenance of intraspecific genetic diversity within typical grassland species, by helping to buffer populations against the negative genetic and demographic consequences of habitat fragmentation and isolation (cf. Ellstrand & Elam, 1993; Oostermeijer et al., 2003).

In many cultural landscapes, efforts to limit future losses of typical grassland species will require not only long-term initiatives to create or restore additional areas of semi-natural grassland, but also the enhancement of connectivity between existing grassland fragments (e.g. Butaye et al., 2005; Bullock et al., 2011). However, the restoration of semi-natural grasslands on abandoned arable fields is a slow process (Walker et al., 2004; Fagan et al., 2008), and "substitute habitat" for lost grasslands, within which typical grassland species may find a temporary refuge until older grasslands can be re-created within the landscape (cf. Wrzesień, 2009; Leppik et al., 2013), may be required. Grasslands on previously arable fields in succession to semi-natural grassland (hereafter "successional grasslands") may already represent a suitable habitat for typical grassland species (Gibson & Brown, 1991), and may therefore function as substitute habitat for lost grasslands.

In the present study, we used a space-for-time approach to analyse changes in species frequencies and soil properties during a long-term (≥280 years) succession from arable fields to grazed semi-natural grasslands. The study was carried out in a landscape consisting of a mosaic of arable fields, grasslands and forests, on the Baltic island of Öland, Sweden (see Johansson et al., 2008). The land-use in the study area is still dynamic: the practice of leaving some arable fields fallow and grazed results in the continuous creation of successional grasslands which may both provide temporary substitute habitat for lost grasslands and increase the connectivity between grassland fragments. We used indicator species analyses and ordinations to analyse frequency data on grassland species, with the aim of: a) identifying typical grassland species which have their highest frequency in transient, successional grasslands and whose populations will be likely to benefit if successional grasslands and land-use dynamics are considered within grassland conservation schemes and b) identifying successional grasslands which already contain typical grassland species and, therefore, have the potential to function as temporary substitute habitat within the landscape until older grasslands can develop.

2. Material and methods

Further details of the methods are provided in Appendix A.

2.1. Study area

The 22.5 km^2 study area (centred on 56°40′49″ N and 16°33′58″ E) on the Baltic island of Öland, Sweden consists of a small-scale mosaic of arable fields, grasslands and forests. The limestone bedrock is covered by coarse glaciofluvial sediments which form a few low ridges on the otherwise flat landscape. The climate is dry, with high summer insolation, a July mean temperature of 17 °C, and a mean annual precipitation of ca. 475 mm (Forslund, 2001).

Within the study area, agricultural intensification has led to the progressive fragmentation of the grazed, semi-natural grasslands over the last 300 years. Semi-natural grasslands covered 80% of the study area in the early 1800s – compared with 5% at the present day (Johansson et al., 2008). The present-day grazing system is still extensive and, within much of the area, cattle and sheep can move freely between grassland fragments belonging to different stages of the arable-to-grassland succession – ensuring seed dispersal between grassland fragments.

2.2. The four time-steps

We used a space-for-time-approach to analyse the long-term, truncated succession (≥280 years) from arable fields to old semi-natural grasslands, and constructed a chronosequence based on grasslands of different ages within the landscape (cf. Walker et al., 2010). Despite its limitations (Pickett, 1988; Johnson & Miyanishi, 2008), a space-for-time approach is the only approach that can be used to investigate long-term successional gradients in the absence of historical vegetation surveys (cf. Walker et al., 2010). We followed the improved space-for-time approach of Molnár & Botta-Dukát (1998), and minimized differences in abiotic and land-use history conditions by using a sampling design that included only grazed grasslands on dry, neutral-to-basic sites. A GIS overlay was carried out using land-use maps from 1730, 1959, 1994 (Johansson et al., 2008) and 2005, to create land-use history polygons (defined by the temporal sequence of land-use) for grasslands within the study area. The land-use history polygons were then classified into four time-steps on the basis of the most recent transition from arable cultivation to grassland. The first three time-steps, t_5, t_15 and t_50, represent successional grasslands on former arable fields that were abandoned 5–14 years, 15–49 years and 50–279 years, respectively (relative to 2010). The first two time-steps (t_5 and t_15) represent early-successional grasslands, whereas the third time-step (t_50) represents mid-successional grasslands within the truncated succession. The fourth time-step, t_280, represents old semi-natural grasslands that have been under continuous grazing management for at least 280 years, and which represent the final stage of the truncated succession. The time-classified, dry grasslands included in the study represented approximately 11% of the study area. The t_5, t_15, t_50 and t_280 grasslands represented, respectively, 4.2%, 3.3%, 0.4% and 3.1% of the study area and 38%, 30%, 4% and 28% of the time-classified, dry grassland area.

A stepwise procedure was used to select 220 sampling areas ("grassland units") within the land-use history polygons. Because an earlier study within the same landscape (Reitalu et al., 2008) showed that patterns of species co-occurrence differed between different scales and because these patterns are already evident at a fine (decimetre) scale, we chose to include two plot scales – to allow for the possibility that landscape-scale patterns of species occurrences and frequencies in the successional grasslands might depend on the plot-level sampling scale. One small (0.4 m × 0.4 m) plot was positioned in each selected grassland unit. Large (2 m × 2 m) plots were positioned in 160 of the grassland units (details in Appendix A.1). All the grassland units were grazed, or showed signs of recent grazing, at the time of sampling.

2.3. Vegetation and soil sampling

Within each small plot, we collected frequency data for all vascular plant species. Within each large plot, frequency data were collected for the 40 most frequent species within the small plot dataset (Appendix A.1).

A soil sample (consisting of three pooled subsamples) was taken from the upper 7.5 cm within each small plot. The soil samples were stored at −20 °C before being analysed for organic carbon content (org_C) by loss-on-ignition (at 600 °C), phosphorus (Bray_P, Bray 1 method (Fransson et al., 2003)), ammonium (amm) and nitrate (nitrate) using barium chloride extraction, and pH measured in water (pH). The soil variables were used to characterise the underlying abiotic (edaphic) environment within each of the time-steps.

2.4. Typical grassland species and red-listed species

Typical grassland species were defined as species that are characteristic of "dry pastures" or "dry pastures and meadows" (Ekstam & Forshed,