



## Temporal dispersal in fragmented landscapes



Jan Plue\*, Sara A.O. Cousins

Department of Physical Geography and Quaternary Geology, Stockholm University, 106 91 Stockholm, Sweden

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### ABSTRACT

Despite a good understanding on how dispersal in space structures plant communities in fragmented landscapes, we know little about dispersal in time. Empirical evidence on temporal dispersal – the soil seed bank – is lacking, with only trait-based evidence on the seed banks' importance for species persistence in fragmented landscapes. Therefore, seed banks of remnant grassland fragments were analyzed in how they changed compared to semi-natural grasslands following fragmentation. We studied the historical trajectories in time since fragmentation, fragment size and habitat quality of 134 grassland plots, linking these to their seed bank and plant community to understand how seed banks temporally connect grassland fragments, potentially conserving the flora of historically large semi-natural grasslands. Seed-banking grassland species were present in similar proportions in all remnant grassland fragments. The seed bank composition changed with time since fragmentation started, triggered by the deterministic loss of grassland species, generating nested subsets of the seed banks of semi-natural grasslands. The spatial heterogeneity in seed bank composition among grassland fragments limited the loss of grassland species at the landscape scale. The seed bank became an increasingly important constituent of total plant diversity with time since fragmentation started, as grassland species stored an increasingly larger proportion of their local diversity in the seed bank. Temporal dispersal enables the prolonged presence and persistence of numerous typical grassland species in fragmented landscapes. The seed banks' storage effect of plant diversity is of considerable significance to efforts aimed at conserving and restoring plant diversity in fragmented landscapes.

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### 1. Introduction

In stable grassland communities, seed banks are an effective feedback and feedforward mechanism to established plant communities. Seedling recruitment from persistent seeds in grasslands has been acknowledged to sustain both population fitness and persistence (feedback; Kalamees and Zobel, 2002), while the seed banks' rescue effect assures local species' persistence as seed-banking enables plant species to re-establish in the vegetation after becoming locally extinct (feedforward; Piessens et al., 2004). Seed-banking thus grants plant species an effective means of temporal dispersal in spatiotemporally variable grassland communities (Seabloom et al., 2005). By storing plant diversity, seed banks enhance species coexistence (Facelli et al., 2005) and buffer against local extinction events (Kalamees et al., 2012). Moreover, its strong small-scale and patchy character in grasslands (Plue and Hermy, 2012) steers early re-colonization after small herbaceous gap-disturbances (Kalamees and Zobel, 2002; Vandvik and Goldberg, 2006) through the availability of seeds altering a plants'

probability to establish at a given location. Hence, the seed bank exerts significant functional control over plant populations and community processes of stable grassland communities, both in space and time.

Large semi-natural grasslands are increasingly rare in North and Western Europe, with a dramatic surface area decline over the last century: e.g. 90% in Sweden (Cousins and Eriksson, 2008), 85% in Estonia (Pärtel et al., 1999) or 97% in England and Wales (Fuller, 1987). Nowadays, this severe habitat fragmentation of Swedish semi-natural grasslands has resulted in few medium-sized and many small remnant grassland habitats embedded in an intensively-used agriculture-forest matrix (Cousins and Lindborg, 2008). The resulting diminished average patch size, the increased patch isolation and altered landscape dynamics threaten future plant distribution patterns, plant species richness and species persistence in the remaining grassland fragments. Moreover, once a species is lost from a grassland patch, re-colonization may be thwarted by dispersal (Tremlova and Münzbergová, 2007), recruitment (Schleuning and Matthies, 2009), microsite and/or seed limitation (Eriksson and Ehrlén, 1992). Hence, the capacity to form a persistent seed bank appears a key survival strategy for semi-natural grassland species in fragmented landscapes (Piessens et al., 2004; Tremlova and Münzbergová, 2007; Lindborg, 2007). Yet,

\* Corresponding author. Tel.: +46 8 674 7884.

E-mail addresses: [jan.plue@natgeo.su.se](mailto:jan.plue@natgeo.su.se), [sara.cousins@natgeo.su.se](mailto:sara.cousins@natgeo.su.se) (J. Plue).

most studies only use trait-based analyses of species assemblages in fragmented landscape to highlight the importance of seed-banking. To our knowledge, empirical evidence from seed banks in support of their importance for species persistence in fragmented landscapes is absent. No direct evidence thus exists on how grassland seed banks may temporally disperse species lost from the vegetation due to habitat fragmentation.

Once a storage mechanism for grassland species in stable grassland communities (Kalamees and Zobel, 2002; Vandvik and Goldberg, 2006; Auffret and Cousins, 2011), the seed bank in remnant grassland fragments may hinder their re-establishment. Indeed, Peterson and Carson (1996) and Devlaeminck et al. (2005) demonstrated consistent seed inflow from adjacent arable land, accumulating vast quantities of competitive ruderal species in the seed bank of temperate forest fragments. Should a similar seed inflow take place in remnant grassland fragments, these ruderals may hamper future restoration efforts where these efforts create the gap-disturbances critical for grassland species establishment (Kalamees and Zobel, 2002; Vandvik and Goldberg, 2006; Schleuning and Matthies, 2009). The consequent seed-bank derived competition in small gaps may outcompete the vulnerable fragmented populations (Endels et al., 2007). Hence, rather than supporting these remnant populations via seed bank-driven seedling recruitment (Auffret and Cousins, 2011), the ruderals' activation from the seed bank may instead trigger local species' extinctions in local plant communities. The remnant habitats' seed bank may still prove a valuable restoration asset (Auffret and Cousins, 2011) where a gradual release of seed-banking species thwarts aggressive colonization by ruderals (e.g. introduction of grazing, Cousins and Lindborg, 2008).

Nonetheless, temporal connectivity provided by the seed bank is often disregarded. For example, Cousins and Eriksson (2008) overlooked temporal connectivity when they argued that remnant grassland habitats are isolated in space and time, due to the loss of functional human landscape connectivity. While temporal connectivity provided by the seed bank is valuable, time is equally an influential factor constraining seed bank composition. Grassland seed banks are no exception given the frequent reports of depleted seed banks in overgrown grasslands (Bakker and Berendse, 1999; Jacquemyn et al., 2011) because of the boundaries on seed persistence (Bekker et al., 2000). Obviously, since empirical evidence on seed bank changes in response to habitat fragmentation is non-existent, the answer on how long temporal dispersal may sustain a species' persistence and potentially re-introduce species in the aboveground vegetation, is unclear.

This study sets out to gather direct empirical evidence to test the hypothesis that seed banks are critical to the prolonged presence, persistence and survival of grassland species in fragmented landscapes. By studying the historical trajectories of current grassland fragments resulting from historical habitat fragmentation (Gustavsson et al., 2007) and linking these to their seed bank records, we address the following research questions: (1) how does the seed bank of semi-natural grasslands change with habitat fragmentation, (2) does the seed bank of remnant grassland fragments conserve part of the flora characteristic of large semi-natural grasslands and (3) does the seed banks' temporal storage effect have a spatial dimension which buffers local species losses at the landscape scale, adding to species persistence and survival in fragmented landscapes?

## 2. Materials and methods

### 2.1. Study site and data collection

The study site covered a 25 km<sup>2</sup> area of the island of Selaön (59°24'N, 17°10'E) in Lake Mälaren, central Sweden. Selaön is an

open agriculture-forest landscape (56% agriculture and 36% coniferous forest) with little semi-natural grassland left (5% in 2011 versus 60% in 1854; Cousins and Eriksson, 2008). Within the 25 km<sup>2</sup> area, ten landscape sections (circles with a 800 m radius) were selected. Within each section, all remnant grassland fragments were sampled (Fig. 1), totalling 134 sampling locations. All 134 locations were visited in September 2010 and at each location a 2 m × 2 m plot was permanently marked. Within each plot, 25 core samples (3.5 cm diameter, 5 cm deep) were collected. The litter layer of each soil core was discarded to remove transient seeds. The 25 soil core samples were pooled to yield one seed bank sample per plot. Samples were stored in a dark and cool environment until processing. The concentrated samples (Ter Heerdt et al., 1996), overlying a layer of steam-sterilized potting soil, were allowed to germinate under a 16 h-day, 8 h-night regime, with daytime temperatures between 25 and 30 °C. Identified seedlings were counted and removed. Unidentified seedlings were transplanted and identified upon flowering. Germination was interrupted after 14 weeks, followed by a cold stratification period (0–2 °C for 10 weeks). The second germination period was terminated after another 24 weeks. Control containers did not detect any contamination from either airborne seeds or seeds present in the potting soil. All 134 plots were revisited in June–July 2011, recording all plant species per plot. Nomenclature follows Mossberg and Stenberg (2003).

### 2.2. Data analysis

#### 2.2.1. Land use trajectory as a factor combining co-occurring fragmentation processes

Habitat fragmentation comprises multiple co-occurring processes such as habitat loss, declining patch size, habitat quality deterioration and changing matrix configuration, implying significant collinearity among variables such as e.g. patch size and habitat quality. To overcome collinearity during statistical modelling, we instead developed one comprehensive factor variable, namely land use trajectory (LUT hereafter). This LUT factor incorporates all co-occurring spatial, temporal and local changes sampled grassland fragments have experienced, grouping grassland fragments with similar historical trajectories (Fig. 1, Gustavsson et al., 2007). We defined LUT classes using digitized historical maps from 1854, and land cover maps based on interpreted and digitized aerial photographs from 1954 to 2011. We assigned a number of characteristics to each plot per time step: (1) surface area of the fragment (per time step 1854, 1954 and 2011), (2) tree canopy presence (in 1954 and 2011), (3) last date of recorded grazing and (4) habitat turn-over. Spatial connectivity was disregarded as historical and contemporary connectivity have limited importance to fragmented central Swedish grassland communities (Cousins et al., 2007; Öster et al., 2007). A hierarchical Wards' clustering based on a Gower dissimilarity matrix was run on the 134 plot × 7 landscape characteristics matrix. Four LUT classes emerged: (1) Old remnant grassland fragments, (2) Young remnant grassland fragments, (3) Recent remnant grassland fragments and (4) Semi-natural grasslands. All seven landscape characteristics and the presence-absence based Ellenberg values for Nitrogen and Reaction were tested along the four LUT classes to describe their spatial, temporal and local characteristics (using ANOVA, Kruskal–Wallis or Chi-square tests). The four LUT classes present a gradient in time since fragmentation started together with a decline in fragment size and increase in the Ellenberg value for Nitrogen ( $F = 19.54$ ,  $p < 0.001$ ) and Reaction ( $F = 11.95$ ,  $p < 0.001$ ) (Table 1 and Appendix A). This suggests stronger nutrient inflow as grassland fragments become older and smaller. LUT will also be referred to as "time since fragmentation started".

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