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Effects of landscape composition, species pool and time on grassland specialists in restored semi-natural grasslands

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ABSTRACT

Habitat restoration is an important complement to protecting habitat for the conservation of biodiversity. Semi-natural grasslands are target habitats for ecological restoration in temperate Europe. Restoration of abandoned semi-natural grasslands often relies on spontaneous colonisation of plant species from the soil seed bank or the surrounding landscape. Although many studies show that the regional species pool is important for upholding local diversity, its effect on restoration outcome in semi-natural grasslands is poorly known. In this multi-landscape study, we examined grassland specialist species occurring in restored grasslands and the effect of specialist species pool, landscape composition and local temporal factors. We found that specialist richness and frequency was positively affected by specialist richness and frequency in the surrounding landscape. Specialist richness in the restored grasslands also increased with time since restoration. Moreover, specialist frequency in the restored grassland increased with the proportion of semi-natural and remnant grassland habitats in the landscape. We also found a positive relationship between the proportion of species occurring in both the restored grassland and its surrounding landscape and time since restoration, in landscapes with high proportions of semi-natural grasslands. This suggests that both temporal factors, as well as the landscape composition and species pool, affect plant recolonisation in restored semi-natural grasslands.

1. Introduction

Habitat restoration is included in the UN Sustainable Development Goals and the Convention for Biological Diversity (2010 Aichi Biodiversity Target D) as a key measure to counteract current losses of biodiversity and ecosystem services. One goal is to globally restore 15% of degraded natural and semi-natural habitats of high biological value by the year 2020 (CBD, 2012). Permanent semi-natural grasslands in Europe have developed through centuries by grazing and mowing to become biological hotspots of high conservation value in the agricultural landscape (Habel et al., 2013; Papanikolaou, Kühn, Frenzel, and Schweiger, 2016). However, due to agricultural intensification and abandonment, remaining semi-natural grasslands are often heavily fragmented (Cousins, Auffret, Lindgren, and Tränk, 2015) and degraded in quality (Kasari, Saar, de Bello, Takkis, and Helm, 2016). Economic compensation to restore abandoned and degraded semi-natural grasslands are therefore incorporated in agri-environment schemes (AES) in many European countries (Stoate et al., 2009).

Previous studies have shown that community assembly and species persistence are influenced by processes acting at both local (Dupre and Ehrlen, 2002; Krauss, Klein, Steffan-Dewenter, and Tscharntke, 2004; Lindborg et al., 2012) and landscape scales (Eriksson, 1996; Kormann et al., 2015; Öckinger, Lindborg, Sjödin, and Bommarco, 2012). Although the influence of the regional species pool is widely acknowledged (Hanski, 1999; Pärtel, Bennett, and Zobel, 2016; Pärtel, Szava-Kovats, and Zobel, 2011; Zobel, van der Maarel, and Dupré, 1998), studies on how it affects restoration outcome in local habitats are rare (but see Conradi and Kollmann, 2016; Prach, Fajmon, Jongepierová, and Řehounková, 2015 regarding species pool effects on recreated grasslands). Whereas creation of new grasslands on ex-arable fields often includes manually sowing target seed mixes, restoration of abandoned semi-natural grasslands in northern Europe most often relies on plants recolonising spontaneously, either from the soil seed bank or the surrounding landscape (Waldén and Lindborg, 2016). This could potentially be a cost-efficient restoration method, but requires that targeted species still occur locally within the site or regionally within the landscape so that they are able to recolonise the restored habitat (Prach and Hobbs, 2008; Török, Vida, Deák, Lengyel, and Tóthmérész, 2011). Many grassland species exhibit a time-lag before they go extinct following grassland abandonment (Bagaria, Helm, Rodà, and Pino,

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2015; Krauss et al., 2010; Kuussaari et al., 2009), persisting either as perennial adults or as seeds in the seed bank (Auffret and Cousins, 2011; Helm, Hanski, and Partel, 2006; Lindborg, 2007). This time delay in the extinction process, the extinction debt (Kuussaari et al., 2009), enables populations to recover rapidly when habitat conditions within restored grasslands have become suitable again (Havrdová, Douda, and Doudová, 2015; Plue and Cousins, 2013).

Nevertheless, a long time between grassland abandonment and restoration has a negative effect on restoration potential in grasslands (Bossuyt, Honnay, Van Stichelen, Hermy, and Van Assche, 2001; Schrautzer, Jansen, Breuer, and Nelle, 2009; Willems, 2001). Long-term effect of abandonment often results in the dominance of few competitive plant species while grassland specialists disappear (Willems and Bik, 1998), especially if the grassland has been fertilised (Fagan, Pywell, Bullock, and Marrs, 2008; Janssens et al., 1998). Another temporal factor affecting restoration outcome is the elapsed time since restoration. Usually the overall plant species richness increase with time since restoration (e.g. Piqueray et al., 2011; Waldén and Lindborg, 2016; Winsa, Bommarco, Lindborg, Marini, and Öckinger, 2015), although this will not necessarily indicate an increase in the species that characterise the habitat (cf. Helm, Zobel, Moles, Szava-Kovats, and Pärtel, 2015). While common species often immigrate to restored grasslands (Kotiluoto, 1998), specialists and rare species often show no or only slight recovery (e.g. Helsen et al., 2013; Pykälä, 2003; Tikka et al., 2001; but see Dzwonko and Loster, 1998). Gijbels, Adriaens, and Honnay (2012) showed that target orchid species were only present in half of the estimated suitable habitats, even three decades after restoration. Due to the low colonisation potential of grassland specialists species (Pywell et al., 2003), reference sites usually have a higher fraction of grassland specialists than restored sites (Lindborg and Eriksson, 2004; Schrautzer et al., 2009).

The potential species to recolonise restored habitats from the landscape species pool is determined by species dispersal ability (Riibak et al., 2015), but also on the landscape structure (Cousins, 2006). In modern European agricultural landscapes, remaining species-rich grasslands are often small and isolated, resulting in low possibilities for species to disperse between grassland fragments (Eriksson, Cousins, and Bruun, 2002). However, except for continuously managed semi-natural grasslands, populations of typical grassland species can also survive in other types of habitats, e.g. in former grasslands that now are abandoned, road verges, gardens and midfield islets (Cousins, 2006; Lindgren and Cousins, 2017; Plue and Cousins, 2013). Such habitats might facilitate species dispersal into restored grasslands, acting as stepping stone habitats (Cousins and Lindborg, 2008; Lindborg, Plue, Andersson, and Cousins, 2014). Excluding these potentially suitable habitats when surveying plant species, could therefore underestimate the available species pool.

Although dispersal from surrounding habitats is a common presumption both in restoration practise and research, few studies exist that build on field surveys of the actual species pool and its potential effect on restoration outcome in restored semi-natural grasslands. One recent study of grasslands recreated on ex-arable fields showed a positive relationship between the number of target plant species in the recreated grasslands and their occurrence in the surrounding landscape (Prach et al., 2015). Remnant grassland habitats may also act as source communities when they are directly connected to recreated grasslands (Cousins and Lindborg, 2008). Even though the abiotic and biotic preconditions in recreated grasslands are fundamentally different from restored abandoned semi-natural grasslands (Fagan et al., 2008; Horrocks et al., 2016), this indicates that target species from a species pool are able to recolonise spontaneously. How large proportion of the species pool in the landscape that is represented in different types of restored semi-natural grasslands is still relatively unknown. Although the surrounding landscape might host a large habitat specific species pool, some species could still be absent in the local restored habitat (i.e. belong to the dark diversity) (Lewis, Szava-Kovats, and Pärtel, 2016; Pärtel et al., 2011). This could for example be due to their low dispersal ability and/or low competitive ability (Poschlod, Kiefer, Tränkle, Fischer, and Bonn, 1998; Riibak et al., 2015), or related to temporal and/or spatial issues, such as to not yet suitable abiotic or biotic conditions (Helsen et al., 2016; Piqueray et al., 2011) or lack of functional connectivity (Auffret et al., 2017).

As a full survey of the total species pool in a landscape is extremely time consuming, using GIS-analyses of landscape features have been suggested as substitute (Perring et al., 2015), where a high proportion of semi-natural grasslands in the landscape could indicate better opportunity for community recovery within restored semi-natural grasslands. However, these methods disregard the possibilities of grassland specialists inhabiting remnant grassland habitats, such as former grasslands or midfield islets (Cousins and Aggemyr, 2008).

In this study, we examined the relationship between the habitat specific plant species pool (including managed semi-natural grasslands and remnant grassland habitats) and the plant specialists species found in restored semi-natural grasslands. The questions we posed were: How is the number and frequency of grassland specialists in restored and reference grasslands affected by (1) the temporal and local factors time since restoration, abandonment time (years without management) and focal grassland area, and (2) by the landscape factors proportion of semi-natural grasslands, remnant habitats and arable fields and the number and frequency of plant specialists found in the surrounding landscape? (3) How is the proportion of shared species (i.e. grassland specialists occurring in both the focal restored/reference grassland and the surrounding landscape) affected by time since restoration, abandonment time, grassland area and semi-natural grasslands, remnant habitats and arable fields in the landscapes?

2. Methods

2.1. Study area and geographical analyses

We selected 20 circular landscapes (1 km radius, no overlap between landscapes) situated in south-central Sweden in the counties of Södermanland, Uppland and Västmanland (Geographical coordinates in Appendix A). Each landscape was centered around one focal grassland; either a restored semi-natural grassland (12 sites) or a continuously managed semi-natural grassland (8 sites). The restored grasslands were abandoned semi-natural grasslands restored 6–23 years before our study. Restoration included clearing of trees and shrubs and reintroduction of domestic grazers (cattle (10 sites), horses (1) and sheep (1)). The continuously managed grasslands here act as reference grasslands, representing intact communities and the desired state after restoration. When discussing the restored and reference grasslands together, we refer to them as 'focal grasslands'. All focal grasslands were chosen by using information from the County Administration Boards, the Municipalities and the Uppland Foundation, combined with information from a national Swedish geographical database of semi-natural pastures (http://www.jordbruksverket.se/tuva), previously described by Winsa et al. (2017). The grasslands were selected according to standardised criteria regarding soil conditions, the state before restoration actions (degree of degradation before restoration and restoration practice and effort), and are all situated in counties with relatively similar abiotic conditions (Lindborg and Eriksson, 2004; Steiner, Öckinger, Karrer, Winsa, and Jonsell, 2016). The average grassland area was similar for restored and reference grasslands (3.23 ± 0.60 and 3.11 ± 0.62 ha, respectively). Information of time since restoration (i.e. years since restoration was initiated) and abandonment time (i.e. years without management) were obtained by asking farmers, landowners and the County Administration Boards. Time since restoration varied between 6 and 23 years and abandonment time varied between 0 and 60 years (where 0 years refers to low intensity grazing, insufficient to fully prevent succession, during the last 50 years). All focal grasslands had dry to mesic abiotic conditions and