Restoration of Plant and Pollinator Communities in Fragmented Grasslands

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Abstract

A large proportion of the former area of species-rich semi-natural grasslands has been lost due to agricultural intensification and abandonment. Remaining small and isolated grassland fragments are often imbedded in more or less intensively managed landscapes. The loss and fragmentation of these grasslands have profound effects on overall biodiversity, and may affect processes and functions in the entire agricultural landscape. Therefore, semi-natural grasslands are key targets for conservation and restoration efforts. Until recently, evaluations have mainly assessed restoration outcomes in terms of species richness and abundance, often only of plants. Contrasting responses among interacting species to landscape and local factors can have consequences for the recovery of community composition, species interactions and ecosystem functions in restored habitat fragments. In this thesis, I examine the response of plant and pollinator (bees; *Apoidea*, and hoverflies; *Syrphidae*) communities to restoration of semi-natural grasslands in fragmented landscapes in south-central Sweden. Restoration effects were measured in terms of species richness, species composition, community trait composition, and composition of species and interactions within plant-pollinator networks. Following restoration, plant communities recovered both in terms of species richness and trait composition. These changes were reflected in a recovery of pollinator composition within plant-pollinator networks, and also a recovery in species interactions. The trait composition among pollinators was sustained both through abandonment and restoration, but responded to structural features of the vegetation. Plant communities had higher species richness in sites adjacent to intact grasslands than in those adjoining croplands. Hoverflies were not affected by grassland connectivity, but high connectivity facilitated the recovery of sedentary and specialized bee species. Time since restoration was an important driver in the recovery of plant communities, but not for pollinators or species interactions. This thesis shows that plant and pollinator communities as well as plant-pollinator interactions can be restored. The dispersal ability of both plants and pollinators, and the resource use of pollinators within and outside grassland fragments affected species responses to grassland connectivity. Connectivity to intact grasslands does not fully reflect the availability of resources and potential source populations within fragmented landscapes. Except for intact grasslands, abandoned and restored grasslands are also important for biodiversity and ecosystem functioning in the agricultural landscape.

Keywords: abandonment, dispersal, isolation, habitat fragmentation, habitat loss, plant-pollinator network, semi-natural grasslands, species interactions, species traits

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Dedication

Till Örjan och Eldar

‘I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations.’

C. Darwin

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Winsa, M., Bommarco, R., Lindborg R., Marini L., Öckinger E. (2015). Recovery of plant diversity in restored pastures depends on adjacent land use. *Applied Vegetation Science* 18(3), 413-422.

II Öckinger E., Winsa M., Roberts S.P.M., Bommarco R. Mobility and resource use influence the occurrence of pollinating insects in restored semi-natural fragments (manuscript).

III Winsa M., Öckinger E., Bommarco R., Lindborg R., Roberts S.P.M., Wärnsberg J., Bartomeus I. Sustained functional composition of pollinators in restored pastures despite slow functional restoration of plants (manuscript).

IV Winsa M., Bartomeus I., Bommarco R., Öckinger E. Plant-pollinator networks in restored semi-natural grasslands (manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Marie Winsa to the papers included in this thesis was as follows:

I Main author. Planned the field work, and performed all statistical analyses. Developed study design together with L.M., E.Ö. and R.B.

II Second author. Planned and performed field work, and performed all statistical analyses. Developed study design together with E.Ö. and R.B.

III Main author. Planned and performed field work, and performed all statistical analyses. Developed study design together with E.Ö., R.L. and R.B.

IV Main author. Planned and performed field work. Performed all statistical analyses with significant contribution of I.B. Developed study design together with E.Ö and R.B.

1 Introduction

1.1 Land-use change in agricultural landscapes

1.1.1 Agricultural intensification and abandonment

During the last century, landscapes in Europe and elsewhere has undergone major changes through the exploitation of natural habitats for forest or agricultural production (Foley et al. 2005; Hoekstra et al. 2005). Since the 1950's, an already intensified agriculture has experienced further large-scale industrialization. On the local scale, farm units have grown bigger and become more specialized. Field size has increased at the cost of natural and cultural (hereafter semi-natural) habitats and wetlands, and the use of agrochemicals has increased (Berglund et al. 1991). In productive regions, the characteristic low-intensity farming of semi-natural habitats have largely been replaced by more intensified practices to increase production, or, in low-productive regions, semi-natural habitats have been actively afforested or abandoned (Foley et al. 2005; Stoate et al. 2001; Cousins 2009). A consequence of the ongoing habitat loss and altered landscape composition are declines in biodiversity (Foley et al. 2005), which in turn has raised concerns about the effect of these changes on ecosystem processes and functions within ecosystems (Stoate et al. 2009).

1.1.2 High Nature Value farmlands

In Europe, about 40% of the land is under agricultural use (Eurostat 2016), and approximately 50% of all species in Europe are dependent on agricultural habitats (BISE n.d.). The definition of habitat has changed throughout time, and it is still used inconsistently depending on context. In the EU Habitats directive[1], habitats are defined as *'terrestrial or aquatic areas distinguished by geographic, abiotic and biotic features, whether they entirely natural or semi-natural'*. Judging whether a habitat is agricultural ("artificial") or semi-natural is not always straightforward, but it can often be determined from the composition of species and the presence of indicator species (Ichter et al. 2014). Semi-natural habitats originate from the long history of low-intensive agricultural management in Europe, where management systems are adapted to the regional environmental conditions, and little interventions to increase productivity have been implemented. In other words, semi-natural vegetation refers to natural vegetation under human management, which host a high biodiversity (Bignal & McCracken 2000; 1996). Among semi-natural habitats, extensively managed grasslands can be exceptionally species rich (Wilson et al. 2012; Kull & Zobel 1991). This is reflected in that these grasslands constitute a large portion of the so called High Nature Value (HNV, Baldock et al. 1993) farmlands in Europe, and that they are highly prioritized targets for conservation and restoration efforts.

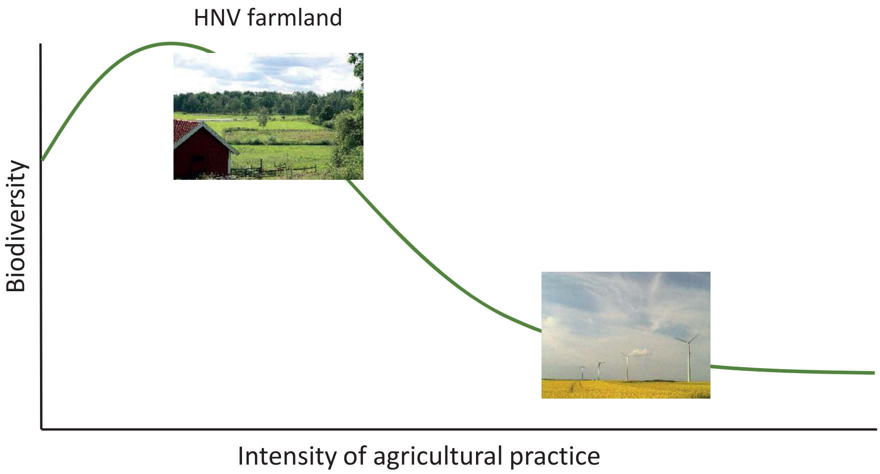

Figure 1. Conceptual figure describing how local biodiversity relate to agricultural intensity, and where on this scale High Nature Values (HNV) farmlands are situated. Photos: M. Winsa. *Adapted from Hoogeveen et al. (2002, 2004).*

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[1]. Council Directive 92/43/EEC adopted 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. European Commission 1992.

Many species are dependent on the vegetation types and structures within HNV farmlands that often only an extensive management can maintain (Hoogeveen et al. 2004; Henle et al. 2008). However, with economic pressure, many farmers have been forced to choose between ceased management (i.e. abandonment) and intensification of agricultural practices on these HNV farmlands. Both scenarios cause biodiversity declines on the local scale, but especially the effects of extreme agricultural intensification can be difficult to reverse (right hand side of Figure 1). Hence, maintenance of extensive land use or restoration of abandoned land (left hand side of Figure 1) are likely the most cost-effective ways to preserve or enhance biodiversity (Hoogeveen et al. 2002).

1.2 Habitat restoration

1.2.1 Aims of ecological restoration of habitats

Ecological restoration is defined by the Society for Ecological Restoration (Gann & Lamb 2006) as *'assisting the recovery of an ecosystem that has been degraded, damaged or destroyed',* and has become an established tool to counteract negative effects of land-use changes on biodiversity and ecosystems. The overarching goal is not only to restore species composition, but also the structures and functions within the ecosystem, and to integrate the ecosystem, its species, processes and functions with a larger landscape context (Gann & Lamb 2006).

The EU Biodiversity Strategy aims at halting the loss of biodiversity and ecosystem services in the EU, and one of its six targets is to *'Maintain and restore ecosystems and their services'*. The target goal is that *'by 2020, ecosystems and their services are maintained and enhanced by including green infrastructure in spatial planning and restoring at least 15 % of degraded ecosystems'* (Lammerant et al. 2013). One measure to reach this target is that incentives are given to landowners who, on voluntary basis, restore degraded habitats. In Sweden, for instance, within The Rural Development Programme instated by the Swedish Board of Agriculture, land owners can be reimbursed for parts of the costs involved in the restoration of for example wetlands, meadows and pastures (Jordbruksverket 2015).

1.2.2 Species responses to habitat fragmentation and restoration

Habitat loss often, but not always, leads to habitat fragmentation. It is the spatial arrangement of remaining habitat patches in the landscape that determines the degree of fragmentation and connectivity among them (Fahrig 2003). With respect to species distributions and community assembly processes, habitat connectivity is a relative measure that is intimately linked to the dispersal ability of species (Lindenmayer et al. 2008; Soons et al. 2005). Remnant natural and semi-natural ecosystems are often small and isolated, and situated in a landscape context that is different from when the ecosystems once developed (Saunders et al. 1991). One of the many challenges within ecosystem restoration is, hence, to deal with the effect of the “new” landscape context of restored habitats, and the effect it might have on the re-colonization of species and recovery of ecosystem processes. When ecological restorations are performed in fragmented landscapes, the degree of isolation from potential source populations in combination with species dispersal ability can therefore affect the prospects and speed of species re-colonization (Stampfli & Zeiter 1999; Ozinga et al. 2004; Helsen et al. 2013). Furthermore, depending on the quality of the landscape surrounding restored habitat fragments, the landscape matrix can either provide additional resources or act as a dispersal barrier for species, and hence affect the persistence within and dispersal into restored habitat fragments (Öckinger et al. 2012). The relationship between landscape configuration and species requirements and qualities (hereafter referred to as traits) is therefore an important aspect to consider in the planning of conservation and restoration efforts (e.g. Matthews et al. 2009; Helsen et al. 2013).

Even though landscape composition in relation to species’ dispersal ability is a key determinant for community recovery in restored habitats in fragmented landscapes, there is no single trait that on its own determines the prospects of community recovery following habitat restoration. For instance, as an alternative to re-colonization through dispersal from source populations in the surrounding landscape, some species, at least among plants, might be able to endure periods of habitat degradation (Lindborg et al. 2005; Eriksson 1996). Thereafter, there are other additional traits related to the local conditions of a habitat that will affect the performance and dynamics of species, for example traits related to competition, specialization, phenology, and reproduction (Pywell et al. 2003; Williams et al. 2010; Bommarco et al. 2010). While our general understanding of how land use changes affects the functional diversity of species has increased (Tscharntke et al. 2008; Rader et al. 2014), there is still much to learn about how landscape and local factors affects the prospects and speed of a functional recovery of communities in restored habitat fragments.

1.2.3 Evaluations of habitat restorations

Restoration ecology as a scientific research area has evolved rapidly since the 1990´s (Wortley et al. 2013). However, to further develop research within this subject area, and to better inform practitioners and decision makers, it has been argued that there is a need for more comprehensive and long term evaluations of restoration techniques and outcomes (Montoya et al. 2012; Suding 2011). Measuring all ecosystem attributes in a restored habitat is rarely feasible due to time and budget constraints, but for a restoration project to be considered successful, processes and functions should display a recovering trajectory where no further restoration intervention is needed (Gann & Lamb 2006).

Until recently, restoration evaluations has mainly targeted the plant community in terms of richness and abundance of species, often assuming a subsequent recovery also of ecological functions (McAlpine et al. 2016; Gann & Lamb 2006). Considering that nearly 90% of the worlds flowering plants are dependent upon pollination for their reproduction and long term persistence (Ollerton et al. 2011), it is surprising that habitat restorations only rarely are targeting pollinator communities (Williams 2011). Moreover, species richness and abundance measures are, indeed, a good starting point to assess the state of a restored habitat and the processes within it (Wortley et al. 2013), but ecosystem functioning is not sufficiently explained by these measures (Gagic et al. 2015).

Species interactions compose the architecture of biodiversity (Bascompte & Jordano 2007), and the structuring of these interactions are the result of complex processes (Bartomeus et al. 2016). Firstly, species' responses to local and landscape conditions (as discussed above) affects species occurrence and abundance distribution, which in turn affect species encountering probability. Secondly, species traits determines if co-occurring species are compatible to interact (morphologically and phenologically), and also, the impact of interactions on ecosystem functioning (here pollination) (Bartomeus et al. 2016). Variation in species' responses to local conditions and landscape composition can, hence, affect the abundance distribution of communities such that both the trait composition of communities and dynamics between species will change (Vázquez et al. 2009; Brosi & Briggs 2013). These alterations, in turn, can cause changes in interaction network structures that feedback both to the community composition and functioning of ecosystems (Bartomeus et al. 2016).

Explorations of species interactions have steadily increased within ecological studies in general (Heleno et al. 2014), as has our knowledge about the biodiversity-ecosystem functioning relationship (Cadotte et al. 2011). However, within restoration ecology, changes in functional diversity of communities and species interaction networks has only begun to be explored (Menz et al. 2011; Montoya et al. 2012). The implementation of functional diversity and interaction network approaches in restoration evaluations has the potential to increase our understanding of mechanisms underlying restoration outcomes, and can improve the planning of successful functional restorations of habitats in fragmented landscapes.

1.3 Semi-natural grasslands

1.3.1 History and current status of semi natural grasslands

Semi-natural grasslands of today can have their history as far back as the early Iron Ages (Pärtel et al. 2007). At this point in time, arable fields and mown meadows were situated near settlements, and outside the settlements grasslands were used as pastures for livestock grazing (Widgren 1983). It was not until the mid-19th century that this system was replaced by a more modernized and intensified agricultural system under which a large portion of semi-natural grasslands were abandoned (Eriksson et al. 2002). With continued agricultural intensification on a regional level, more and more grasslands have been lost (Figure 2), with grasslands on productive soils being converted for arable use, and grasslands on poor soils becoming abandoned or converted for forest production (Cousins 2009). In an area in south-eastern Sweden for instance, Cousins *et al.* (2015) found that in the early 1900, grasslands made up 46% of the total land cover, whilst the land cover of grasslands in 2013 only reached 2%.

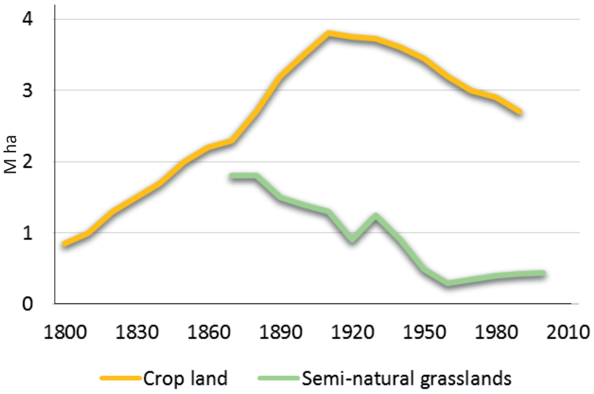

Figure 2. Trends in amount of cropland and semi-natural grasslands (million ha.) in Sweden in the period 1800-2006. Included in 'semi-natural grasslands' are grasslands of varying quality, which makes the amount of grasslands reported here higher than what has been reported in other national surveys of High Nature Values (HNV) grasslands. *Adapted from Olsson et al. (2008).*

1.3.2 Plants and pollinators in semi-natural grasslands

Semi-natural grasslands were traditionally managed through mowing or late season grazing, allowing both plants and other species associated with these to complete their life cycle (Plantureux et al. 2005; Dahlström et al. 2008). The effect of this type of management is reflected in the high small-scale plant species richness that characterises semi-natural grasslands (Kull & Zobel 1991; Eriksson & Eriksson 1997; Wilson et al. 2012). Furthermore, nutrient poor conditions in combination with suppression of strongly competitive species through grazing or mowing promotes the persistence of slow growing plant species (Plantureux et al. 2005). As a result, plant communities in semi-natural grasslands host many rare species that are restricted to this type of habitat (Cousins & Eriksson 2001).

Diverse plant communities often promote high diversity of other species groups (e.g. Öckinger et al. 2006; Steffan-Dewenter & Tscharntke 2001; Duelli & Obrist 1998). In addition, the local structural heterogeneity of semi-natural grasslands is beneficial for biodiversity, as it provides resources and microhabitats for many species (Söderström et al. 2001). For instance, many bee species (*Apoidea*) and to some degree hoverflies (*Syrphidae*) are associated with semi-natural habitats (e.g. Westrich 1996; Kleijn & van Langevelde 2006). Both groups are frequent flower visitors and considered to be key pollinators of plants, but they can differ greatly in their requirements and traits, and hence also in their dependence on semi-natural habitats (Winfree et al. 2011). One crucial difference lies in the reproduction and foraging patterns of these two pollinator groups. Non parasitic bees are often bound to semi-natural habitats through their nest sites (Westrich 1996). After foraging, these species need to return to their nests to feed their offspring. In contrast, once hoverflies have oviposited in a suitable microhabitat with sufficient resources for their larvae, they can track floral resources freely in the landscape (Kleijn & van Langevelde 2006; Jauker et al. 2009). Therefore, depending on the quality of the matrix surrounding semi-natural habitats, bees more often than hoverflies display decreasing diversity and abundance with increasing distance from semi-natural habitats (Jauker et al. 2009; Ekroos et al. 2013; but see Kohler et al. 2008).

1.3.3 Species responses to altered grassland management

Alterations in management of semi-natural grasslands can have profound effects on both plant and pollinator communities. Intensified grassland management and conversion to arable use often implies ploughing, fertilization, increased use of agrochemicals and, for intensified grassland management, increased grazing pressure (Plantureux et al. 2005), resulting in declines in species richness (e.g. Weiner et al. 2011). Industrialized farming systems at large have also led to the abandonment of semi-natural grasslands or conversion for forest production. This trend is most pronounced in regions where intensified grassland management or conversion for arable use is not economically justifiable or practically possible due to poor soil conditions (Cousins 2009). When grasslands are abandoned, the cessation of grazing can initially lead to increasing diversity of plants and high flower abundance, but relatively soon after abandonment litter accumulation and encroachment of trees and shrubs leads to declines in plant species richness and floral resources for pollinators (Prévosto et al. 2011; Wissman 2006; Pykälä et al. 2005; Hansson & Fogelfors 2000). Pollinator responses to land use changes are often mediated by alterations in the floral community caused by the changes in land use, rather than by the management changes themselves (Winfree et al. 2011). Also, since pollinators are mobile and can utilize resources from several habitats, pollinator response to local land use change can be affected by landscape scale factors such as landscape heterogeneity and regional flower abundance (Meyer et al. 2009).

1.3.4 Restoration of semi-natural grasslands

Maintaining and restoring biodiversity within semi-natural grasslands is not only of importance on the local scale, but also provides benefits for the surrounding agricultural landscape as source populations and ecosystem services (e.g. Öckinger & Smith 2007; Cousins & Lindborg 2008; Potts et al. 2010). To counteract the immense loss of semi-natural grasslands, many grasslands are now being subject to habitat restorations (Keenleyside et al. 2014). In many parts of Europe, restoration from arable use is common. This type of grassland restoration often requires a relatively active restoration approach, including removal of nutrients and sowing and/or transplantation of plants (e.g. Walker et al. 2004; Török et al. 2011, see also Figure 1). However, in some parts of Europe, for instance in Scandinavia, grassland restorations are most often done from an abandoned state, and entails the cutting and clearing of trees and shrubs and re-instatement of grazing (Lindborg & Eriksson 2004). The restoration of semi-natural grasslands from abandoned state has the advantage that plants, who are relatively long-lived, can persist for quite some time after abandonment (Pykälä et al. 2005; Pärtel et al. 1998). The often observed shifts in species richness and composition that follows with grassland abandonment (Hellström et al. 2006; Pykälä et al. 2005) can be at least partly reverted over time if suitable management regimes are re-instated (Waldén & Lindborg 2016; Pykälä 2003; Pärtel et al. 1998). However, despite efforts that have been made on both national and EU-level to conserve and restore species rich grasslands, it has not been enough to sufficiently improve the state and future prospects of remaining European grasslands. In a report from the period 2007-2012 on the state of ecosystems within habitats included in the EU Habitats directive[2], grasslands had the lowest proportion of favourable and the highest unfavourable conditions of all terrestrial ecosystems (Romão et al. 2015). Increased knowledge on how to best restore these species rich and functionally important grasslands is, hence, an urgent matter.

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[2]. Council Directive 92/43/EEC, European commission 1992

2 Objectives

The central theme of my thesis is the effect that habitat fragmentation has on the recovery of plant and pollinator communities in restored semi-natural pastures. To increase the understanding of underlying mechanisms behind plant and pollinator community recovery in relation to space and time, my thesis evaluates restoration outcomes in terms of species richness, species composition, and in terms of trait and plant-pollinator network composition.

The main questions were:

- Does the recovery of plant communities in restored semi-natural pastures depend on adjacent land use? (Paper I)

- Does the mobility and niche breadth of pollinators influence species recovery in restored semi-natural pastures? (Paper II)

- How does *i)* grassland management (abandonment and restoration), *ii)* landscape composition (grassland connectivity), and *iii)* time since restoration affect the functional composition of plants and pollinators (Paper III), and plant-pollinator interaction networks (Paper IV)?

3 Methods

3.1 Study area and grassland selection

Plant and pollinator surveys for this thesis were conducted in south-central Sweden during 2011-2012, in the counties of Uppsala, Stockholm, Västmanland, Södermanland and Östergötland. Paper I included six pastures that were unique to that study (Figure 3a), and the remaining eight pastures were also used within a larger study design including 38 pastures (Figure 3b), on which paper II-IV were based upon.

Paper I included 14 pastures that had been restored from an abandoned state. These restored pastures were either located adjacent to a crop field, or adjacent to an intact (continuously grazed) pasture. Paper III and IV included 10 abandoned, 18 restored and 10 continuously grazed pastures. The larger study design comprise a space-for-time substitution, where the abandoned state represents the state prior to restoration, and the continuously grazed pastures represent the target state which restoration actions aim at reaching. All continuously grazed and restored pastures were grazed by cattle, horses and/or sheep. The study in paper II was based on the 18 restored pastures of the study design used in paper III and IV, and also on intact grasslands in the landscapes surrounding the restored pastures.

Abandoned pastures and continuously grazed pastures were identified using a national Swedish geographical database on semi-natural grasslands, named TUVA (http://www.jordbruksverket.se/tuva). To standardize vegetation types between pastures as much as possible, the continuously grazed pastures were selected among habitat types classified in TUVA as ‘Semi-natural dry grasslands and scrublands facies on calcareous substrates’, ‘Fennoscandian lowland species-rich dry to mesic grasslands’, ‘Lowland hay meadows’, ‘Fennoscandian wooded meadows’ and ‘Fennoscandian wooded pastures’. This habitat classification follows to the classification of Natura 2000 habitats

(European Commission 2013), although most grasslands in the database are not Natura 2000 sites. The Uppland foundation, County Administrative Boards, and municipalities in the region provided information to locate and select restored pastures for which the landowners have received economical compensation to restore from an abandoned state. Abandoned and some of the restored pastures were not classified in the TUVA database, but were classified during the selection process to belong to any of the mentioned habitat types.

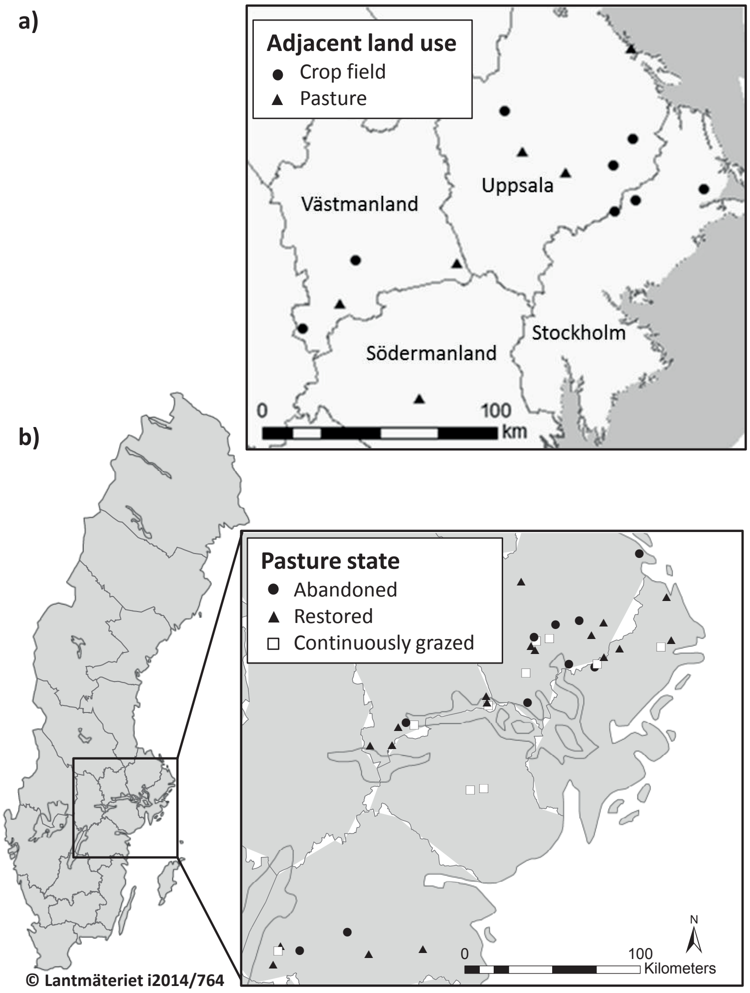

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Figure 3. Overview maps of study sites located in south-central Sweden, where a) plant communities were surveyed in restored pastures adjoining intact pastures and crop fields respectively (Paper I), and b) where plant and pollinator communities were surveyed in abandoned, restored and continuously grazed pastures (Paper II-IV). As a subset of the larger study design, paper II was based on data from restored pastures.

For restored pastures, pasture selection was partly based on the time since restoration, which ranged from 1 to 13 years in paper I, and 1 to 16 years in paper II-IV. Further, pastures in the larger study design (N = 38) were selected to achieve a similar gradient in connectivity within all three pasture states (abandoned, restored, and continuously grazed, Figure 4). This enabled us to assess the effect of time since restoration and landscape composition on the recovery of plant and pollinator communities in terms of community and functional composition and species interactions. The area and distance to other intact semi-natural grasslands within a 5 km radius around the focal pastures were used to calculate connectivity index (described in Hanski et al. 2000).

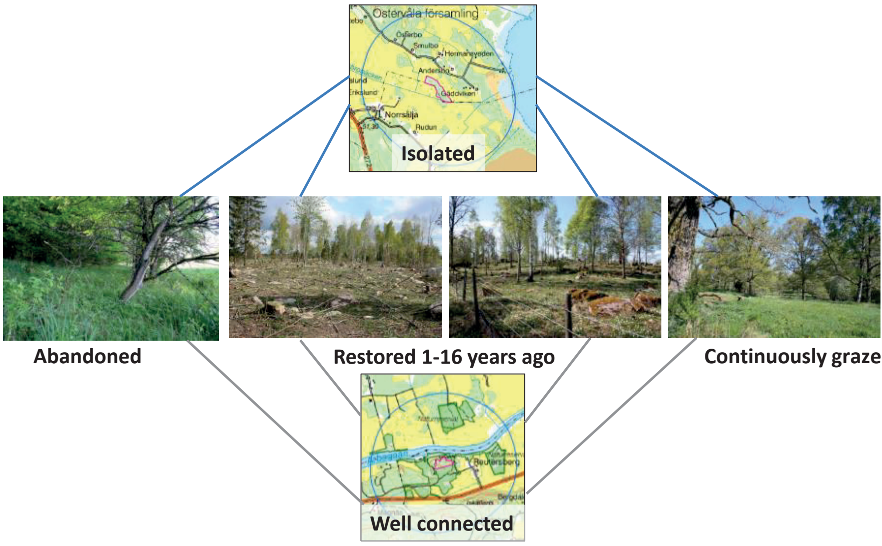

Figure 4. Schematic overview of the study design including 38 semi-natural pastures of different management state (abandoned, restored and continuously grazed), located in south-central Sweden. The pastures ranged in both connectivity to intact grasslands in the surrounding landscape (5 km radius) and time since restoration (1-16 years). Paper II was based on pollinator data from the restored pastures, and Paper III and IV on plant and pollinator data from all pastures in the study design. Photos: M. Winsa.

3.2 Data collection

3.2.1 Paper I

To investigate if plant community recovery in restored pastures depend on adjacent land use, vascular plants were surveyed in along a 50 m transect from the border towards the centre of the restored pasture. Ten sampling plots of 1 x 1 m were placed in a quasi-logarithmic fashion along the transect, at distances of 0, 1, 2, 3, 4.5, 8, 12.5, 20, 31.5 and 49 m from the border (Figure

5). Sampling was more intensive near the border of the pastures, such that possible edge effects on plant communities could be recorded. Due to the shape or the size of three pastures, only 9 plots could be sampled (up to 31.5 m from the border) to avoid passing the centre of the sites. For sites where the restored pastures bordered to an intact pasture, three sampling plots were also surveyed in the adjoining pasture, with the distances of 0, 1 and 4.5 m from the border (Figure 5). The sampling plots were divided into 25 small squares of 20 x 20 cm. To estimate the relative frequency of vascular plant species, each species was recorded as present or absent in the small squares. To assess if specialist species that are dependent on grassland management responded differently than more generalist plant species, all species recorded in the surveys were classified as either semi-natural grassland specialists, or non-specialist species (Ekstam & Forshed 1997).

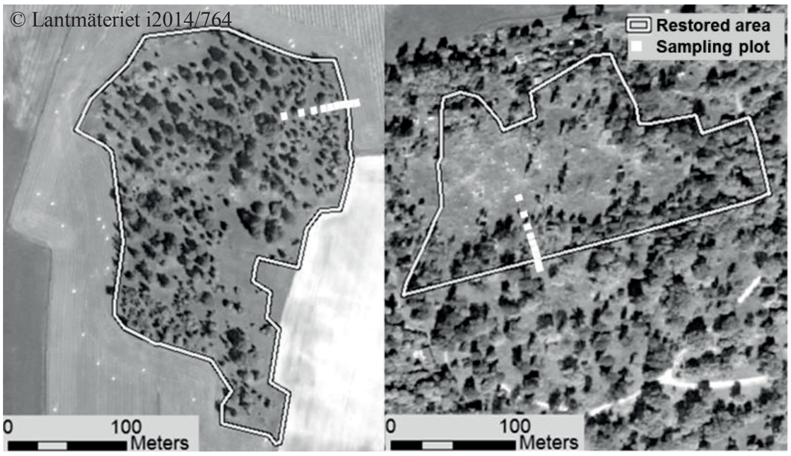

Figure 5. Aerial photos exemplifying sampling in restored semi-natural pastures in south-central Sweden. The pastured were either located adjacent to crop fields (left) or continuously grazed pastures (right). Within restored pastures the vegetation sampling plots were placed an a quasi-logarithmic fashion at distances of 0, 1, 2, 3, 4.5, 8, 12.5, 20, 31.5 and 49 m from the pasture edge, and in adjoining field at 0, 1 and 4.5 m from the border (Paper I).

3.2.2 Paper II-IV

In the large study design, bees (excluding honey bees, *Apis mellifera* L.) and hoverflies were surveyed along four 50 m transects per site (i.e. total transect length = 200 m). The width of transects were two meters, and the placement of transects aimed at capturing within-site habitat variability. In 2011, surveys were performed during June-August, with four visits per pasture during the sampling season (Paper III). In 2012, surveys were performed from May to

July, with five visits per site (Paper II and IV). The pollinators were collected with sweep nets and were later identified in the lab. The time spent on each transect was fixed after handling time of pollinators was discounted. Pollinator surveys were conducted during standardized weather conditions, i.e., temperature ≥16°C, no precipitation and low wind (≤ 4m/s).

Additional sampling for papers II-IV was also made. For paper II, with the purpose of assessing the composition of the species pool from which pollinator communities in the restored pastures could recover, pollinators were surveyed in intact semi natural grasslands within a 1 km radius in the landscape surrounding the restored pastures (N = 18, Figure 6). The total transect length in the landscape was set in relation to the amount of grassland available within the radius (20 m transect/ha).

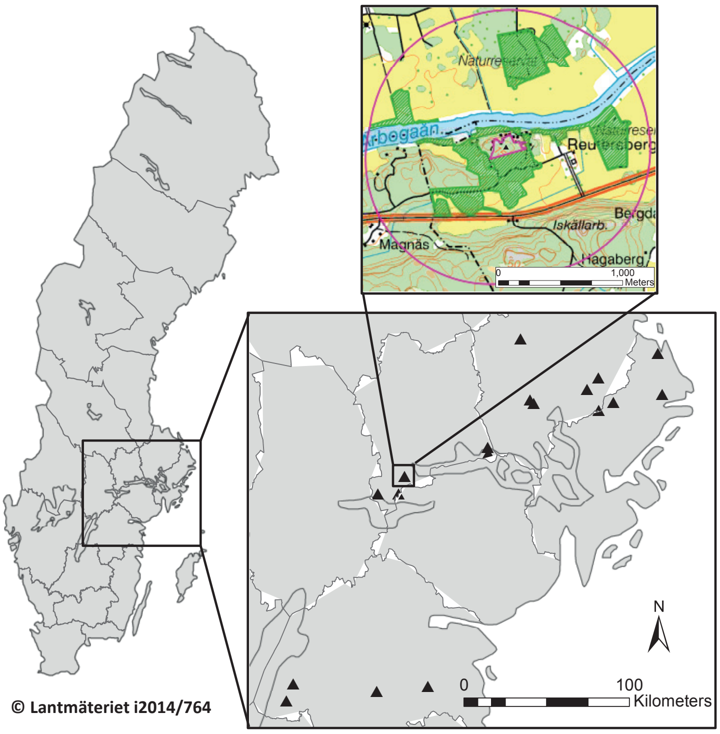

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Figure 6. Overview map showing locations of restored pastures in south-central Sweden, where pollinators were surveyed within the focal pastures, and in grasslands in the surrounding landscape (radius 1 km). The top right panel exemplifies the landscape surrounding one of the restored pastures (pink polygon), with all surveyed grasslands (green polygons) in the landscape (Paper II).

For paper III, the plant community of all 38 pastures were sampled from June to September in 2011. In 10 randomly selected 1 x 1 m plots per pasture, with each plot divided into 100 small squares of 10 x 10 cm, the frequency of each vascular plant was estimated by counting the number of small squares per plot where each species was present. To describe the habitat characteristics in the pastures, mean seasonal vegetation height and flower abundance was estimated from three 1 x 1 m plots placed along each 50 m pollinator transect (i.e. 12 plots per pasture and visit). Tree and shrub cover and abandonment time was estimated from aerial photographs (Wärnsberg 2013). For paper IV, flower visitation by bees and hoverflies was also documented along the transects, and estimates of floral resources in the pastures were obtained from the three square meter plots per pollinator transects (12 plots per pasture and visit, same as in Paper III). Species traits for pollinators (Paper II and III) and plants (Paper III) were compiled from literature (Krok et al. 2012; Bartsch et al. 2009a; 2009b; Mossberg & Stenberg 2003), Biolflor database (Klotz et al. 2002), Syrph the Net database (Speight et al. 2013) and an unpublished database held by the University of Reading (for bees).

3.3 Statistical analyses

Most statistical analyses were performed in R (R Development Core Team 2014). EstimateS (Colwell 2006) was used to analyse plant community similarity (Paper I). An overview of main focus of each paper and the explanatory variables included in the analyses are presented in Table 1.

3.3.1 Community similarity

To compare plant community composition along the gradient in the restored pastures with the plant community in adjacent grassland (Paper I), two complementary similarity indices were used. Sørensen index is a qualitative index that is based on presence/absence of species, while the Bray–Curtis index include the frequency of plant species occurrence (Magurran 2004).

3.3.2 Indicator species analyses

Indicator species analyses were used to identify pollinator species that were under-represented in restored pastures compared to their occurrence in intact grasslands in the surrounding landscape, and vice versa (Paper II).

3.3.3 Community trait composition

Community weighted trait mean

To assess the trait composition of plant and pollinator communities in each pasture (Paper III), calculations of the community-weighted trait mean (CWM) for plants, bees and hoverflies were made (Garnier et al. 2004). Due to the interdependence between flowering plants and pollinators, the trait composition of flowering plants were also analysed separately. Vegetation height and tree and shrub cover were included in the CWM for plants to describe the vegetation structure within pastures. A distance matrix was created from pairwise comparisons of community trait composition, and to explore differences and variations in trait composition among management states the distance matrix was analysed using permutational analysis of variance (PERMANOVA, Anderson 2001), permutational analysis of dispersion (PERMDISP, Anderson 2006), and non-parametric multidimensional scaling (NMDS, Oksanen 2015).

Table 1. *The central theme of my thesis is to assess the effects of habitat fragmentation on plant and pollinator community recovery following grassland restoration. In four papers I evaluate the recovery of plant and pollinator communities from different perspectives. Listed are the main focus of each paper (marked in grey), and the explanatory variables included in the analyses. The papers are based surveys conducted in semi-natural grasslands in south-central Sweden in 2011 and 2012.*

	Paper I	Paper II	Paper III	Paper IV
Main response variables				
Species richness	x			
Species composition	x	x		
Trait composition		(x[i])	x	
Network beta diversity				x
Explanatory variables				
Connectivity		x	x	x
Adjacent land use	x			
Management state			x	x
Time since restoration	x	x	x	x
Abandonment time			x	
Pasture area		x	x	
Distance from edge	x			
Species traits		x	x	
Shrub cover			x[j]	
Vegetation height			x[j]	
Flower abundance			x[j]	x

i indirectly through exploration of the effect that species traits have on species composition

[j] only for pollinators

RLQ/ Fourth corner analysis

Assessments of how local and landscape environmental factors affect species traits composition in restored pastures (Paper III) was made using a method that combines two complementary approaches: the Fourth corner analysis (Legendre et al. 1997) and RLQ analysis (Dolédec et al. 1996). The combined approach makes it possible to relate species traits to environmental variables via species abundance (Dray et al. 2014), explores relationships between all environmental variables and all species traits, as well as accounts for co-variations among them. Trait environmental relationships were analysed for the entire plant community, flowering plants, bees and hoverflies. The environmental variables tested for were pasture area, connectivity to intact grasslands in the landscape, time since restoration and abandonment time. In addition, vegetation structure in terms of tree and shrub cover, vegetation height and flower abundance were included in the analyses for pollinators.

3.3.4 Network analyses

Plant-pollinator interaction networks were analysed in terms of species number, number of links per species and beta diversity of species and interactions among pastures (Paper IV). Beta diversity of species and interactions were obtained from pairwise comparisons between all local networks, and between local networks and the compiled web of all interactions observed across all study sites, referred to as the ‘metaweb’. By applying classic beta diversity to a pairwise comparison of networks it is possible to disentangle the effect of species turnover and rewiring of interactions on network dissimilarity (Poisot et al. 2012). PERMANOVA and NMDS (see CWM analyses above) were used to assess if the beta diversity of species and interactions differed among pasture states.

3.3.5 Linear and mixed models

General linear mixed models were used to test for *i)* time and edge effects on plant species richness and similarity in plant community composition compared to that in adjacent intact grassland (Paper I), and *ii)* the effect of environmental variables and species traits on pollinator species occurrence probability in restored pastures (Paper II). ‘Site’ was used as a random factor to account for site specific patterns in the datasets (Bunnefeld & Phillimore 2012).

Linear models were used to investigate *i)* if pollinator species occurrence probability in restored pastures differed among species groups (solitary bees, bumble bees and hoverflies) and among species with different traits (Paper II), and *ii)* if environmental variables affect plant-pollinator network properties (IV).

To facilitate the interpretation of main and interaction effects of continuous environmental predictor variables, distance, area, connectivity, time since restoration and abandonment time were scaled in all models by subtraction of the mean from all data points to give a mean of zero. Thereafter all points were scaled to 1 SD by division with the sample SD (Schielzeth 2010).

In paper I and IV, models were compared based on AICc (which account for small sample size) and Akaike weights. Models with delta AICc >2 were considered to differ in fit (Burnham & Anderson 2002). In paper I, because no single best model was found, model averaging was used to assess the contribution of each explanatory variable to observed richness and similarity patterns. Model averaging gives average parameter estimate based on the weighted estimate from all candidate models. The relative variable importance is the summed Akaike weight for the subset of models for which each explanatory variable is included (Burnham and Anderson 2002). In paper IV, models were compared to the null model to assess if the effect of environmental variables on networks structures were real, or part of the variation within the dataset.

4 Results and discussion

4.1 Plant community recovery in relation to adjacent land use

Restored pastures located adjacent to intact grasslands had a higher species richness than those adjoining crop fields (Figure 7a and b). Also, plant communities in restored pastures had the highest similarity to intact pastures near the border between the two pastures, which decreased with increasing distance from the border. This indicates that nearby grasslands act as population sources for recovering plant communities, with species colonizing restored pastures in a stepwise manner from intact grasslands (Cousins & Lindborg 2008; Hutchings & Booth 1996). It appeared, however, that additional processes were involved in the observed plant community recovery. Specifically, time since restoration and distance from the pasture border were the two variables that had the strongest effect on small-scale (1 m^2) plant species richness patterns within restored pastures: species richness increased with time since restoration and decreased with distance from the pasture border. These patterns were not affected by adjacent land use, which would be expected if short distance dispersal from nearby population sources were the only mechanism behind plant community recovery. Furthermore, grassland specialist species did not respond as strongly as total species richness to adjacent land use. This suggests that the recovery of target species for grassland restorations recover by other means than short distance dispersal from adjoining population sources. Species persistence during habitat degradation (Pykälä et al. 2005; Pärtel et al. 1998), species potential for long distance dispersal by different vectors (Ozinga et al. 2004), seed bank longevity (Bossuyt & Honnay 2008), and historical land use within the restored pasture and its surroundings (Bommarco et al. 2014; Helm et al. 2006) are examples of factors that also could influence the chance of successful plant community recovery after restoration. These factors should, together with adjacent land use, be considered in the planning of restoring plant communities in grasslands.

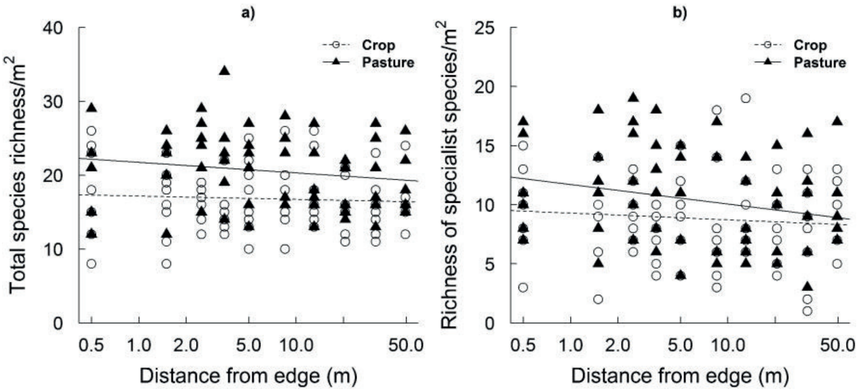

Figure 7. Species richness of a) the total plant community and b) grassland specialist species within restored semi-natural pastures in south-central Sweden, measured in 1 m^2 plots placed along a distance gradient (0-50 m) from the border of the restored pastures towards the pasture centre. Trends in species richness in relation to distance from the pasture border are given for pastures adjoining crop land and intact semi-natural pastures, respectively. Each data point represents a single 1 m^2 plot. Note the quasi-logarithmic scale on the x-axis.

4.2 Pollinator community recovery in relation to species traits

When comparing the pollinator community composition within restored pastures to the composition in intact grasslands in the surrounding landscape, six hoverfly and seven bee species were found to be characteristic for intact grasslands, whereas no species were characteristic for restored pastures only. This means that the pollinator communities in restored pastures consisted of a subset of the species pool observed in the surrounding landscapes. In relation to the landscape species pool, the occurrence probability within restored pastures differed for bumblebees, solitary bees and hoverflies. Among the three pollinator groups, solitary bees were most often absent from restored pastures as compared to the regional species pool (Figure 8a), and also displayed increasing occurrence probability in restored pastures with increasing grassland connectivity (Figure 8b). The dispersal ability of species is generally correlated to their body size (Gathmann et al. 1994), and mobile species are better adapted to re-colonize restored habitats than are sedentary species (Baur 2014; Bakker & Berendse 1999). Indeed, among hoverflies, both species with larger body size and migratory species were more likely to occur in restored pastures compared to small and non-migratory species. For bees, no effect of body size within any of the two groups was found. However, if all bees were pooled, larger (bumblebees), and hence more mobile bee species (Greenleaf et al. 2007; Steffan-Dewenter et al. 2002), were more likely than small species (solitary bees) to occur in restored pastures. The difference in occurrence probability in restored pastures between bees and hoverflies is likely also related to differences in resource use. Hoverflies are not strictly dependent on semi-natural grasslands and can more freely utilize resources within the larger landscape, whereas solitary bees often display decreasing densities with increasing distance to semi-natural grasslands (e.g. Ekroos et al. 2013; Jauker et al. 2009).

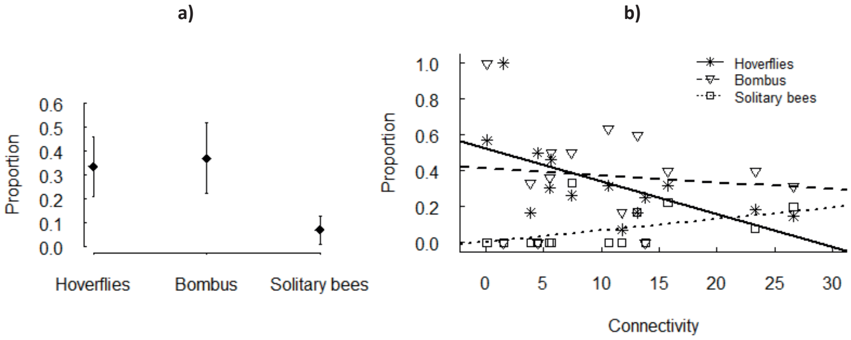

Figure 8. The proportion of pollinator species present in the surrounding landscape also occurring in restored pastures was lower for solitary bees than hoverflies and bumble bees (a). For solitary bees, the occurrence probability in restored pastures increased with increasing connectivity, whereas it decreased for hoverflies (b). Pollinator surveys were conducted in semi-natural pastures in south-central Sweden during the period May-July in 2012.

The availability of and preferences for nest sites have been shown to structure bee communities (Forrest et al. 2015; Kremen & M'Gonigle 2015; Potts et al. 2005). Accordingly, the occurrence probability for bumblebees and solitary bees within restored pastures were related to species nesting traits. Parasitic species of both bumblebees and solitary bees had low probability to occur in restored pastures. The slow recovery of parasitic bee species could be an effect of their regularly high degree of specialization (Løken 1984), and their dependence on well-recovered populations of their host species. Furthermore, ground excavating solitary bees displayed low occurrence. This was unexpected considering that the clearing of trees and shrubs during restoration creates patches of bare ground, which should offer suitable nest sites for many ground excavating species (Westrich 1996).

Prioritizing grassland restoration sites where nearby population sources are available can promote the recovery of sedentary and specialized bees and improve recovery of pollinator communities. However, it is still unclear what possible effects the observed differences in trait composition between restored pastures and the surrounding landscape might have for species interactions and ecosystem functions.

4.3 Restoration and landscape effects on plant and pollinator trait composition

The trait composition of plant communities differed among management states of pastures. For instance, the vegetation in continuously grazed pastures was dominated by forbs and species with grazing adapted growth forms, whereas abandoned and restored pastures held a larger proportion of grasses and species with erosulate growth form. Despite the similarity between abandoned and restored pastures in these traits, their overall plant trait composition differed. The composition in restored pastures was more similar to that in continuously grazed pastures than that in abandoned pastures, which was clearly differentiated from that in both restored and intact pastures (Figure 9a). Among plants, the trait composition of flowering plants in restored pastures displayed recovery with time since restoration (Figure 9b). In contrast, the trait composition of pollinators was not influenced by either grassland management or time since restoration.

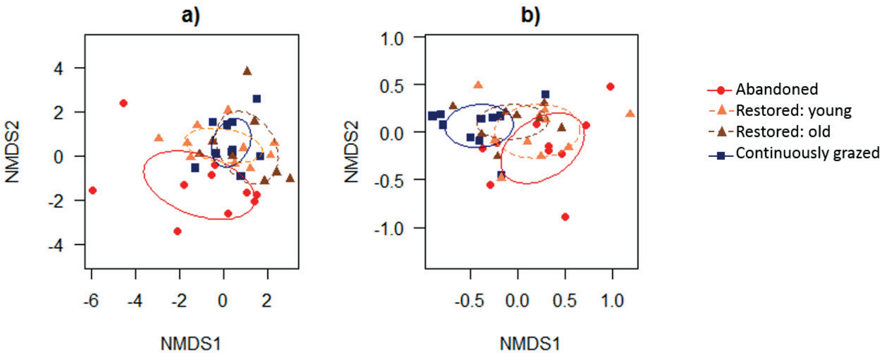

Figure 9. Non-parametric multidimensional scaling (NMDS) visualizing the trait composition of a) the 'entire' plant community (excluding trees, woody plants and shrubs with a maximum height of >1 m) and b) flowering plants in semi-natural pastures of three pasture states (abandoned, restored and continuously grazed), located in south-central Sweden. The NMDS was based on distance matrices of community-weighted trait means (CWM) for dominating (or most relevant) trait levels within local plant communities. To visualize the effect of 'time since restoration', restored pastures were plotted in two age classes: 'young' and 'old' (restored 1-5 and 8-15 years prior to the study in 2012, respectively). NMDS stress = 0.18 and 0.03 respectively.

If resources that are required by species are not sufficient within a habitat fragment, mobile organisms such as pollinators can utilize complementary resource in the surrounding landscape (Dunning et al. 1992). This type of landscape complementarity is probably an important factor behind the sustained pollinator trait composition across management states and over time since restoration. Within restored pastures, the exploration of relationships between species traits and environmental factors revealed that pollinator trait composition was affected by vegetation structure (shrub cover, flower abundance and vegetation height) and to some extent (only for bees) by connectivity to intact grasslands. High flower abundance was related to decreasing feeding specialization among bees, and high shrub cover was associated with hoverfly species with wood-living larvae. Vegetation height affected bee trait composition, such that the proportion of parasitic bees increased when the vegetation was low, and the proportion of nest-renting species when vegetation was high. With equally abundant floral resources across management states, the availability of woody species and the vegetation height could, thus, be important to keep a sustained trait composition among pollinators on a landscape scale.

Plant trait composition was not affected by connectivity to intact grasslands. Considering that many grassland specialist species have a limited long distance dispersal capacity (Verkaar et al. 1983), the observed changes in plant trait community is likely a result of that species are able to survive as remnant populations during periods of abandonment (Eriksson & Eriksson 1997; Lindborg & Eriksson 2004), and/or recover from the seed bank (Fagan et al. 2008). Among pollinators, only the trait composition of bees was affected by connectivity. The contrasting effects among pollinator groups could, again (see previous section), be due to differences in resource use, dependency upon semi-natural grasslands (e.g. Jauker et al. 2009; Ekroos et al. 2013), and species mobility. Whereas most hoverflies are relatively mobile (Schweiger et al. 2005), the dispersal ability of bees ranges from highly mobile bumblebees (Greenleaf et al. 2007) to very sedentary solitary bees (Franzén et al. 2009). Among bees, small-bodied species were negatively affected by isolation, probably as an effect of low mobility (Schweiger et al. 2005; Greenleaf et al. 2007).

The gradual recovery of plant trait composition after grassland restoration, and the sustained pollinator trait composition even during grassland abandonment demonstrates how interacting plants and pollinators are under influence of different trait-environmental relationships. Even if important relationships between traits and environmental variables that shapes plant and pollinator communities in restored pastures was identified, the underlying processes behind the observed patterns were not fully explained. For this purpose, assessments of seed bank longevity for grassland plant species and the availability of resources for pollinators within the landscape would be a step in the right direction.

4.4 Restoration and landscape effects on interaction networks

The overall richness and abundance of flowering plants (measured independently from networks) did not differ among management states, whereas the richness and abundance of pollinators (flying and flower-visiting combined) were highest in restored pastures. The beta diversity of species and interactions, obtained from pairwise comparisons of local networks (Poisot et al. 2012), revealed that the compositional turnover of species among networks was very high across study sites, both for flowering plants (β_L, mean = 0.89, where $\beta_L = 1.0$ would mean no species overlap), and for pollinators (β_U, mean = 0.92). The turnover of species among sites was the main driver in the observed turnover of interactions (β_{WN}), but also species behavioural shifts contributed, as reflected by re-wiring of interactions among co-occurring species (β_{OS}). Pollinators are known to be able to switch interaction partner if their preferred partner go extinct or declines in abundance (Fründ et al. 2010; Petanidou et al. 2008). This re-wiring of interactions makes communities less vulnerable to secondary extinctions (Kaiser-Bunbury et al. 2010). Also, it means that it would not have been possible to predict interaction composition from species co-occurrence patterns.

Whereas plant composition within networks could not be explained by grassland management (Figure 10a), the composition of pollinators and interactions were different in abandoned pastures compared to restored and continuously grazed pastures, and displayed a recovering trend when abandoned pastures had been restored (Figure 10b and c). Pollinator response to land use change has been shown to largely follow changes in floral resources imposed by land use change (Winfree et al. 2011). Since the three management states held similar flower abundance, the effect of grassland restoration on pollinator communities was likely due to changes in floral traits (Potts et al. 2003), or in other resources and conditions important for pollinator survival and reproduction. Abandoned pastures have higher cover of shrubs and trees, higher vegetation and deeper litter layer than continuously managed grasslands (Wissman 2006; Plantureux et al. 2005; Hansson & Fogelfors 2000). After restoration, when grassland are opened up through clearing and management is re-instated (Lindborg & Eriksson 2004), the structures and microclimatic conditions alters again (Suggitt et al. 2011; Thomas 1983). With pollinator richness and diversity being highest in restored pastures, it appears, thus, that the early stages of grassland restoration offers unique resources and conditions that are beneficial for a rich pollinator community, probably due to high environmental heterogeneity.

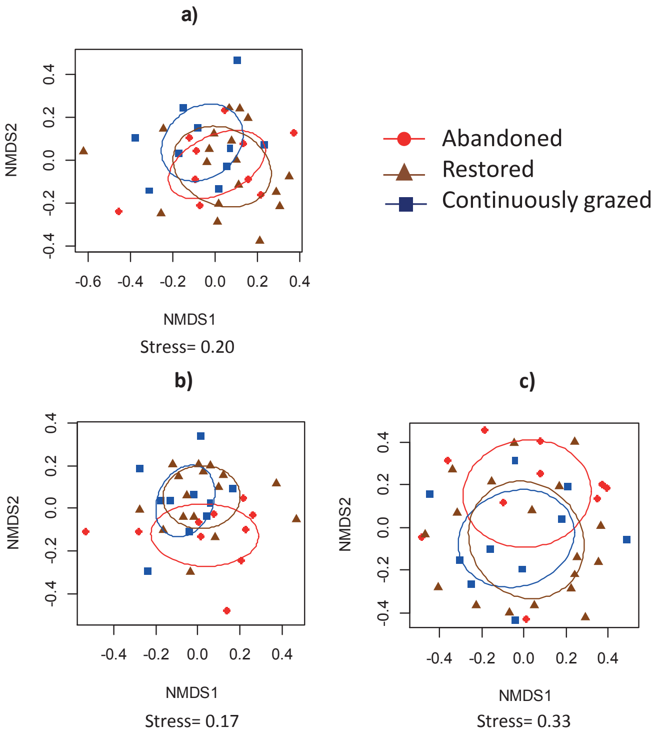

Figure 10. Non-parametric multidimensional scaling (NMDS) visualizing beta diversity of a) plant composition, b) pollinator composition and c) interactions within plant-pollinator networks of abandoned, restored and continuously grazed semi-natural pastures in south-central Sweden. The NMDS was based on distance matrices from pairwise comparison of local networks. For the pollinator composition, one outlier obscured the patterns, and made it difficult to assess how pollinator beta-diversity differed among pasture states. Therefore, this data point was removed from the pollinator beta diversity plot (b), but was included in all other figures and analyses.

The often observed declines in plant species richness and altered plant community composition in abandoned grasslands (Galvanek & Leps 2008; Pykälä 2003) was not reflected in either the richness of flowering plants or in the plant composition within networks. However, compared to the regional network of interactions compiled across all study sites, beta diversity of interactions among co-occurring species ($\beta_{OS'}$) was highest in abandoned grasslands, lowest in continuously grazed, and intermediate in restored pastures. This means that grazed pastures had a higher proportion of rare species and interactions than abandoned pastures.

Neither grassland connectivity nor time since restoration affected network size or local network similarity to the regional network composition. The turnover of species and interactions among sites are, hence, mainly driven by local scale factors, and plant-pollinator interactions can be restored without delay even in fragmented landscapes. Furthermore, since both abandoned and restored grasslands can contribute to the overall diversity and functioning of the agricultural landscape, temporary abandonment of semi-natural grasslands does not have to be negative.

4.5 Concluding remarks

At the outset of my work, I expected more pronounced effects of grassland connectivity on plant and pollinator community recovery and on plant pollinator interaction networks than what I actually found. Still, the observed effects show that especially two mechanisms behind community recovery relates to connectivity: dispersal of plant and pollinator species, and the resource use by pollinators within and outside grassland fragments. Also, when the goal is to restore communities of interacting groups of species, my results highlight the importance of considering the scale of fragmentation and its effect on organism groups. Plants respond to grassland connectivity on a local scale, and bees on a larger landscape scale. Hoverflies appear to respond to land use intensity and resource availability within landscapes in general, rather than to grassland connectivity *per se*.

Assessments of landscape connectivity are often based on human perception of habitats, but this type of classification does not always reflect the way that organisms utilize resources in the landscapes (Lindenmayer et al. 2008). Indeed, restored pastures appear to offer conditions that support a richer pollinator community than intact grasslands. Using connectivity to intact grasslands as a measure of habitat fragmentation might, hence, underestimate available resources and the amount of potential source populations within landscapes. Also, abandoned pastures supports a distinct set of pollinators and plant-pollinator interactions compared to restored and intact pastures, which is interesting from a biodiversity and functional point of view for the agricultural landscape as a whole. In summary, even though intact semi-natural grasslands are key habitats for maintaining overall biodiversity and functioning within the agricultural landscape, also abandoned and restored grasslands are important habitats and can provide source populations.

Since grasslands are still being lost and degraded due to abandonment and intensification (Romão et al. 2015), it could be argued that efforts should focus more on maintenance of remaining intact grasslands, rather than on the restoration of degraded grasslands. Plant species recovery after restoration has been thoroughly explored in restoration evaluations (McAlpine et al. 2016), and as many of these (e.g. Waldén & Lindborg 2016; Lindborg & Eriksson 2004; Pykälä 2003), my results show that restoration of grasslands from an abandoned state can revert declines in plant species richness. In addition, my thesis shows that both the functional composition of plants, the composition of pollinators within networks, and interactions between plants and pollinators can recover following restoration. In light of the possibility to restore plant communities and plant-pollinator interactions, the contribution of abandoned and restored grasslands to biodiversity and functioning suggests that abandonment does not necessarily have to be negative. Finding ways to maintain grasslands of different successional stages within landscapes could, rather, be beneficial for pollinator communities and ecosystem functioning. However, since plant community recovery following restoration takes considerable time, the practical implementation of such a landscape approach is a challenging task. Temporary abandonment of previously restored sites probably has more severe consequences for biodiversity than temporary abandonment of ancient intact grasslands. Especially rare plant species are slow or might even be unable to recover following restoration (Lindborg & Eriksson 2004; Pykälä 2003). Also, I found that specialized bee species were largely lacking in restored sites even if they were present within the nearest landscape. This means that abandonment can lead to the irreversible loss of rare and perhaps functionally important species. Therefore, before the implementation of a grassland management regime, where abandonment is part of a biodiversity conservation measure, there is a need for further investigation of mechanisms behind plant and pollinator community recovery beyond species dispersal from nearby source populations.

In this thesis, I have used methods to evaluate habitat restoration outcomes that extends beyond the commonly used measures of species richness and abundance. By considering also the functional response of plants and pollinator communities to habitat restoration and landscape composition, my thesis brings insights into parts of the mechanisms behind plant and pollinator community responses in fragmented landscapes. Even though connectivity to intact grasslands explains parts of the observed patterns in the recovery of plant and pollinator communities, other possible mechanisms behind species responses needs to be further investigated for full understanding.

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