

Restoration of semi-natural grasslands

Impacts on biodiversity, ecosystem services and stakeholder perceptions

Emelie Waldén

Academic dissertation for the Degree of Doctor of Philosophy in Physical Geography at Stockholm University to be publicly defended on Thursday 14 June 2018 at 13.00 in Högbomsalen, Geovetenskapens hus, Svante Arrhenius väg 12.

Abstract

Humans play a major role shaping the living conditions for not only ourselves, but also all other species on Earth. In fact, some species-rich habitat types require human management to uphold the biodiversity and related ecosystem services. One of the world's most biodiverse habitats on small spatial scales, semi-natural grasslands, have been formed over the course of centuries through extensive grazing and mowing. However, due to political and economic reasons, up to 90% of the European semi-natural grasslands have been lost during the 20th century. To counteract these drastic losses, restoration actions are implemented in environmental policies across Europe. Yet, knowledge of the long-term restoration effects on biodiversity and ecosystem services is still limited. The vast need for future restoration also requires a better understanding of how different pre-conditions affect the restoration outcome, as well as how stakeholders perceive restoration, to be able to prioritise between sites and recognise the limitations of the restoration process. In this thesis, I examine restoration outcomes in Swedish semi-natural grasslands, in terms of plant diversity, associated ecosystem services and from the farmers' and land-owners' perspective. The outcome is also analysed in relation to environmental factors at the local and landscape scale. I found that the overall community composition recovered to resemble intact reference communities, but it took relatively long time (12-20 years). Moreover, the reference sites still had higher species richness both at large and small spatial scales, more grassland specialist species and a higher abundance of plant species important to the five tested ecosystem services (meat production, pollination, water retention, temperature regulation and cultural heritage). My results show that prioritising large, unfertilised, newly abandoned grasslands situated in landscapes containing a large grassland specialist species pool and high amounts of intact and remnant semi-natural grasslands, could speed up the plant recovery. However, prioritising fast results does not necessarily ensure long-term success at a larger spatial scale. Since restoration success can be interpreted differently depending on evaluation measure used, pre-defined, clear and realistic goals are essential. While the surveyed farmers and landowners overall perceived the restoration as successful, 40% were unsure whether the grasslands will be managed in the future. Low profitability still poses a threat to their maintenance and thus, also to the coupled biodiversity and ecosystem services. Policy changes are therefore urgently needed to facilitate incentives for sustained management of restored and intact European semi-natural grasslands in a long-term perspective.

Keywords: *Biodiversity, Ecosystem services, Farmer, Landscape ecology, Plant, Policy, Restoration, Semi-natural grassland.*

Stockholm 2018

<http://urn.kb.se/resolve?urn=urn:nbn:se:su:diva-153905>

ISBN 978-91-7797-171-9
ISBN 978-91-7797-172-6
ISSN 1653-7211

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ISBN print 978-91-7797-171-9

ISBN PDF 978-91-7797-172-6

ISSN 1653-7211

Cover art: Emelie Waldén

Type set with LATEX using Department of Physical Geography dissertation template

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Printed by: Universitetsservice US-AB, Stockholm, Sweden 2018

Distributor: Department of Physical Geography, Stockholm University

Abstract

Humans play a major role shaping the living conditions for not only ourselves, but also all other species on Earth. In fact, some species-rich habitat types require human management to uphold the biodiversity and related ecosystem services. One of the world's most biodiverse habitats on small spatial scales, semi-natural grasslands, have been formed over the course of centuries through extensive grazing and mowing. However, due to political and economic reasons, up to 90% of the European semi-natural grasslands have been lost during the 20th century. To counteract these drastic losses, restoration actions are implemented in environmental policies across Europe. Yet, knowledge of the long-term restoration effects on biodiversity and ecosystem services is still limited. The vast need for future restoration also requires a better understanding of how different pre-conditions affect the restoration outcome, as well as how stakeholders perceive restoration, to be able to prioritise between sites and recognise the limitations of the restoration process. In this thesis, I examine restoration outcomes in Swedish semi-natural grasslands, in terms of plant diversity, associated ecosystem services and from the farmers' and land-owners' perspective. The outcome is also analysed in relation to environmental factors at the local and landscape scale. I found that the overall community composition recovered to resemble intact reference communities, but it took relatively long time (12-20 years). Moreover, the reference sites still had higher species richness both at large and small spatial scales, more grassland specialist species and a higher abundance of plant species important to the five tested ecosystem services (meat production, pollination, water retention, temperature regulation and cultural heritage). My results show that prioritising large, unfertilised, newly abandoned grasslands situated in landscapes containing a large grassland specialist species pool and high amounts of intact and remnant semi-natural grasslands, could speed up the plant recovery. However, prioritising fast results does not necessarily ensure long-term success at a larger spatial scale. Since restoration success can be interpreted differently depending on evaluation measure used, pre-defined, clear and realistic goals are essential. While the surveyed farmers and landowners overall perceived the restoration as successful, 40% were unsure whether the grasslands will be managed in the future. Low profitability still poses a threat to their maintenance and thus, also to the coupled biodiversity and ecosystem services. Policy changes are therefore urgently needed to facilitate incentives for sustained management of restored and intact European semi-natural grasslands in a long-term perspective.

Sammanfattning

Människan har sedan länge påverkat jordens ekosystem, där vissa habitat numer är beroende av skötsel för att upprätthålla biologisk mångfald och ekosystemtjänster. I naturbetesmarker och ängar (traditionella gräsmarker) har århundranden av hävd genom bete och slåtter format en artrikedom att jämföra med tropisk regnskog, med skillnaden att många av dessa arter är beroende av hävden för sin överlevnad. På grund av det senaste århundrandets jordbruksintensifiering har dock upp till 90% av de europeiska gräsmarkerna vuxit igen eller omvandlats till åkermark eller skogsplantering. För att motverka detta är restaurering av dessa habitat en viktig åtgärd som ingår i bl.a. EU:s ekonomiska stödsystem till lantbrukare. Ekonomiska incitament för restaurering har funnits i flera decennier, men kunskapen om långsiktiga effekter på biologisk mångfald och ekosystemtjänster är fortfarande relativt begränsad. För att möta det omfattande framtida restaureringsbehovet behövs också mer information om hur olika miljöfaktorer kan påverka resultatet, samt hur berörda aktörer uppfattar restaureringen. I denna avhandling undersöker jag restaurering av svenska traditionellt hävdade gräsmarker, med fokus på mångfald av växter och ekosystemtjänster, samt ur lantbrukares och markägares perspektiv. Detta analyseras i förhållande till lokala förhållanden i gräsmarkerna och omgivande landskapsfaktorer. Jag fann att artsammansättningen i restaurerade gräsmarker utvecklades till att likna sammansättningen i kontinuerligt hävdade (intakta) referensgräsmarker, men att denna återhämtning tog relativt lång tid (12-20 år). Referensmarkerna hade dock fortfarande högre artrikedom, fler gräsmarksspecialiserade arter och högre abundans av växter viktiga för fem ekosystemtjänster: köttproduktion, pollinering, vattenhållningsförmåga, kolinlagring och kulturarv. Mina resultat visade även att prioritering av stora, ogödslade, nyligen övergivna gräsmarker belägna i landskap med många intakta gräsmarker och resthabitat, samt en stor artpool med gräsmarksspecialister, skulle kunna påskynda växters återetablering. Det bör dock påpekas att restaurering av gräsmarker kan ge goda effekter också i andra slags landskap, även om det kan ta längre tid. Sammantaget synliggör min avhandling att beroende på vilken utvärderingsmetod som används kan restaureringsresultatet tolkas på olika sätt. För att kunna göra en korrekt utvärdering behövs därför tydliga och realistiska mål som definierats innan restaureringen. Lantbrukarna och markägarna upplevde överlag att restaureringen varit framgångsrik. Trots detta var 40% osäkra på huruvida dessa gräsmarker kommer att skötas i framtiden, framför allt på grund av låg lönsamhet. Därmed är det av yttersta vikt att stödsystemen utformas för att gynna hållbar och långsiktig hävd av både restaurerade och intakta naturbetesmarker och ängar i Europa.

Thesis content

This doctoral thesis consists of a summary and the four papers listed below (I-IV). The published papers are reprinted with permission from the respective copyright holder.

- I** **Waldén E**, Lindborg R. (2016) Long Term Positive Effect of Grassland Restoration on Plant Diversity - Success or Not? *PLoS ONE* 11(5): e0155836.
- II** **Waldén E**, Öckinger E, Winsa M, Lindborg R. (2017) Effects of landscape composition, species pool and time on grassland specialists in restored semi-natural grasslands. *Biological Conservation* 214, 176–183.
- III** **Waldén E**, Queiroz C, Lindborg R. Biodiversity mitigates trade-offs among multiple ecosystem services. *Manuscript*
- IV** **Waldén E**, Lindborg R. Facing the future of grassland restoration – What about the farmers? *Under review in Journal of Environmental Management*

Author contributions

The contributions from listed authors are divided as follows for each article.

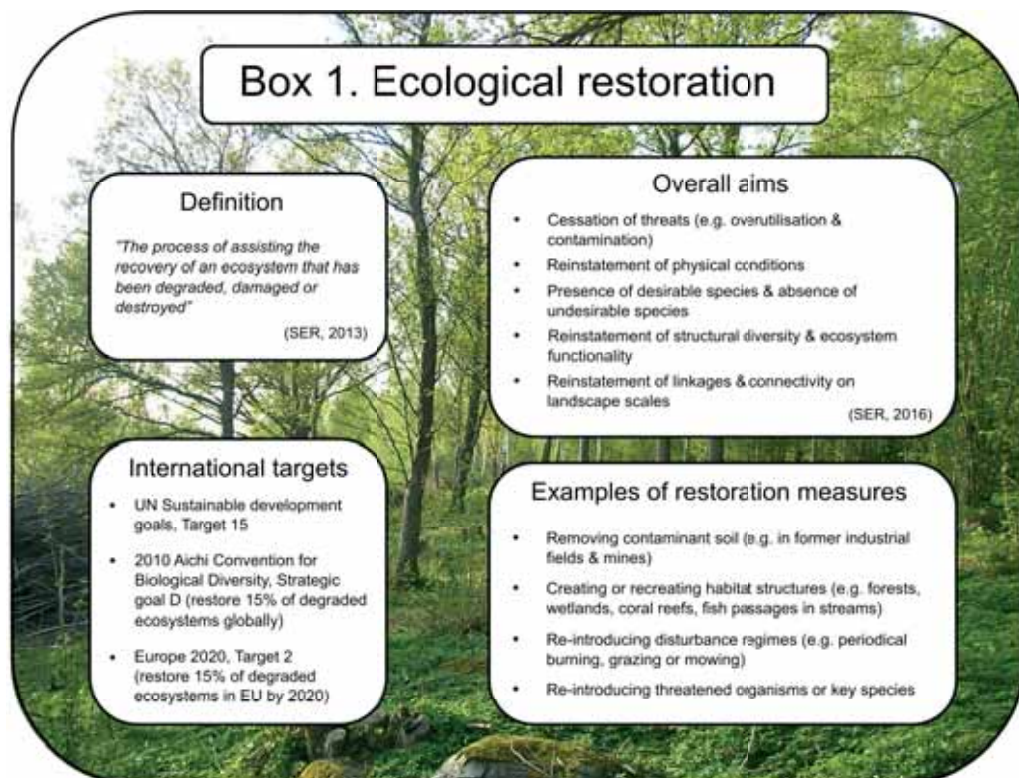
- I** Conceived and designed the study: EW, RL
Performed the field work and data collection: EW, RL
Analysed the data: EW
Wrote the paper: EW, RL
- II** Conceived and designed the study: EW, RL
Performed the field work and data collection: EW, MW
Analysed the data: EW
Wrote the paper: EW, EÖ, MW, RL
- III** Conceived and designed the study: EW, CQ, RL
Performed the data collection: EW, CQ
Analysed the data: EW
Wrote the paper: EW, RL, CQ
- IV** Conceived and designed the study: EW
Performed the field work and data collection: EW
Analysed the data: EW
Wrote the paper: EW, RL

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1 Introduction

Today we face worldwide ecosystem changes, directly or indirectly caused by humans (Ellis and Ramankutty, 2008; Hooke and Martín-Duque, 2012). Across the globe, habitat destruction and degradation combined with rapid climate change and invasions of alien species have led to major losses of biodiversity (Brook et al., 2008). Biodiversity is important, not only for its intrinsic value, but also for all the benefits people obtain from it. In fact, our way of life depends on other species providing us with many different kinds of ecosystem services (Díaz et al., 2006; Millennium Ecosystem Assessment, 2005). To promote biodiversity and ensure functioning ecosystems for future generations, various measures are being implemented on different spatial scales and political levels in order to conserve remaining natural habitat. Since this may not be sufficient, the restoration of degraded and destroyed ecosystems (Box 1) is also considered as high priority (Suding et al., 2015).



Habitat restoration is a costly procedure involving a range of different priorities, where not only natural habitats require consideration, but also semi-natural habitats, of which many harbour high biodiversity and contribute to multiple ecosystem services. Examples of such habitats are European semi-natural grasslands, which are ancient pastures and meadows traditionally managed by grazing or mowing, without the use of pesticides

or fertilisers in modern time (Box 2). These habitats have developed through centuries by human maintenance to become biological hotspots of high conservation value in agricultural landscapes (Habel et al., 2013; WallisDeVries et al., 2002). They are included in the European Union (EU) Rural Development Programme as key features in the so called *High Nature Value farming*, where biodiversity is maintained by low-intensity farming (Beaufoy, 2011; Lomba et al., 2014; Paracchini et al., 2008). Semi-natural grasslands also play a major role in the supply of multiple regulating ecosystem services in agricultural landscapes (García-Feced et al., 2014), such as pollination (Öckinger and Smith, 2007), natural pest control (Bianchi et al., 2006; Gardiner et al., 2009), water regulation (Macleod and Ferrier, 2011; Souchère et al., 2003) and temperature regulation (Guo and Gifford, 2002; Ostle et al., 2009; Soussana et al., 2010). They are also important for many cultural ecosystem services, including recreation, tourism, cultural heritage and aesthetics (Garrido et al., 2017; Plieninger et al., 2015; Southon et al., 2017). However, due to agricultural intensification, but also abandonment (Romão et al., 2015), relatively few semi-natural grasslands remain and restoration efforts could be crucial for their future existence (BIO by Deloitte, 2015; Helsen et al., 2012).

Global meta-analyses covering restoration of all kinds of habitat types often show low success rates of restoration actions (Jones et al., 2018; Suding, 2011). Even where restoration of degraded semi-natural grasslands has been implemented for several decades, relatively few studies of its outcome have been performed, especially over long time-series (Prach and Walker, 2011; Pykälä, 2003). Targeting efficient restoration measures and pinpointing limitations might be necessary, given the high need for future restoration in remaining degraded and destroyed European semi-natural grasslands (BIO by Deloitte, 2015). In this thesis, I will summarise the current knowledge and present new results on semi-natural grassland restoration, how it can affect biodiversity and ecosystem services and the perceptions of stakeholders.

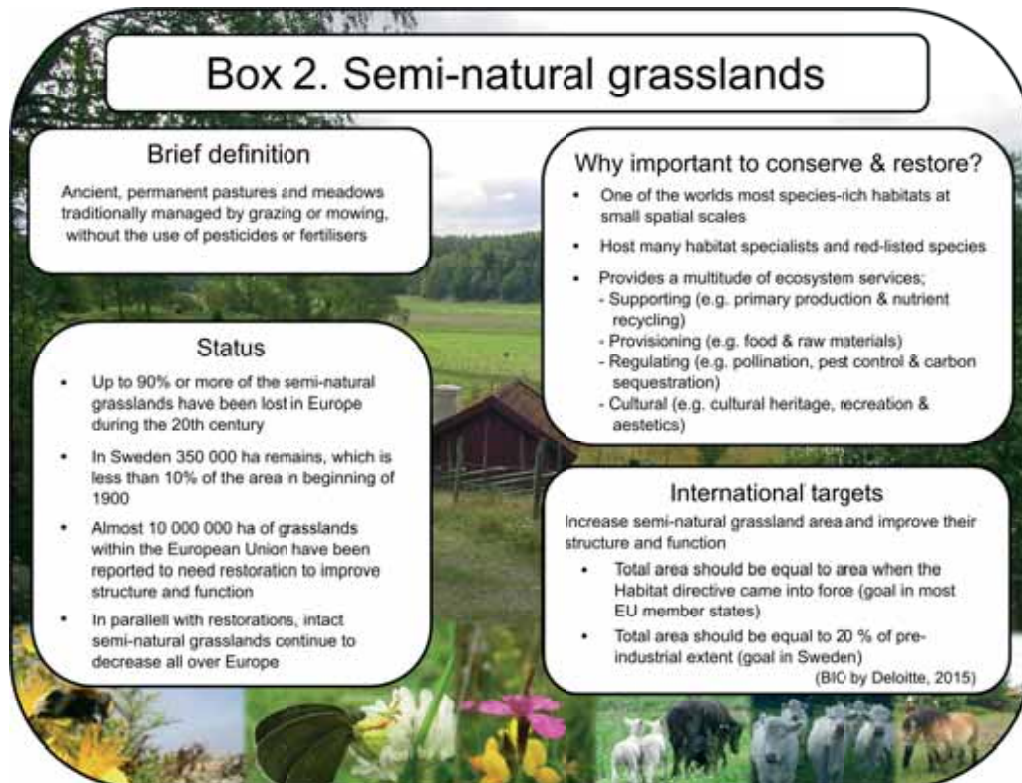
1.1 Background

1.1.1 Historical background of European semi-natural grasslands

The maintenance of semi-natural grasslands has a long history in Europe. Typically, today's species-rich grasslands originate from forest clearance for agriculture several thousand years ago (Ellenberg, 2009) and were used for haymaking and as grazing land for livestock (Hartel and Plieninger, 2014; Poschlod and WallisDeVries, 2002; WallisDeVries et al., 2002). The permanent meadows and pastures were often located in parts of the landscape that were unsuitable for cultivation, such as stony and hilly habitats (Fuller et al., 2017) or on wet soils dominated by clay (Cousins, 2009). The distance to the farm was important, where close-by grasslands often were used more intensively, creating an open or semi-open environment with scattered trees, while vast areas of forest were used for extensive grazing (Dahlström et al., 2006; Fuller et al., 2017; Jørgensen and Quelch, 2014).

Large areas of Scandinavia were covered by such grasslands, due to the need for grazing grounds and production of winter fodder for livestock (Ekstam and Forshed, 2000; Eriksson et al., 2002). Throughout centuries, humans managed them by traditional extensive grazing and mowing, which created a unique habitat containing among the highest small-scale density of plant species to be found in terrestrial environments (Austrheim et al., 1999; Eriksson et al., 2002; Habel et al., 2013; Wilson et al., 2012). One square me-

tre has been reported to harbour more than 60 plant species (Eriksson et al., 2006; Kull and Zobel, 1991), including many species only to be found in this habitat. Semi-natural grasslands are also important for several other organisms not studied in this thesis, such as insects (Steiner et al., 2016; Söderström et al., 2001; Öckinger and Smith, 2007), earthworms (Ivask et al., 2012), soil microorganisms (Strecker et al., 2016), birds (Jakobsson and Lindborg, 2017; Pärt and Söderström, 1999) and bats (Wood et al., 2017). To maintain their high biodiversity, it is crucial that disturbance by traditional grazing or mowing is continued (Aavik et al., 2008; Eriksson et al., 2002; Schrautzer et al., 2011).



1.1.2 Ecological processes forming grassland biodiversity

Local environmental conditions such as light availability, soil moisture and nutrient content highly affect plant community composition. In semi-natural grasslands, the natural succession into forest is prevented by grazing or mowing. Due to a continuous removal of plant material, dry species-rich semi-natural grasslands are also relatively nutrient-poor (Kull and Zobel, 1991). The removal of plant material along with livestock trampling also create gaps, allowing less competitive species to co-exist with more competitive species (Kalamees and Zobel, 2002). This historical disturbance regime has shaped the species community existing at each specific site (Dahlström et al., 2008; Eriksson et al., 2015). In traditional semi-natural pastures, typical grassland plants (grassland specialist species) have evolved strategies to avoid or cope with intermediate grazing. These evolutionary adaptations could for example be expressed as chemical properties (e.g. unpalatability or high amounts of silica), morphological structures (e.g. thorns/spikes/hairs, or nutrient storage close to ground/in roots), or in the plant phenology (e.g. early seed set) (Diaz et al., 2001; Lavorel et al., 1997; Ågren et al., 2006). Some of these traits can also be found in grassland plants typical for traditional meadows, for example early flowering and seed set (Eriksson et al., 2015).

The spatial conditions, in terms of habitat area and surrounding landscape composition, also affect local diversity. In line with island biogeography theory (MacArthur and Wilson, 1967), larger semi-natural grasslands tend to contain more species (e.g. Bruun, 2000; Cousins et al., 2007; Krauss et al., 2004), probably due to the increased variation in microhabitats (Eriksson et al., 1995; Gazol et al., 2012; Öster et al., 2007). As both inbreeding and stochastic population extinction can occur even in good local conditions, long-term population persistence depends on species being able to disperse and establish at other sites. This ability is highly affected by the surrounding landscape configuration, i.e. the habitat connectivity (the distance to and size of similar habitats) and landscape composition (the number of and relative abundance of habitat types) (Brückmann et al., 2010; Hanski, 1999; Öckinger et al., 2012). The surrounding landscape configuration similarly affects presence of species that are available for habitat colonisation, i.e. the species pool (Cornell and Harrison, 2014). Moreover, effective dispersal among habitat patches is also related to plant functional traits, as well as the interactions between these traits, dispersal vectors and landscape composition (Auffret et al., 2017). Plant dispersal traits mainly relate to reproduction propagules, e.g. pollen or seeds. For example, seed dispersal capacity encompasses size, amount and form of the seeds, where some species have evolved seeds with hooks that can attach animal fur. Besides spatial dispersal, some species can also store their seeds in the soil seed bank (Bekker et al., 1997), allowing for temporal dispersal when conditions are suitable (Havrdová et al., 2015; Plue and Cousins, 2013; Vandvik et al., 2016). Seed bank storage and traits related to persistence (e.g. perennation) can therefore create a temporal time-lag in species extinction following a degradation of habitat conditions.

1.1.3 Relationships between biodiversity, species traits, ecosystem functions and services

While ecosystem processes affect biodiversity, biodiversity can also in turn affect ecosystem processes, e.g. by altering resource fluxes and changing abiotic conditions (Chapin et al., 2000; Jones et al., 1994). While the role of biodiversity in ecosystem functioning has been explored in, for example, many field experiments (Cardinale et al., 2012), measuring ecosystem services is still difficult and time-consuming (Malinga et al., 2015; Manning et al., 2018). One relatively recent method to assess ecosystem services via biodiversity, is by using ecosystem functions coupled to species functional traits, as an intermediate step (Díaz et al., 2007; Lavorel, 2013; Moor et al., 2017). As an example, the plant traits *nectar and pollen quantity* can be associated with the function *food provision for pollinators*, leading to the ecosystem service *pollination* (Fornoff et al., 2017). According to the mass-ratio theory (Grime, 1998), ecosystem functioning is primarily driven by the dominant species in a community. Since a species' functional role in the ecosystem is determined by its effect traits (see Violle et al., 2007), increased abundance of species with certain traits should increase ecosystem functioning and related services. There could also be trade-offs, whereby an individual species contributing strongly to one ecosystem function can at the same time exhibit traits with low or no impact on other functions. Therefore, a high trait diversity in a system promotes high functional diversity, i.e. many functionally disparate species (Petchey and Gaston, 2006, 2002).

Even though biodiversity can correlate with functional diversity (Petchey and Gaston, 2002), individual species may be redundant in the function they perform (Johnson et al., 1996; Loreau, 1998; Naeem, 2002). Nevertheless, biodiversity has been shown to have a strong positive effect when considering multiple functions and services. This has been

shown in field experiments (Hector and Bagchi, 2007; Isbell et al., 2011; Meyer et al., 2018), in natural few-species systems (Gamfeldt et al., 2013; van der Plas et al., 2016) and in data-simulations (Gamfeldt and Roger, 2017). High biodiversity may also act as a buffer to ensure ecosystem functioning and services during environmental changes (Fetzer et al., 2015; Hooper et al., 2005; Isbell et al., 2011; Walker, 1992; Yachi and Loreau, 1999). While the relationship between biodiversity and ecosystem functioning is still debated, studies linking biodiversity and multiple ecosystem services are comparably few. Disentangling this relationship is of high interest for researchers and stakeholders, but also urgent, due to the continued loss of biodiversity and habitats worldwide.

1.1.4 Semi-natural grasslands – a threatened habitat in need of conservation and restoration

Land-use changes during the last century have completely modified the traditional agricultural landscape in Europe (Benton et al., 2003; Krebs et al., 1999; Stoate et al., 2009). The intensification of agriculture, based on the use of pesticides, synthetic fertilisers and large monocultures, has replaced the former small-scale farming (Naylor et al., 2005; Strijker, 2005). On a landscape scale, agriculture is now concentrated and intensified in productive regions, while low-productive regions have been abandoned (Queiroz et al., 2014; Strijker, 2005). A persistent trend within the EU is that the farms are becoming fewer and larger, but also more specialised (European Union, 2016). For example, between 1980 and 2015, the amount of cattle reduced by 24% and the number of cattle holdings decreased by 75% in Sweden (Statistics Sweden, 2016). These large-scale land use changes have caused a dramatic loss of managed low-productive habitats. Up to 90% of semi-natural grasslands in some European areas have been lost during the last century (Cousins et al., 2015; Poschlod and WallisDeVries, 2002; Pärtel et al., 1999; WallisDeVries et al., 2002). Extensive areas of grasslands have been completely transformed into arable land or forest plantations (Fuller, 1987; Poschlod and WallisDeVries, 2002; Romão et al., 2015). Management abandonment and lack of grazing and mowing have also highly affected these habitats and were the most reported threats to grassland ecosystems reported within EU between 2007-2012 (Romão et al., 2015). Today, unfertilised semi-natural grasslands are almost absent in western and central Europe (except in Spain) and only relatively few remain in northern Europe (Fuller, 1987; Pärtel et al., 1999; WallisDeVries et al., 2002). In Sweden, 350 000 ha of semi-natural grasslands still exist (ArtDatabanken, 2014), which represents less than 10% of such grasslands in the beginning of the twentieth century (Bernes, 2011; Ekstam and Forshed, 2000). The remaining species-rich grasslands are often small and isolated, resulting in a heavily fragmented landscape (Cousins et al., 2015). Due to the low profits of managing traditional semi-natural grasslands, grazing and mowing today mainly occur on improved grasslands, often sown leys on former arable fields (Beaufoy et al., 2011; Swedish Board of Agriculture, 2009).

All across Europe, the biodiversity associated with semi-natural grasslands has been radically reduced and a large number of species dependent on these habitats are threatened (ArtDatabanken, 2015; Pöyry et al., 2004). When grasslands are abandoned or fertilised, their biodiversity declines drastically (Jacquemyn et al., 2011; John et al., 2016; Mitlacher et al., 2002; Wahlman and Milberg, 2002), with notable differences even after one year (Galvánek and Lepš, 2009). Management abandonment often results in the encroachment of trees and shrubs, leading to low light availability in the field layer (Hansson and Fogelfors, 2000; Stoate et al., 2009; Willems and Bik, 1998). The declining population sizes, particularly among species that are poor dispersers and live in isolated habitats

with low colonisation rates, also leads to elevated extinction risks (Cousins et al., 2007). Grassland specialists have been more vulnerable to habitat loss and thus become rare (Cousins and Eriksson, 2001), which is reflected by the Swedish Red Data List containing several hundred species of plants, fungi, and animals inhabiting semi-natural grasslands (ArtDatabanken, 2015). Abandonment also affects functional diversity negatively (Neuenkamp et al., 2016; Winsa et al., 2017), i.e. decreasing the number of functionally disparate species within a population, which can reduce ecosystem stability and function.

To reverse this negative trend and increase the amount of managed semi-natural grasslands, economic compensation to conserve and restore semi-natural grasslands has been incorporated in agri-environment schemes in many European countries (Stoate et al., 2009). Within the Swedish Rural Development Programme, more than 14 200 ha of semi-natural grasslands were restored with agri-environment payments to a cost of approximately €26 million (256 million SEK) during 2000-2013 (Andersson et al., 2009; Swedish Board of Agriculture, 2016). Still, EU member states have reported that almost 10 million ha (97 000 km²) of European semi-natural grassland habitats need restoration for improved structure and function to reach the Habitat and Birds Directives (BIO by Deloitte, 2015).

1.1.5 Restoration to what?

Having clear restoration goals is fundamental for the evaluation of restoration projects, irrespective of habitat type (Hobbs and Norton, 1996). Even though this has been known for decades, setting up specific and quantitative goals for restoration in practice is still uncommon (Borgström et al., 2016; Wortley et al., 2013). The over-arching aim when restoring semi-natural grasslands is often to restore the habitat type to a previous state, or a specific grassland type (Swedish Board of Agriculture, 2014). What the previous state encompasses is difficult to address, since explicit data from the previous states rarely exists. It also depends on which aspect of the previous state that is desirable. Focusing on e.g. biodiversity conservation, cultural values or different ecosystem services may differ in restoration procedure and outcome.

So far, most restoration goals have targeted biodiversity (Borgström et al., 2016). This has previously been evaluated scientifically by measuring overall species richness, but studies can also focus on the occurrence and abundance of grassland specialists, indicator species or threatened species (Pykälä, 2005; Schrautzer et al., 2011). In line with international guidelines from the Society for Ecological Restoration (SER, 2004), many studies use biodiversity in reference habitats (i.e. continuously managed semi-natural grasslands) for comparison (e.g. Blanckenhagen and Poschlod, 2007; GalvANEK and Lepš, 2009; Piqueray et al., 2011; Pykälä, 2003; Schrautzer et al., 2009). Moving beyond biodiversity, recent studies suggest alternative goals connected to ecosystem functionality, for example re-establishing plant-pollinator networks (Forup et al., 2008; Menz et al., 2011; Shackelford et al., 2013). Until recently, ecosystem services were rarely mentioned in specific restoration aims and therefore seldom evaluated afterwards (Rey-Benayas et al., 2009). Another underrepresented perspective in semi-natural grassland restoration is the socio-economical dimension, both regarding the restoration process and for evaluation of the outcome. Clearly, there is not yet a consensus what semi-natural grassland restoration should aim at or how the outcome should be measured.

1.1.6 Grassland restoration in practice and research

In parts of Europe, semi-natural grassland restoration includes creation of grasslands on former arable fields (e.g. Conrad and Tischew, 2011; Fagan et al., 2008; Horrocks et al., 2016; Prach et al., 2015), although I will refer to this as *re-creation* rather than *restoration* (see Palmer and Filoso, 2009). The direct effects of re-creation are more radical than restoring degraded, but not fundamentally altered, permanent semi-natural grasslands (see Suding et al., 2004), which is a more common method in northern Europe due to the nature of land-use change that has occurred there. However, restoring abandoned grasslands could be more successful in the long-term perspective, since nutrient levels, soil structure and presence of arbuscular mycorrhizal fungi is more comparable to continuously managed (*intact*) semi-natural grasslands (see Honnay et al., 2017; Neuenkamp et al., 2018), and as many grassland plants may occur as remnant populations or in the soil seed bank (Auffret and Cousins, 2011; Bakker et al., 1996). Common practice during restoration in northern Europe does not usually include any kind of seed sowing or seedling planting, which implies that restoration success requires the presence of target species in the vegetation, in the soil seed bank, or in seeds dispersing from habitats nearby (Eriksson, 1996; Strykstra et al., 1998; Willems and Bik, 1998). In Sweden, restoration practice often involves the removal of trees and shrubs to increase light availability, and reintroducing appropriate grazing or mowing regimes (Swedish Board of Agriculture, 2014). As a financial incentive, agri-environment payments are given during the initial five years, with a precondition that the farmer will continue the management for an additional five years (Swedish Board of Agriculture, 2004).

Semi-natural grassland restoration has been implemented for several decades, yet there are still knowledge gaps to fill. There are, for example, multiple experimental studies of grassland re-created on ex-arable fields, whereas long-term studies of restored semi-natural grasslands are relatively few. Re-created grasslands show large differences between initial short-term effects and long-term outcome (Conrad and Tischew, 2011; Fagan et al., 2008), indicating difficulties of making long-term predictions. Short-term studies on restored semi-natural grasslands have reported various results for e.g. how grassland size affects species recovery (e.g. Dahms et al., 2010; Lindborg and Eriksson, 2004a). Negative effects of other local factors, such as period of abandonment (i.e. the time between ceased management and restoration) and extent of previous fertilisation, have been observed in such studies (e.g. Willems, 2001; Öckinger et al., 2006). However, long-term effects of different local biotic and abiotic conditions are still relatively unknown. Moreover, although studies show that landscape configuration and species pools affect local species distribution within landscapes (Cornell and Harrison, 2014; Lindborg et al., 2014; Öckinger et al., 2012), better knowledge of how this affects restoration outcome is needed.

Broadening the previous focus on biodiversity within restoration to also include ecosystem services is of high interest among stakeholders and researchers (see also Blicharska and Hilding-Rydevik, 2018). Biodiversity is often seen as a prerequisite that underlies provision of many ecosystem services (Millennium Ecosystem Assessment, 2005). Restoration aiming at increasing biodiversity may therefore also have a positive effect on ecosystem services. This is a relatively new research area, both in terms of studying ecosystem service recovery post-restoration *per se*, as well as disentangling potential linkages between biodiversity and ecosystem services. Studies of ecosystem services in restored species-rich habitats are scarce and eventual links to biodiversity recovery needs to be explored further. There is also a lack of interdisciplinary studies combining effects

on biodiversity with stakeholder perspectives. Incorporating socio-economical factors in restoration is especially necessary when considering the long-term engagement needed for semi-natural grassland restoration (see McDonald et al., 2016; Perring et al., 2015). The present large-scale need for restoration requires better knowledge regarding how to target the appropriate restoration measures and how to prioritise between candidate sites.

2 Thesis objectives

The main aim of this thesis is to investigate restoration outcomes in semi-natural grasslands, focusing on different aspects of biodiversity, functions and ecosystem services, the effects of local and landscape factors and how stakeholders perceive the procedure, outcome and future grassland management. The aim is subdivided into three objectives (A-C) and analysed in four papers (I-IV) (Table 2.1).

Objective A

The first objective focuses on restoration effects on biodiversity and how it relates to local and landscape aspects. I assessed this by inventorying vascular plant species richness and abundance in semi-natural grasslands and comparing it to reference sites (intact semi-natural grasslands). Paper I focused on how the species community changed over time, while Paper II addressed the impact on habitat specialist species. This was set in relation to local conditions (habitat area, degree of fertilisation, vegetation height, tree and shrub abundance, period of abandonment and time since restoration), as well as landscape factors (species pools and proportion of present and remnant semi-natural grasslands in the surrounding landscape).

Objective B

Under objective B, the restoration outcome in terms of ecosystem services is assessed through plant functional traits (Paper III). First, plant traits beneficial for five different provisioning, regulating and cultural ecosystem services (ES) were selected. As a second step, I used these trait data to calculate individual ES-values for all plant species present in restored and reference semi-natural grasslands. The ES-values were then combined with data of the species' presence and abundance following restoration, to detect community average changes over time, and compared with reference grasslands.

Objective C

The final objective includes stakeholder perspectives on the future of restored semi-natural grasslands. As continued management is necessary to uphold and improve the restoration outcome, opinions and experiences from involved stakeholders need to be acknowledged. In Paper IV, I surveyed and interviewed farmers and landowners of restored grasslands, focusing on their views on the restoration process and outcome and how they perceive the future management possibilities. This was combined with biodiversity data from field inventories and data of received agri-environment payments from County Administrative Boards.

Table 2.1. Thesis objectives covered by the thesis papers (I-IV).

Objective		I	II	III	IV
A	Effects on biodiversity	•	•		
	Outcome affected by local conditions	•	•		
	Outcome affected by time	•	•		
	Outcome affected by landscape		•		
B	Effects on ecosystem services			•	
	Outcome affected by time			•	
C	Stakeholder perceptions				•

3 Methods

3.1 Study area and restoration measures

The 35 restored and 12 continuously managed reference semi-natural grassland sites studied in this thesis are all located in fragmented agricultural landscapes in south-eastern Sweden, in the counties of Östergötland, Södermanland, Västmanland, Stockholm and Uppsala. These sites were chosen either because they had been inventoried previously, or because they represented a gradient in terms of time since restoration and surrounding landscape connectivity. Paper I and III are based upon plant re-inventories performed in 16 restored and 5 reference semi-natural grasslands (Fig. 3.1a). In Paper II, specialist plant inventories of 12 focal restored and 8 reference semi-natural grasslands were combined with field inventories and GIS-analyses of the surrounding landscapes (Fig. 3.1b). In the final paper (IV), survey data of farmers and landowners managing 30 restored grasslands and eight in-depth interviews were combined with agri-environment payment data from County Administrative Boards (Swedish: *Länsstyrelser*) and plant inventory data (Fig. 3.1c).

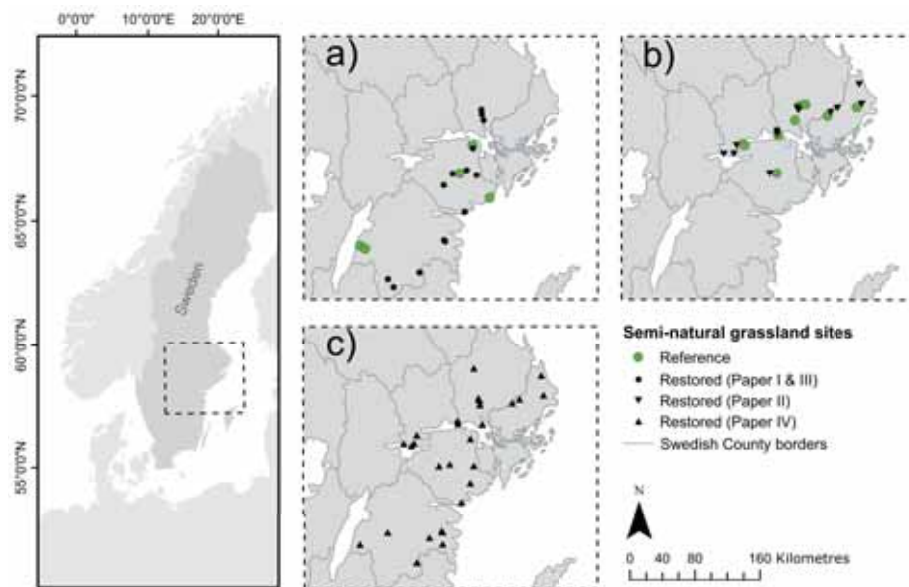


Figure 3.1. Restored and reference (i.e. continuously managed) semi-natural grasslands in south-eastern Sweden studied in this thesis for (a) Paper I and III, (b) Paper II and (c) Paper IV.

The grassland sites were selected by using information from the County Administrative Boards, the Municipalities and the Uppland Foundation (Swedish: *Upplandsstiftelsen*), combined with information from the national Swedish geographical database of semi-natural grasslands TUVÅ (<http://www.jordbruksverket.se/tuva>). In Paper I-III, restored and reference semi-natural grasslands with dry to dry-mesic abiotic conditions

were studied, while Paper IV also included moist to wet restored grasslands. The reference semi-natural grasslands (Fig. 3.2) were chosen to resemble the desired state after restoration and have thus been managed continuously. Moreover, they were located in the vicinity of the restored grasslands and had the same average size. The restored grasslands were abandoned prior to restoration and restored 6-26 years before the inventories carried out for this thesis. As detailed inventories from before restoration were not performed, the study design comprised a space-for-time substitution (Pickett, 1989), where time since restoration was used as a measure to assess community change over time.

In all restored sites, restoration involved the clearing of unwanted trees and shrubs and resuming previous management, i.e. re-introducing domestic livestock (cattle, sheep or horses) and at some wet sites (in Paper IV) also re-instating a mowing regime after cutting reed and removing tussocks. Restoration was in most cases economically financed through agri-environment schemes and the restoration procedures planned in detail by the County Administrative Boards. However, the restoration goals were vague or non-existent for most restorations in this thesis, making evaluations difficult or subjective. The existing aims generally considered increased biodiversity and cultural values, but some also mentioned preserving grassland species (not specified further), ancient stone monuments and small-scale agricultural landscapes as a whole.



Figure 3.2. Example of four different semi-natural grasslands in the Swedish county Östergötland; (from left to right) abandoned for more than 50 years, recently restored, restored 13 years ago and continuously managed (intact) reference grassland.

3.2 Data collection

To address the three thesis objectives, I used a combination of different data collection measures (Table 3.1). I performed field inventories of vascular plant species, both in restored and reference semi-natural grasslands, and also in the surrounding landscapes. Moreover, I collected data of the grasslands' history and surrounding landscape from County Administrative Boards, the Swedish National Land Survey (*Lantmäteriet*), the Swedish Board of Agriculture (*Jordbruksverket*) and by surveying farmers and landowners. The spatial information was further processed in ArcGIS to be included in the following analyses. To assess ecosystem functioning, five ecosystem services (meat production, pollination, temperature regulation, water retention and cultural heritage) were targeted, for which I compiled data of related plant traits from public trait databases and literature and combined this with our previous plant diversity data. For the final objective, I surveyed and interviewed farmers and landowners of restored semi-natural grasslands.

Table 3.1. Response and explanatory variables examined and the data collection methods used in the thesis papers (I-IV).

Main response variables	Collection method	Paper
Vascular plant species richness & abundance	Field inventories	I
Vascular plant habitat specialist species richness & abundance	Field inventories	II
Ecosystem service provision based on plant traits	Field inventories, Trait databases & Literature	III
Stakeholder perspectives on restoration	Survey & Interviews	IV
Explanatory variables	Collection method	Paper
Time since restoration	Acquired from farmers & County Boards	I, II
Period of abandonment	Acquired from farmers & County Boards	I, II
Tree & shrub abundance	Field inventories	I
Vegetation height (proxy for grazing intensity)	Field inventories	I
Degree of fertilisation	Acquired from farmers	I
Grassland area	Acquired from County Boards	I, II
Landscape specialist species pool	Field inventories	II
Proportions of semi-natural grasslands & remnant habitats in surrounding landscape	Aerial photos, Historical maps & GIS analysis	II
Proportions of arable fields in surrounding landscape	Aerial photos & GIS analysis	II

3.2.1 Field inventories of plant diversity in focal restored and reference grasslands and in surrounding landscapes

Plant inventories followed the same protocol in restored grasslands and in reference grasslands. In Paper I, all vascular plant species were inventoried, whereas Paper II focused on 30 grassland specialist plants. Vascular plant species richness and abundance were inventoried in 10 plots of 1 m × 1 m, subdivided into 100 smaller squares of 10 cm × 10 cm to estimate occurrence frequency in each focal grassland. In Paper I (data used also in Paper III and IV) the inventories were carried out at two time steps, in 2001 (Lindborg and Eriksson, 2004a) and 2012. The ten plots were equally distributed along two transects per site at both time steps. In Paper II (data also used in Paper IV) the plots were randomly distributed on a map to cover the entire grasslands (Winsa et al., 2017).

In Paper II, I also inventoried the specialist species pool of the surrounding landscape (1 km radius), recording specialist presence and frequency (scale 0-100) in 70 1 m × 1 m plots per landscape. The 70 plots were placed randomly on set distance intervals using ArcGIS, according to a priority order of probable habitats: [1] semi-natural grasslands managed today, [2] former semi-natural grasslands managed in the 1950s and [3] midfield islets (small bedrock outcrops situated in crop-fields, historically grazed post-harvest). A total of 1400 plots were sampled in the landscapes.

3.2.2 Data collection of local and landscape factors

To see which factors that could affect the restoration outcome, I examined different environmental factors at the local and landscape scale in Paper I and II. The temporal factors ‘time since restoration’ and ‘period of abandonment’ were acquired by asking farmers and County Administrative Boards. They also provided information regarding site area and degree of fertilisation. Abundance of trees and shrubs in the grassland and vegetation height (as a proxy for grazing intensity) were obtained through field inventories. Moreover, by using aerial photographs and the Economic map (from 1950s) provided by the Swedish National Land Survey, combined with information of managed semi-natural grasslands from the TUVa-database, I calculated present and historical proportions of

intact semi-natural grasslands, remnant grassland habitats and arable fields in the landscape using ArcGIS.

3.2.3 Plant trait collection to estimate ecosystem service provision

In Paper III, ecosystem service (ES) provision in restored semi-natural grasslands over time, and in relation to reference grasslands, was estimated using a five-step procedure based upon available plant traits (Fig. 3.3). Based on literature, plant traits positively related to each of the five ecosystem services (meat production, pollination, water retention, temperature regulation and cultural heritage) were selected, resulting in five different ES trait-sets. In some cases, other or additional traits would have been preferred, but were not included due to high levels of missing data for the studied species. Secondly, I collected and compiled data for these traits from public databases (Hoes and Pluym, 2007; Kattge et al., 2011; Kleyer et al., 2008; Klotz et al., 2002; The Centre for Swedish Folk Music and Jazz Research, 2017) and literature (Ekstam and Forshed, 1997; Mossberg and Stenberg, 2010). All traits were standardised into a 0-1 scale based on the community maximum, where higher values indicated higher contribution to the ES. In the third step, I calculated species-specific ES-values for all five ES by averaging the standardised traits in the associated ES trait-set for each species in the community. Fourthly, the species-specific ES-values were paired with previously collected species presence and abundance data in the 16 restored and 5 reference semi-natural grasslands from 2001 and 2012 (also used in Paper I). In the final step, I calculated community-weighted mean (ES community average) for each grassland (restored, reference), time-step (2001, 2012) and ES, using data based on either the species presence or the abundance, to be able to analyse whether ES provision had changed and in which direction.

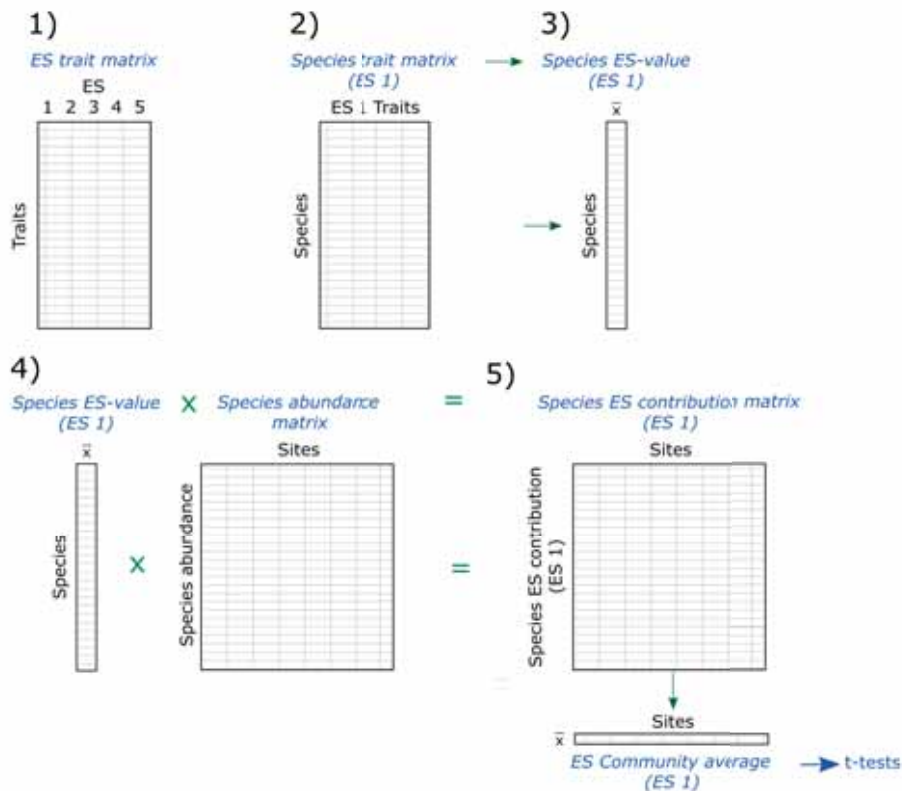


Figure 3.3. Stepwise procedure to estimate ecosystem service (ES) provision of five ecosystem services in restored and reference semi-natural grasslands based upon plant functional traits.

3.2.4 Survey and interviews

In Paper IV, I sent out a short survey to the farmers and landowners of restored semi-natural grasslands whose biodiversity was inventoried in previous studies (Paper I-II and unpublished data). The survey consisted of questions regarding the restored grasslands' history, the restoration outcome and future management. All 29 farmers and landowners of 30 restored grasslands who ended up contributing to the survey, were then asked to participate in an in-depth interview. In the eight semi-structured interviews that followed, the respondents (six farmers and two landowners) were asked to further elaborate their experiences, thoughts and opinions regarding the restoration procedure and outcome, and semi-natural grassland management as such, both today and in the future.

To find patterns of similarities and dissimilarities in their answers, I analysed the quantitative and qualitative survey data and qualitative interview data both separately and together. The transcribed interviews were analysed in a qualitative, deductive manner based upon the over-arching themes in the semi-structured interview guide (Elo and Kynäs, 2008). Similarities and dissimilarities within and between the different interview respondent types' perceptions (farmer and landowner), as well as in relation to the survey answers, were also analysed for comparison. These results were also discussed in the context of the restored grasslands' plant diversity and received restoration agri-environment payments from the County Administrative Boards.

3.3 Statistical analyses

In this thesis, I have used different statistical methods depending on the response and explanatory variables examined in each paper. Paired t-tests were used to compare community changes in species richness (at different spatial scales, in total and for grassland specialists (Paper I)) and ES community average over time (Paper III), and Welch t-tests to compare with the reference grasslands (Paper I-III). I also used regression analyses (linear and multiple) in Paper I to examine whether the species richness change over time was related to any of the explanatory variables. In Paper II, the relationship between the different species diversity metrics and the temporal, local and landscape factors were analysed in Spearman Monte Carlo tests. This method was also used to test whether the proportion of shared species between the focal grassland and surrounding landscape was related to any of the explanatory variables and if it differed between the restored and reference sites.

Changes in species composition over time, in comparison with reference grasslands, and in relation to explanatory variables were analysed using multivariate methods; ordinations (DCA, NMDS and CCA), similarity- (ANOSIM, based on Bray-Curtis distance measure) and evenness analyses (Simpson's Index of Diversity; Oksanen et al. 2016) (Paper I and III). Most of the statistical analyses were performed in R 2.15.0 – 3.3.0 (R Core Team, 2016), with additional analyses using CANOCO (Smilauer and Lepš, 2014) and PAST 2.17b (Hammer et al., 2001) in Paper I.

4 Results and Discussion

4.1 Restoration effects on biodiversity in relation to local and landscape aspects

(Paper I and II)

4.1.1 Plant species richness, abundance and composition (Paper I)

If species are able to colonise from surrounding landscape or recover from a dormant seed bank, the effect on the vegetation after semi-natural grassland restoration can be relatively quick (Dzwonko and Loster, 1998; Hellström et al., 2003; Willems and Bik, 1998). This fast response in terms of a higher species richness can be due to the creation of a wider range of habitat niches, where the community shortly after restoration can comprise a larger range of species, including grassland specialists, generalists, nutrient demanding species and forest specialists (Kotiluoto, 1998). Fast responses can indicate successful restoration, although it might not reveal the long-term outcome. In Paper I, I found a long-term increase in total species richness at site level, but not at the smaller spatial scale (1 m²; Fig. 4a). Other studies have also shown increased species richness with time since restoration (Kotiluoto, 1998; Willems, 2001; Winsa et al., 2015), however the recovery is slower at small spatial scales (Austrheim and Olsson, 1999). This can be an effect of an overall higher probability of environmental heterogeneity at larger scales (Pykälä, 2003), where a larger variety of microhabitats can benefit a wider variety of species (Gazol et al., 2012; Pihlgren and Lennartsson, 2008; Söderström et al., 2001). Nevertheless, the continuously managed reference grasslands still had higher total species richness at both site- and square-metre scales (Fig. 4.1a).

Even though traditionally managed semi-natural grasslands often are characterised by having high species richness at small spatial scales (Austrheim et al., 1999; Eriksson and Eriksson, 1997; Eriksson et al., 2002; Habel et al., 2013; Wilson et al., 2012), using species richness as a measure of restoration success could be criticised for not considering species identity (see Kasari et al., 2016). By including the identity and abundance (i.e. frequency) of each species, changes in the species composition towards reference states can be better detected. In a species composition analysis, I found that the plant community had changed over time and resembled the reference state 12-20 years after restoration (Fig. 4.1b). Local environmental factors had low effects on the tested biodiversity measures. Species composition was only affected by period of abandonment and degree of fertilisation, whereas time since restoration, site area, tree and shrub abundance and vegetation height had no effect. These results might change with more precise data for some of the variables, but could also be due to high environmental similarity between the investigated sites.

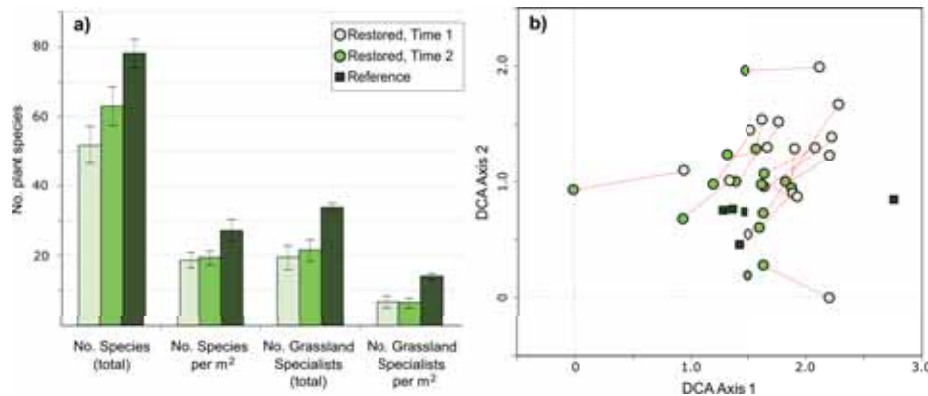


Figure 4.1. *a)* Vascular plant species richness (95% CI) in restored semi-natural grasslands measured at time 1 (1-9 years after restoration) and time 2 (12-20 years after restoration) and in relation to reference grasslands (intact continuously managed semi-natural grasslands). The overall number of plant species, as well as the number of grassland specialist species was measured at site level (total) and per 1×1 m plot. *b)* Detrended correspondence analysis (DCA) showing a species composition shift in the restored grasslands over time towards reference conditions. Modified from Paper I.

4.1.2 Grassland specialist species (Paper I and II)

Habitat restoration can also aim to increase certain key species or habitat specialist species (Borgström et al., 2016; John et al., 2016), for example typical grassland specialist species. Most grassland specialists have evolved to tolerate low-intensity disturbance, which in today's landscape requires continuous management by grazing or mowing (see Grime, 1973). Nevertheless, perennial grassland specialists and specialists with long-lived seed banks may still survive if management ceases (Auffret et al., 2016; Lehtila et al., 2006; Lindborg, 2007; Saar et al., 2012) and then repopulate the grassland after restoration. Specialists may also disperse from surrounding intact or remnant habitats, although it can take time depending on the species' dispersal capability and the structural connectivity between habitats (Aavik and Helm, 2017; Winsa et al., 2015). In Paper I, I found that the number of grassland specialist species did not change during the eleven years of study, at neither the site- nor the square metre level (Fig 4.1a). The reference grasslands had more than double the amount of specialists per square metre (Fig 4.1a). These findings are in line with other studies showing a less successful recovery of specialists and rare species (e.g. Gijbels et al., 2012; Pykälä, 2003; Tikka et al., 2001). However, I also found that the specialist species composition had changed and had become similar to the reference community composition. These contrasting results could be explained by reference grasslands containing many species at comparably low abundances; species which therefore have little statistical impact in species composition analyses.

Of the environmental factors tested in Paper I, specialist species composition was only affected by site area. Previous studies have shown a positive dependency on habitat area for long-lived grassland specialists (Lindborg et al., 2012; Lindgren and Cousins, 2017). This could be due to higher probability of habitat heterogeneity (Öster et al., 2007) and reduced risks of generalist species competition caused by habitat fragmentation and edge-effects (Kiviniemi and Eriksson, 2002). Moving beyond local conditions, I studied the effect of surrounding landscape composition and species pool in Paper II. I targeted 30 grassland specialist species and found a positive relationship between specialist species richness in the restored grasslands and richness in surrounding landscapes. The specialist frequency in the restored grasslands was also positively related to the proportion of intact semi-natural grasslands and remnant habitats (former semi-natural grasslands

and midfield-islets). Other studies finding that past, rather than contemporary, landscape composition reflects present-day grassland diversity (Cousins and Vanhoenacker, 2011; Helm et al., 2006; Krauss et al., 2010; Lindborg and Eriksson, 2004b), further highlighting restoration possibilities in landscapes where intact semi-natural grasslands are scarce. However, this historical legacy is of course affected by the time at which fragmentation started, how severe the landscape transformation has been and whether the matrix can support remnant populations (see e.g. Steffan-Dewenter, 2003). Paper II also shows that the proportion of shared species between focal restored grassland and surrounding landscape (i.e. occurring in both focal grassland and landscape) was related to the interaction between temporal and spatial factors. Proportion of shared specialist species correlated positively with time since restoration in landscapes with high proportions of semi-natural grasslands, suggesting that specialists can recolonise in landscapes with a high amount of suitable habitats, given enough time (Fig. 4.2). This supports the findings of previous research showing higher specialist recovery at sites adjacent to intact semi-natural grasslands with source populations (Conradi and Kollmann, 2016; Winsa et al., 2015; but see Piqueray et al., 2011).

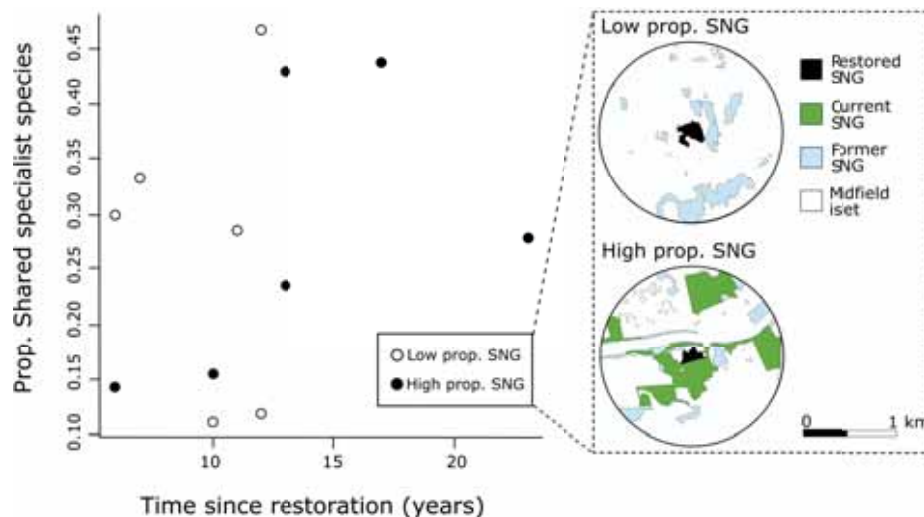


Figure 4.2. Relationship between the proportion of grassland specialist plant species occurring in both the restored semi-natural grassland and its surrounding landscape (i.e. proportion shared) and the time since restoration (in years). Black and white circles indicate high (>0.08) and low (<0.05) proportion of semi-natural grasslands (SNG) in surrounding landscapes (circular radius 1 km). Modified from Paper II.

4.2 Restoration effects on ecosystem services assessed via plant traits

(Paper III)

As a complement to the traditional focus on biodiversity recovery, emphasis on restoring ecosystem services is emerging in research and policy (Borgström et al., 2016; Kollmann et al., 2016; McDonald et al., 2016). In Paper III, I found that the presence of plant species with traits contributing to the five selected ecosystem services (meat production, pollination, temperature regulation, water retention and cultural heritage) increased over time, and values for meat production and pollination resembled levels in reference grasslands 12-20 years post-restoration (Fig. 4.3, top panel). However, when accounting for

species abundance in the calculations, there was no significant change over time and the reference semi-natural grasslands had higher values for all five services (Fig. 4.3, bottom panel).

Species with traits contributing to several services were present post-restoration, although not in the same abundances as in the reference habitats (Fig. 4.3). According to Bullock *et al.* (2011), ecosystem services and biodiversity recovers at different rates during restoration. A follow-up study of the sites studied in Paper III could reveal if this is an ongoing trend towards reference levels, or if species are functionally extinct due to rareness or absence. A long-term study including the reference sites might also detect an eventual time-lag in ecosystem service provision (Isbell *et al.*, 2015), where current provision relies on species undergoing a time-delay in their extinction process.

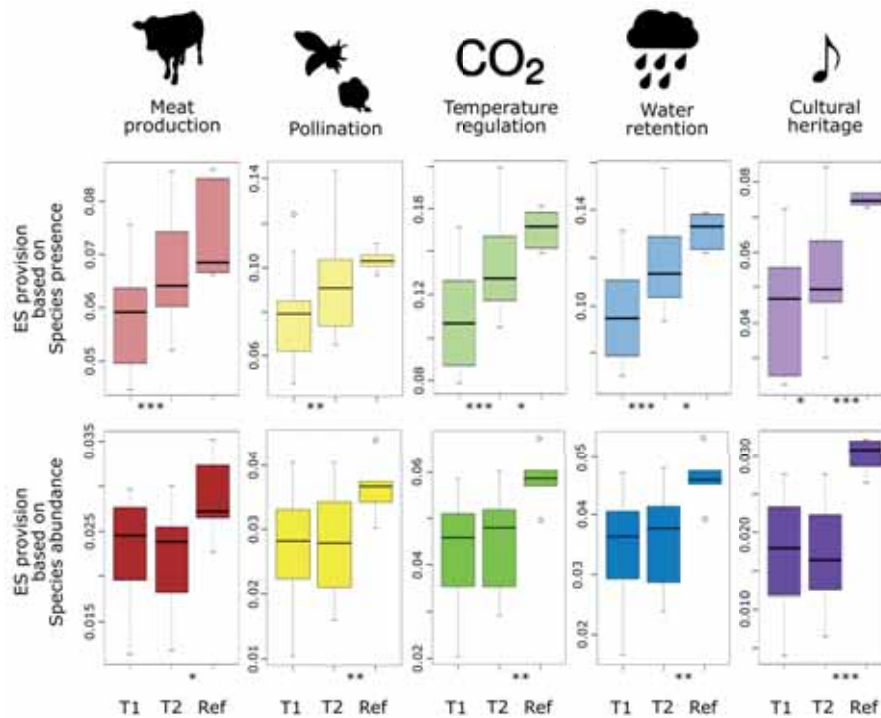


Figure 4.3. Boxplots showing ecosystem service provision for meat production, pollination, temperature regulation, water retention and cultural heritage in restored semi-natural grasslands at time 1 (T1, 1-9 years after restoration) and time 2 (T2, 12-20 years after restoration), as well as in reference grasslands (intact continuously managed semi-natural grasslands) at time 2. The ecosystem service provision (community average) is based on plant species traits connected to the specific ecosystem functions and services, and the species' presence (top panel) or abundance (bottom panel). Significant differences between Restored at T1 and T2, and Restored T2 and Reference, indicated by asterisks (* $p < 0.05$ -0.01, ** $p < 0.01$ -0.001, *** $p < 0.001$). Analysed in paired t-tests and Welch t-tests, respectively. Figure from Paper III.

There were strong positive correlations between the five ecosystem service community averages, both shortly (1-9 years) and longer (12-20 years) after restoration (Fig. 4.4). This indicates that increasing provision of one service simultaneously could increase the other four services. Simultaneous recovery of biodiversity and supply of regulating and supporting ecosystem services in restored agroecosystems has been shown in a global meta-study (Barral *et al.*, 2015). However, these results were based mainly on habitat recreation and organic farming, and did not cover restored semi-natural grasslands. Since conflicts between provision of different ecosystem services have been detected in other studies (e.g. Birkhofer *et al.*, 2018; Bullock *et al.*, 2011), more studies addressing the po-

tential need to account for trade-offs and synergies are needed. Interestingly, I also found that all services were highly positively correlated with species richness, a relationship that became stronger as species richness increased over time (Fig. 4.4). Relating this to the increased species community evenness over time, further implies that service provision shortly after restoration relied on a few key species and with time became dependent on more species (Fig. 4.5). Hence, with a more evenly distributed abundance over more species, the communities have become more resilient to natural and non-natural disturbances (Folke, 2006).

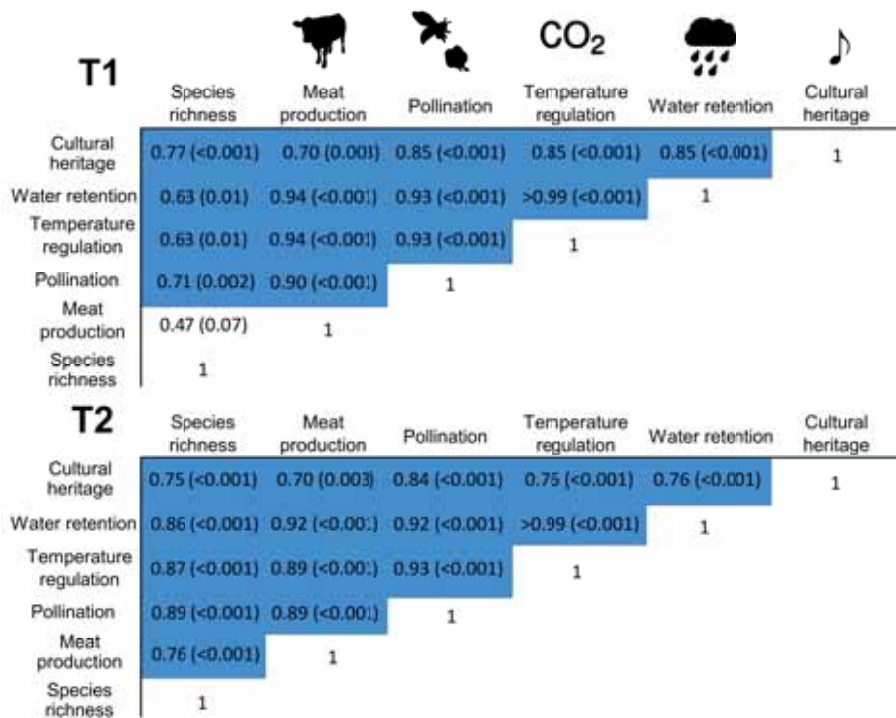


Figure 4.4. Correlations between provision of five different ecosystem services (community averages) and species richness in restored semi-natural grasslands, at T1 (Time 1, 1-9 years after restoration) and T2 (Time 2, 12-20 years after restoration). Analysed with Spearman's rank correlation (Spearman's ρ and p-value, positive significant relationship indicated by blue colour). Figure modified from Paper III.

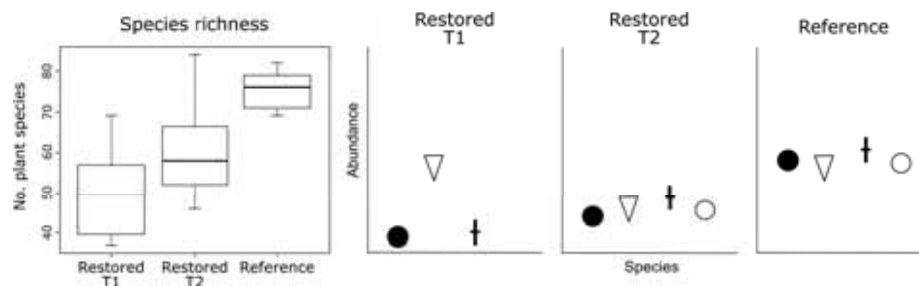


Figure 4.5. *Left*: Species richness increase over time in restored semi-natural grasslands (T1: 1-9 years post-restoration vs. T2: 12-20 years post-restoration) and in comparison to reference grasslands (intact continuously managed semi-natural grasslands). *Right*: Illustration of a community evenness shift, where number and abundance of different species important to an ecosystem service increase and become more evenly distributed with time (Restored T1 vs T2) and in comparison with reference state. Figure from Paper III.

4.3 Stakeholder perspectives on the future of restored semi-natural grasslands

(Paper IV)

Social and economical factors are often neglected, but nevertheless central, in habitat restoration (Burke and Mitchell, 2007; Shackelford et al., 2013; Temperton, 2007). People willing and able to continue managing the restored semi-natural habitats are crucial for a successful outcome, especially in a longer time perspective. In Paper IV, I found that farmers and landowners mostly considered the restoration successful, which also was reflected in the overall increased plant diversity. However, irrespective of the result, 10% of the restored grasslands were abandoned again post-restoration. Moreover, 40% of the surveyed farmers and landowners were unsure if they would be able to manage their restored grasslands in the future. This was strongly related to how they perceived their (or their tenant farmers') future farm economy and if they (or their successors), would continue farming with grazing animals. Therefore, receiving financial support for both restoration and post-restoration management were essential to the farmers. Similar results have been found in other studies, where the ageing farming population and low financial motivation to manage traditional grasslands highlights a significant risk of future management abandonment (McGinlay et al., 2017; Raatikainen and Barron, 2017). Besides financial support, the interview respondents in this study also requested support from their local communities, alongside more and better feedback and advice from authorities. Less frequent regulation changes, a more simplified subsidy system adjusted to national and local conditions, as well as an increased societal demand to produce more livestock products, were believed to benefit the long-term management. The interview respondents highly appreciated the semi-natural grasslands for their plants and animals, for providing a healthy environment for the livestock and for their beauty in the landscape. Nevertheless, as one farmer put it: *“Semi-natural grasslands will only remain semi-natural grasslands as long as they continue to be managed”*.

At a European level, management abandonment and land-use transformation of traditional semi-natural grasslands is an ongoing trend (Beaufoy et al., 2011; Stoate et al., 2009). A rapid and continuous decrease in the quality of remaining semi-natural grasslands has also been reported across Europe (BIO by Deloitte, 2015; Swedish Board of Agriculture, 2013). As an example, 18% of Swedish semi-natural grasslands reported as “valuable” in 2002-2004, were no longer considered valuable ten years later, due to management abandonment or loss of species (Swedish Board of Agriculture, 2013). Loss of species also in managed grasslands, whether this indicates inappropriate management, realisation of a time-lagged extinction (Cousins, 2009), or both, could potentially affect future restoration outcomes. Nonetheless, the ongoing abandonment of valuable grasslands shows that the need for policy-driven restoration is only going to increase.

Box 3. Key results & Implications

Objective A

- Site-scale plant species richness increased over time. Yet, there were more species, grassland specialist species and higher species density in the intact reference grasslands, even 12-20 years post-restoration (Paper I).
- Species community composition, on the other hand, resembled the reference community composition 12-20 years post-restoration (Paper I).
- Local factors affecting biodiversity were time since restoration, period of abandonment, degree of fertilisation and site area (Paper I, II).
- Landscape factors with a positive effect on specialist species recovery were species pool occurrence and high proportions of intact and remnant semi-natural grasslands in surrounding landscape (Paper II).

Objective B

- The number of plant species contributing to the five ecosystem services meat production, pollination, temperature regulation, water retention and cultural heritage, increased over time (Paper III).
- However, when accounting for their abundance, there was no difference in their contribution over time. Intact reference grasslands had higher contributions to all tested services. Nevertheless, the increased evenness over time suggests that the communities with time became more resilient (Paper III).
- The ecosystem service provision was highly correlated with species richness (Paper III).

Objective C

- Almost all surveyed farmers and landowners perceived their restoration successful. However, 40% were unsure if their restored semi-natural grassland will be managed in the future (Paper IV).
- Low profitability, both for the semi-natural grassland management itself and for traditional agriculture as a whole, was considered the greatest threat to continued management (Paper IV).

Management implications

- Pre-defined, clear and realistic goals are highly needed for evaluation, especially since restoration success can be interpreted differently depending on evaluation measure used.
- Restoration to intact reference conditions takes time. For faster biodiversity recovery, large, unfertilised, newly abandoned grasslands situated in landscapes containing a large grassland specialist species pool and high amounts of intact and remnant semi-natural grasslands, could be prioritised. However, focussing on fast results might overlook the importance of biodiversity recovery also in homogenous landscapes.
- Aiming for increased species richness does not necessarily benefit grassland specialist diversity. However, species richness can correlate positively with provision of multiple ecosystem services.
- Policy change is urgently required to facilitate incentives for management of restored and intact semi-natural grasslands in a long-term perspective. Farmers call for a more simplified and trustworthy subsidy system, better feedback and advice from authorities, and support from society as a whole.

5 Addressing future semi-natural grassland restoration

5.1 The importance of having well-defined goals

As seen in Paper I and III, using different diversity measurements could lead to different results, and thus different conclusions of restoration success (Box 3). This could be problematic and ultimately stresses the importance of well-defined initial goals. The widely used goal “increased biodiversity” could be interpreted as increased number of species; i.e. the more the better. However, although species richness may increase post-restoration, it is unclear if the additional species are desired habitat specialists or just a result of heterogeneity following restoration (see Kasari et al., 2016). If the main goal is recovery of habitat specialists or rare species, monitoring species frequency before and after restoration would better detect population trends. Including data of species frequency would also enable species composition analyses where trends towards target communities could be detected (Paper I). Nonetheless, it should also be noted that I found a positive relationship between species richness and calculated ecosystem service provision of all five services (Paper III).

The vague goals set on a European level, but also for each specific site (Paper I), lead to difficulties evaluating restoration success and incorporating cost-effectiveness (see also Ansell et al., 2016; Smith et al., 2016). The goals mostly relate to conservation and an increase of biodiversity and cultural values, which correspond to the overarching goals for High Nature Value farmlands in the EU Rural Development Programme (Beaufoy, 2011). These broad goals are important for habitat restoration in general, but there is still a need for measurable goals that can be evaluated through follow-up studies (Paper I). They may, for example, specifically target different aspects of biodiversity conservation (see de Bello et al., 2010) or be of interest for recreational or historical reasons. It is important to clarify that one site cannot incorporate all desirable aspects simultaneously. Some sites are better suited for e.g. farmland bird conservation (see Pärt and Söderström, 1999), while others might harbour remnant populations of red-listed plants (Schrautzer et al., 2011) or have recreational value for local communities (Swedish Board of Agriculture, 2014). This is why we need to have a wider ecosystem or landscape approach including many sites, where both function and structure is included and also where quantitative evaluation parameters are incorporated (de Bello et al., 2010; Miteva et al., 2012; Perring et al., 2015; Suding et al., 2015).

Moreover, there are several issues to control for when aiming at restoring towards reference conditions, especially when lacking pre-restoration data. The first involves choosing a proper reference site or state, which in turn is highly dependent on the main goal. Secondly, the reference conditions should be achievable within a relevant time-scale (Paper

I, III and IV). Different sites have different prerequisites to reach a certain goal (Suding, 2011), which emphasises the need for site-specific goals and measures. At sites where desired plant species are missing in both the soil seed bank and the surrounding species pool, recolonisation needs to be enhanced by e.g. manual hay-transfer or plug-plants from donor sites (Bischoff et al., 2018; Coiffait-Gombault et al., 2011; Wallin et al., 2009).

5.2 Restoration takes time and is context-dependent

Regardless of restoration measure, it is important to evaluate restoration outcomes, especially in long-term follow-up studies. Short-term studies may reveal temporary trends, but the results might not be stable over time (Auestad et al., 2015; Drayton and Primack, 2012; Huhta et al., 2001). A recent meta-study showed that the recovery rate slowed down with progressed time and full recovery was rarely achieved (Jones et al., 2018). As an example, Woodcock et al (2011) found that it might take over 150 years for target species to recolonise re-created European floodplain meadows. The majority of governmentally financed ecological restoration initiatives are short-term and project-based (Borgström et al., 2016), where the current time-scale for agri-environment restoration schemes is set to five years (Swedish Board of Agriculture, 2004). If semi-natural grassland restoration to reference conditions is even possible, it takes longer than five years, i.e. more than 12-20 years for some aspects (Paper I and III). Species potentially targeted in restoration aims, such as specialist species or species contributing to different ecosystem services, are present, although not in the same amount or abundance as in reference grasslands (Paper I and III). Whether this is due to unsuccessful restoration of important functions, such as pollination and seed dispersal, or lack of necessary soil conditions or biota, such as arbuscular mycorrhizal fungi, requires further investigation. Inappropriate biotic or abiotic conditions could be implied e.g. if species were found to be present in the seed bank, but not the vegetation. Continued monitoring of the restored grasslands investigated in this thesis could reveal such constraints.

Suding et al. (2011) reviewed restoration projects worldwide and found that the level of success is highly coupled to historical and geographical context. For restoration of degraded systems, between a third and a half of projects were considered successful (Suding, 2011). Hence, evaluating drivers behind successful restoration is important, especially for prioritising between sites to meet the high demand for restoration. To increase the chances of meeting the fast results required by current payment regulations, semi-natural grassland restoration should prioritise large, newly abandoned and unfertilised sites situated in landscapes containing high amounts of semi-natural grasslands (preferably intact, but also remnant) (Paper I and II). Increasing functional connectivity (see Auffret et al., 2017) through e.g. green infrastructure (Jakobsson et al., 2016) and rotational grazing networks (Auffret et al., 2012; Plue and Cousins, 2017), would also improve dispersal between restored and intact sites (Aavik and Helm, 2017) as it better reflects the historical plant dispersal mechanisms (Fuller et al., 2017). However, if restoration aims at increasing biodiversity on a landscape scale, restoring a degraded grassland in a homogeneous landscape could, in comparison, result in a higher effect at the overall landscape scale (see Rundlöf and Smith, 2006). Nevertheless, to maintain population fitness in a long-term perspective, restoring additional semi-natural grasslands would be needed in such landscapes. Restoration should also target sites with high probability of future management to limit risks of re-abandonment post-restoration (Paper IV).

Although it is known that far from all reported restorations succeed (Jones et al., 2018; Maron et al., 2012), there are to date no scientific studies reporting the consequences of failed habitat restoration. Besides altering biological and abiotic circumstances, restoration also involves stakeholders, and a failed restoration affects all of these aspects. Restoration can be considered failed both due to unsuccessful results immediately following restoration, but also as a consequence of management abandonment later on (Paper IV). If restored semi-natural grasslands are re-abandoned, efforts of restoring the same site again could potentially be more complicated. Opening up a wooded habitat and then ceasing the management might cause a more rapid encroachment of trees and shrubs, due to the natural processes of e.g. re-sprouting (see Rydberg, 2000) and released nutrients from root decomposition (see Coleman et al., 2004). The risk of depleting a previously dormant seed bank before it is replenished (see Fenner and Thompson, 2005) could also affect future restoration potential. From a socio-economical point-of-view, failed restoration could affect managers' trust and willingness to put time and effort into future restoration (Paper IV). These social, economical and ecological aspects could, in turn, affect management of remaining semi-natural grasslands. The lack of research regarding failed restoration and its consequences is therefore relevant and highly important to achieve social-ecological resilience.

5.3 Restoring for the future or the past?

The increasing emphasis on ecosystem functions and services in policy and restoration (Bouwma et al., 2018; Jones, 2017; Kollmann et al., 2016), reveals a trend of restoring processes, rather than re-creating past conditions (Higgs et al., 2014). Restoring a historical past is problematic for many reasons, ranging from impossibilities to reach biological and abiotic preconditions, to changed socio-economical conditions in modern society and purely philosophical questions of which refined part of history to aim at. Still, one should also keep in mind the contemporary dimension of ecosystem service valuation; what we value today will not necessary be valued similarly in the future (see e.g. Kesebir and Kesebir, 2017).

There is also a need for a more proactive approach when setting restoration goals, i.e. we should set realistic and dynamic goals for the future environment rather than the past (Choi, 2004; Hilderbrand et al., 2005; Shackelford et al., 2013), where eventual effects of climate change could be important to take into account (Papanikolaou et al., 2016; Prober et al., 2017; Tainio et al., 2014). Moreover, while EU policies, and thus also farmers, mostly focus on the patch scale, species pool patterns and ecological processes affecting local management, occur on larger scales (Aavik and Helm, 2017; Tscharrntke et al., 2012). Since ecological, social and economic patterns changes across different scales (Schröter et al., 2018), unravelling this spatial scale mismatch in agri-environment scheme design could potentially have high impact on biodiversity conservation and ecosystem service provision (Isbell et al., 2017; Lindborg et al., 2017). One improvement could for example be to include landscape connectivity design in EU policies and food certification.

Setting specific and detailed restoration goals at site level is complex for many of the reasons described above. Specifying goals in detail also implies in-detail evaluation, which requires further prioritisation due to finite resources in terms of time and money.

Nevertheless, with high restoration needs (BIO by Deloitte, 2015) and fairly low outcome success (Jones et al., 2018; Suding, 2011), targeting a selected range of sites or landscapes where goals are specified in detail, data before restoration is collected and long-term outcome is measured appropriately, would highly improve our current knowledge on effects of restoration.

Today, restoring and managing semi-natural grasslands is generally associated with high effort and low financial profits. To uphold biodiversity and ES provision in a long-term perspective, strategies for post-restoration management are urgently needed. For a sustainable future management, I think that the emerging mental shift among farmers to become stewards (see Chapin et al., 2010; Gordon et al., 2017), rather than strictly producers, is key to success. Re-designing agri-environment schemes to support this trend and increasing public awareness of grassland biodiversity and ecosystem services could be necessary to secure continued management. In contrast to the large-scale restoration goals, intact grasslands are still under the threat of abandonment and insufficient management; a pattern seen both on a national and European scale (Romão et al., 2015; Swedish Board of Agriculture, 2009). In order to reverse this trend, it is necessary to combine efforts of restoration and conservation, to also include future perspectives.

6 Concluding remarks

The overall aim of this thesis was to evaluate restoration outcomes in semi-natural grasslands, in terms of plant diversity, associated ecosystem services and from important stakeholder perspectives. In order to improve future site selection, I also analysed how this can be affected by local and landscape factors. A constant thought during this project is that we need to be clear what we aim at in order to evaluate restoration outcome. This is essential, not only from a scientific and policy perspective, but also to provide relevant guidance for grassland managers. In this thesis I have shown that semi-natural grassland restoration can indeed be successful, but that this is highly dependent on what we decide to measure and how. For proper evaluation we also need pre-restoration data and longer time series in follow-up studies, in order to distinguish between fast initial responses and long-term outcomes.

Another important perspective emerging during these years is that irrespective of the restoration outcome, the long-term management needed in both restored and intact grasslands is highly dependent on social and economical factors. These factors largely affect the potential future for these habitats both locally, nationally and internationally.

Restoring a threatened and highly fragmented habitat type requires a holistic approach that includes a multitude of perspectives. As shown in this thesis, if it is possible to restore into intact reference conditions, it takes time and is case-dependent. Therefore, I think it is crucial that further loss of intact habitats is not justified by their eventual future restoration potential. Instead, restoration should be seen as an important complement to the conservation of already well-managed semi-natural grasslands.

Acknowledgements

This PhD project was funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS, grant number 2009-1105). Many thanks to my supervisors, to Lan Wang-Erlandsson and Alistair Auffret for reading and commenting on an early version of this thesis summary. Thanks also to A. Auffret for language corrections.

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Thank you!

First of all, many thanks to all farmers and conservation practitioners, especially the ones involved in this thesis, for your hard work keeping our precious remnants of semi-natural grasslands managed. You are truly my heroes.

I'm also very grateful to my main supervisor Regina Lindborg for guiding my way throughout this journey, with positive comments, great feedback and interesting discussions. Thanks for letting me try out different ideas and go my own way, with all its twists and turns. Thanks also to my co-supervisors Erik Öckinger and Sara Cousins for being there when I needed you. Fellow co-authors, Marie Winsa and Cibele Queiroz, and members of the Biogeography and Geomatics research unit, it has been a pleasure working with so many curious, creative and friendly people. Many thanks also to the HR personnel for facilitating practical issues, to my field assistants Evelina Lindgren and Vanna Lindgren for making my months in field so great and to all involved County Administrative Boards for helping me with grassland information.

Very dear colleagues (past and present), you really made my days at the department better in so many ways. Thanks for all intriguing science and non-science discussions, very interesting side-projects, music/books/movies exchanges, themed Thursdays, walks in the University agro-forestry garden and never-ending hunts for soft ice-cream. I know I will miss you.

Thanks also to my family and friends for standing by my side and involving me in the rest of the world out there. Last, but definitely not least, Hilma, for all the joy you bring into my life and for reminding me what is most important.

