Small remnant habitats
Important structures in fragmented landscapes

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Abstract
The world-wide intensification of agriculture has led to a decline in species richness due to land use change, isolation, and fragmentation of natural and semi-natural habitats in agricultural and forestry landscapes. As a consequence, there is a current landscape management focus on the importance of green infrastructure to mitigate biodiversity decline and preserve ecosystem functions e.g. pollination services and pest control. Even though intensification in agriculture has been ongoing for several hundreds of years, remnant habitats from earlier management practices may still be remaining with a surprisingly high plant richness. Preserving these habitats could help conserving plant species richness in agricultural landscapes, as well as other organisms that are dependent on plants for food and shelter.

In this thesis I focus on two small remnant habitats; midfield islets and borders between managed forest and crop field in southeastern Sweden. In the past, both habitats were included in the grazing system and therefore often still have remnant population of grassland specialist species left today. I have used these two remnant habitats as model habitats to investigate the effect of landscape factors and local factors on species richness of plants, flower morphologies and plants with fleshy fruits. Additively, I analysed the effect of surrounding landscape and local openness on the functions; pollination success, biological pest control of aphids and seed predation on midfield islets.

One of my studies showed that spatial distribution and size of the habitat affected plant species richness. Larger habitat size and higher connectivity between habitats increased species richness of plants in the habitats. Openness of the habitats was shown to be an important factor to increase species richness and richness of flower morphologies, both on midfield islets and in forest borders. Even though midfield islets had the highest species and morphology richness, both habitat types are needed for habitat complementary as forest borders have more plants with fleshy fruits and a higher richness of plant species that flowers in spring/early summer. It was also shown that a more complex forest border, not just with gaps in the canopy, but also with high variation in tree stem sizes increases plant species richness in the field layer. The conclusion is that by managing small remnant habitats to remain or become more semi-open and complex in their structure, would increase species richness of plants, grassland specialist species, and flower morphologies. It would also increase some ecosystem functions as seed predation and biologic pest control of aphids are more effective close to trees. If both midfield islets and forest borders would be managed to be semi-open, the area and connectivity of semi-open habitat would increase in the agricultural landscape, which may also improve pollination success as the connectivity between populations has a possibility to increase. Grassland specialist species are clearly abundant in the small remnant habitats. As the decline of semi-natural grasslands is causing a decline in grassland specialists’ species, not only plants, I recommend that small remnant habitats are included in conservation and management plans and strategies to improve habitat availability and connectivity for grassland species in agricultural landscapes.

Keywords: Alpha-diversity, Beta-diversity, Biological pest control, Canopy cover, Connectivity, Ecosystem function, Fleshy fruits, Forest edge, Forest management, Forest specialist species, Fragmentation, Functional diversity, Gamma-diversity, Grassland specialist species, Green infrastructure, Habitat amount hypothesis, Island biogeography, Midfield islets, Plant diversity, Plant-pollinator interaction, Pollination, Remnant habitat, Seed predation, Small habitats, Species richness, Structural heterogeneity.

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Dedicated to Loke and Mira
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In this thesis I focus on two small remnant habitats; midfield islets and borders between managed forest and crop field in southeastern Sweden. In the past, both habitats were included in the grazing system and therefore often still have remnant population of grassland specialist species left today. I have used these two remnant habitats as model habitats to investigate the effect of landscape factors and local factors on species richness of plants, flower morphologies and plants with fleshy fruits. Additively, I analysed the effect of surrounding landscape and local openness on the functions; pollination success, biological pest control of aphids and seed predation on midfield islets.

One of my studies showed that spatial distribution and size of the habitat affected plant species richness. Larger habitat size and higher connectivity between habitats increased species richness of plants in the habitats. Openness of the habitats was shown to be an important factor to increase species richness and richness of flower morphologies, both on midfield islets and in forest borders. Even though midfield islets had the highest species and morphology richness, both habitat types are needed for habitat complementary as forest borders have more plants with fleshy fruits and a higher richness of plant species that flowers in spring/early summer. It was also shown that a more complex forest border, not just with gaps in the canopy, but with high variation in tree stem sizes increases plant species richness in the field layer. The conclusion is that by managing small remnant habitats to remain or become more semi-open and complex in their structure, would increase species richness of plants, grassland specialist species, and flower morphologies. It would also increase some ecosystem functions as seed predation and biologic pest control of aphids are more effective close to trees. If both midfield islets and forest borders would be managed to be semi-open, the area and connectivity of semi-open habitat would increase in the agricultural landscape, which may also improve pollination success as the connectivity between populations has a possibility to increase. Grassland specialist species are clearly abundant in the small remnant habitats. As the decline of semi-natural grasslands is causing a decline in grassland specialists’ species, not only plants, I recommend that small remnant habitats are included in conservation and management plans and strategies to improve habitat availability and connectivity for grassland species in agricultural landscapes.
Sammanfattning

Världens jordbrukslandskap är under stor omvandling från ett småskaligt och lågintensivt brukande till ett storskaligt intensivt jordbruk. Omstruktureringen av det svenska jordbrukslandskapet under de senaste 150 åren har resulterat i större åkrar, planterade artfattiga skogar och färre naturliga eller lågintensivt skötta habitat (platsen där t.ex. växten växer). Exempel på dessa mins- kande lågintensivt skötta habitat är naturbetesmarker och traditionellt skötta ängar, som har betats eller sköts med slåtter under flera hundra år. Denna lågintensiva skötsel, utan gödsling eller plöjning, har lett till att naturbetesmarker och traditionellt skötta ängar idag är ett av världens mest artrika växthabitat. Till följd av fragmentering, isolering och förlust av lågintensivt skötta habitat har artrikedomen i landskapet minskat kraftigt; 33 % av Sveriges rödlistade arter är direkt kopplade till jordbrukslandskapet. Ett varierat landskap med en hög artdiversitet och livskraftiga populationer med spridningsmöjligheter mellan populationer av samma art, anses vara mer motståndskraftigt mot störningar, t.ex. miljö- och klimatförändringar, till skillnad från ett landskap domineras av monokulturer, med lite variation av växtarter och långa avstånd mellanilda växtpopulationer.

Ekosystemfunktioner kan beskrivas som interaktionen mellan en organismer i ekosystemet, t.ex. pollinering, eller mellan organismer och miljön. Till naturbetesmarkernas växter är även andra organismgrupper, t.ex. insekter, knutna. Flera av dessa bidrar till viktiga funktioner i jordbrukslandskapet, som exempelvis skadedjursbekämpning eller pollinering. En annan viktig ekosystemfunktion som växterna bidrar med är föda i form av frukt, frön eller bär till andra organismgrupper, t.ex. insekter, fåglar och gnagare. Utan tillgång till denna föda i landskapet blir resultatet färre djur i landskapet. En minskad mängd av naturbetesmarker påverkar därför inte bara växtnäringen i landskapet negativt utan även förekomsten av andra organismer som direkt eller indirekt är beroende av växterna. Förutom att växter behöver pollineras så sprids många växter med hjälp av andra organismer som rör sig i landskapet. Hur habitatens ligger i landskapet, hur isolerade habitaten är, är betydelse för interaktionen mellan pollen/pollinatörer/fröspridare och växten. Den faktiska kontakten mellan habitaten, d.v.s. om en växt nås av pollen/pollinatören/fröspridaren eller om avståndet är för långt, är en viktig faktor som påverkar artrikedomen i växthabitaten.

Även om många naturbetesmarker har försvunnit i jordbrukslandskapet, finns många små resthabitat kvar som inte inkluderats i vare sig jord- eller skogsbruket, t.ex. åkerholmar och skogsbyrn. Små resthabitat kan vara viktiga för mängdagen som mange organismer är hänvisade till dem och därmed skapar några av de ekosystemfunktioner förklaras, som är kopplade till sådana organisationer i två typer av små resthabitat; åkerholmar och skogsbyrn. Både på åkerholmar och i skogsbyrn kan växter som förknippas med tidigare gräsmarksskötsel finnas kvar än idag. Eftersom skogen historiskt användes till att valla betesdjur (så kallat utmarksbete) kan fortfarande gräsmarksspecialister finnas i byn, där skogen inte planterats helt i skog, utan över- och under- och iEducation anslutning. Jag har fokuserat på skogsbyrn som visar en tydlig övergångszone mellan planterad skog på ena sidan och åker på andra sidan. Skogsbyrn har en varierande fuktighet och är idag ofta täta med övervägande lövträd. Åkerholmar användes ofta för slåtter men kunde också betas när skördernas var intagen eller under de är åker låg i träda. Dessa habitat sköts idag ibland till viss del genom att ta bort barträd och spara lövträd och buskar som är anpassade till halvöppna habitat, som är en bristvärn i dagens jordbrukslandskap. Åkerholmar består delvis av berggrund och sten med ett mycket tunt jordläge och är därför en torr växtplats som kan vara begränsande för vissa växter men är andra sidan gynnar andra växter. Dessutom har åkerholmar generellt färre träd (d.v.s. en lägre krontäckning) vilket ger markfloran mer ljuus.
I den här avhandlingen undersökte följande faktorer i resthabitaten; rikedom av växter generellt, men även av så kallade specialistarter anpassade till gräsmark och skog, av växter med olika blomform och antal arter med bär och frukt. Detta relaterades sedan till olika funktioner i landskapet: pollinering, biologisk bekämpning av bladlöss och fröpredation. Fröpredation kan anses vara positivt, t.ex. om det förhindrar ogrässpridning till åkern, eller negativt om den sådda grödan åts upp. Jag inventerade växter på 205 åkerholmar, i 50 skogsbryg och 13 naturbetesmarker inom 10 större landskapsutsnitt runt Mälaren i sydöstra Sverige, med varierande andel åker i respektive landskap. Avhandlingen består av fyra delar. I de två första studierna inventerade jag växter (artikel 1) och undersökte ekologiska funktioner (artikel 2) på åkerholmar, i den tredje studien fokuserade jag på skogsbryg och i den fjärde använde jag data från både åkerholmar, bryn och naturbetesmarker. För att studera hur landskapets struktur påverkar mängden växter i ett resthabitat, undersökte jag mängden av eller storleken på åkerholmar (totalt 131 stycken) i olika landskap i relation till deras respektive mängd fält av arter.

Tidigare forskning har lagt fram en hypotes om att flera mindre habitat kan kompensera för ett större habitat, vilket skulle vara en viktig aspekt när prioriteringar ska göras inom naturvård. Min första studie visade dock att större åkerholmar och de med kortare avstånd till andra åkerholmar är viktigare för mängd fält än den totala arean av flera åkerholmar i närområdet (inom 100 m). En annan faktor som kan påverka artsammansättningen av växter är hur mycket ljus som når markfloran. Detta undersöktes både på åkerholmar och i skogsbryg. Resultaten visade att gräsmarksspecialister gynnas i mer öppna habitat med träd av varierande storlek medan skogsarter gynnas av mer slutna habitat med en hög mängd fält av trädarter. Den vetskapen är viktigt att ta hänsyn till vid en eventuell framtida skötsel för bevarandet av hotade arter, eftersom målet med skötseln kan variera i olika landskap.


Även vikten av åkerholmar och skogsbryg för att gynna tillgången på föda för pollinatörer och fruktätare mättes genom att mäta mängd fält av blomformer och antal arter med bär och frukt i de olika habitaten. Åkerholmar utgjorde växtplats för arter med flest olika blomformer och växtarter överlag medan det i brynen växer flest arter med frukt och bär. Växtsamhällena på de olika habitaten varierade i betydelse under växtsäsongen, där växtsamhället i brynen har flest arter som blommar tidigt på säsongen jämfört med åkerholmarna, och därmed kompletterar habitaten varandra som födosourcesområden. Det kan vara speciellt viktigt i landskap med få andra naturliga eller lågintensivt skötta habitat. Sammantaget för studierna hittade jag totalt sett 470 antal olika växtarter, inklusive buskar och träd, där en stor del (122) var typiska gräsmarksspecialister på åkerholmar och i skogsbryg. Det visar tydligt att små resthabitat är viktiga för mängd fält av växter och speciellt för många växter som annars är knutna till naturbetesmarker.

Resultaten i denna avhandling bidrar till att öka förståelsen kring små resthabitat för att bibehålla mängd fält av växter och funktioner kopplade till växterna i dagens jordbrukslandskap. I intensivt brukade områden är oftast resthabitat små och isolerade vilket gör att växtpopulationerna är hårt utsatta av både lokala förändringar så som minskad skötsel och igenväxning och landskapsförändringar som t.ex. fragmentering av gräsmarker och lövskogar. När få lämpliga växtplatser för en art eller ett växtsamhälle finns kvar i landskapet blir varje växtplats placering ännu viktigare. Ett för långt avstånd mellan habitaten leder till isolering av växtsamhället med en nedgång av arter som följd. Genom att sköta små resthabitat för att öka komplexiteten (heterogenitet i öppenhet/krontäckning, gylnna lövträd i olika storlekar och buskar) är därför viktigt för att skapa en ökad sammanlagd area av halvöppna habitat samt en ökad konnektivitet och variation mellan halvöppna habitat i landskapet. Detta gynnar inte typiska lövskogsarter men däremot
mångfalden av växter i jordbrukslandskap som har ett förflutet med betesdjur i löshrift på utmarksbete. Samtidigt gynnas pollinering, biologisk bekämpning av bladlöss och fröpredationen intill buskar och träd.

I resthabitaten i studieområdet växer gräsmarksspecialister. Av alla arter (n=352) som hittades i 13 naturbetesmarker fanns 60 % av arterna också på åkerholmar och 40 % av arterna i skogsbrynen i landskapet. Även om små resthabitat inte kan kompensera för nedgången av naturbetesmarker så kan de fungera som komplement och som ”stepping stones” mellan kvarvarande naturbetesmarker och andra halv-öppna habitat. Småhabitats funktionskvalitet kan bli ännu viktigare i framtiden för att arter ska kunna förflytta sig för att undvika klimat- och miljöförändringar.Idag har resthabitaten litet eller inget skydd. Eftersom arttrikedomen av gräsmarksspecialister har minskat i och med nedgången av naturbetesmarker, rekommenderar jag att kvarvarande resthabitat i landskapen ska ingå och skötas som en del av landskapets gröna infrastruktur i förvaltningsplaner.

List of papers*

This doctoral thesis consist of this summary section and the following papers, which are referred to by their Roman numerals in the text.


II. Lindgren, J., Lindborg, R. and Cousins, S.A.O. 2018: Local conditions in small habitats and surrounding landscape are important for pollination services, biological pest control and seed predation. In press *Agricultural, Ecosystem and Environment*, volume 251 (2018): 107-113


*Author contributions*

**Paper I** Conceived and designed: JL, SAOC. Fieldwork and data analysis: JL. Wrote the paper: JL, SAOC

**Paper II** Conceived and designed: JL with input from SAOC and RL. Performed the experiment and analysed data: JL. Wrote the paper: JL, SAOC with input from RL

**Paper III** Conceived and designed: JL, SAOC. Fieldwork and data analysis: JL. Wrote the paper: JL, AK, SAOC.

**Paper IV** Conceived and designed: JL. Fieldwork: JL. Data preparation and analysis: JL, AK. JL wrote the paper in collaboration with AK, OE and SAOC.
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1. Introduction

“A small natural feature is a site with ecological importance that is disproportionate to its size; sometimes because it provides resources that limit key populations or processes that influence a much larger area; sometimes because it supports unusual diversity, abundance, or productivity. The recognition and management of small natural features as distinct entities is primarily a means to facilitate pragmatic conservation of their associated biodiversity and ecosystem services” (Hunter 2017, page 2).

1.1. Biodiversity in managed landscapes

Slowing the ongoing global loss of biodiversity in today’s changing world is one of the greatest challenges facing humanity (Foley et al. 2005; Haddad et al. 2015). Major drivers of biodiversity loss are destruction and fragmentation of natural and semi-natural habitats, caused by intensified agriculture and forestry (Foley et al. 2005; Fischer & Lindenmayer 2007; Haddad et al. 2015). Despite a dramatic homogenization of our managed landscapes during the last century, there are still small semi-natural habitats remaining. These often support a surprisingly high biodiversity, and potentially provide positive effects for multiple crucial ecosystem functions, both locally and in the landscape. Greater knowledge of the effects of land use homogenization on biodiversity and ecosystem functioning is needed to increase the resilience of ecosystems to negative changes. Ecosystem functions can be explained as interactions between organisms within the ecosystem, for example pollination, or between organisms and the environment, such as nutrient cycling. The species composition in different habitats and in landscapes affects ecosystem functions and it has been suggested that higher species diversity increases the possibility for communities to be resilient to environmental challenges (Foley et al. 2005; Klein et al. 2007; Mace et al. 2012). Hence, there are substantial risks that ecological functions will decline or be lost altogether if the diversity of certain key functional groups drops below certain thresholds. To maintain viable populations in managed landscapes, it is crucial that species can disperse and persist in natural and semi-natural habitat remnants (Clobert 2012). Hence both local and landscape processes can be steering factors for many species in a plant community assembly. Many ecological studies which have focused on community assembly and functions have used large and species-rich habitats, whereas less attention have been given to more species-poor habitats in managed landscapes (but see some exceptions below).

1.2 Semi-natural grasslands

Many plant communities in today’s rural landscapes are associated with and adapted to centuries of small-scale traditional farming (Eriksson 2013; Olsson & Paik 2016). In some cases species are now actively favoured by management (so called grassland specialist species). Long continuity of grazing or mowing in northern Europe’s semi-natural grasslands has influenced the species composition of plants present, supporting many grassland specialists and leading to semi-natural grasslands being amongst the most species-rich plant habitats globally today (Wilson et al. 2012) (Box 1).
Mowing hay and grazing animals are also effective vectors for dispersing seeds from within and between grasslands. These grasslands are also rich in organisms from other taxonomic groups, especially pollinating insects (Öckinger & Smith 2007). This can contribute with positive spillover effects to surrounding landscapes (Öckinger & Smith 2007; Ekroos et al. 2013). In Sweden, semi-natural grassland are also an important habitats for a high diversity of deciduous tree species and shrubs (Pihlgren & Lennartsson 2008; Jakobsson & Lindbärg 2015) and are one of few semi-open habitats in managed landscapes. However, the semi-natural grasslands have declined dramatically during the last 150 years (Cousins et al. 2015).

1.3 Small remnant habitats

Intensively managed landscapes all over the world often contain small habitats not included in management, which have been shown to be important for biodiversity such as road verges and midfield islets (Cousins 2006), borders between two different land uses (Herlin & Fry 2000), hedgerows (Herlin & Fry 2000; Schlinkert et al. 2016), field margins (Marshall & Moonen 2002; Weibull et al. 2003a; Aavik & Liira 2010; Jakobsson et al. 2016), stone walls (Poschlod & Braun-Reichert 2017) and ditches (Aavik et al. 2008). Some of the small habitats fulfil a specific function to land users, like field margins, ditches or hedgerows, and others are left in the landscape as they are hard to remove, particularly in the case of midfield islets, which often have a core of bedrock. Small habitats can serve as refuges for organisms in agricultural landscapes, for example beetles (Wermelinger et al. 2007), reptiles (Pulsford et al. 2017), pollinators and birds (Öckinger & Smith 2007; Terraube et al. 2016) and also plant species in the field layer (Lindgren & Cousins 2017) or in the seed bank (Auffret & Cousins 2011; Plue & Cousins 2013). In small habitats species otherwise adapted to natural or semi-natural environment have limited opportunities to grow, forage, hide and nest in intensively managed landscapes. Intensification of agriculture and forestry has destroyed many of these small habitats and there is a concern that the decline will continue if their conservation value is not recognized (Poschlod & Braun-Reichert 2017). More knowledge is, however, urgently needed on what is affecting species richness and ecosystem functions on small habitats.
Some small habitats are remnants that hold populations matching functions of earlier land use (Cousins & Eriksson 2001; Auffret & Cousins 2011; Koyanagi et al. 2012a; Poschlod & Braun-Reichert 2017) (Box 2). These remnants can serve as additional habitats for specialist species alongside any key remaining habitats (e.g. small remnant of grasslands and semi-natural grasslands). The plant species composition in remnant habitats are affected by the past land use and local environment (Cousins & Eriksson 2001), in addition to the species composition in the surrounding landscape (Marteinsdottir & Eriksson 2014). Cousins and Lindborg (2008) and Koyanagi et al. (2012b) suggest that small remnant habitats may have an important function as a reservoir of grassland species for restoration of grassland communities in fragmented landscapes. Both from plants in the field layer but also because seeds can be stored in the soil seed bank from earlier land use (Auffret & Cousins 2011; Plue & Cousins 2013). The seed bank can add species to the above-ground plant community if environmental conditions improve, for example by increasing light availability or small scale disturbances in the soil caused by the reintroduction of grazing animals (Plue et al. 2017). Despite that most natural small habitats in agricultural landscapes contains fewer specialist species compared to key habitat semi-natural grasslands, small remnant habitats increases the heterogeneity and thus increase the biodiversity in the landscape (Poschlod & Braun-Reichert 2017). In this thesis, I have chosen to study two remnant habitats, one typically present in agricultural landscapes; midfield islets, and one on the border to forested landscapes; forest borders (Fig. 1). Both midfield islets and forests around farms were used for grazing and hay-making in the past, and today they hold a high richness of grassland specialist species in the field layer (Cousins & Eriksson 2002; Cousins 2006; Lindgren & Cousins 2017).
1.4 Habitat size and connectivity affecting plant species richness (paper I)

There is an ongoing debate over which factors that are most influential in controlling species richness in a given area, an essential question in conservation management. Fundamentally, a larger area will have more species than a smaller area according to the species-area relationship (Arrhenius 1921). A classical approach in conservation, originating from the species-area relationship, is the island biogeography theory, stipulating that area and distance between key habitats are the best predictors of immigration and extinction rates of populations, thus species richness (MacArthur & Wilson 1967) (Fig. 2). Island biogeography theory was developed using data from islands and is today commonly extended to model biodiversity patterns in fragmented habitats in terrestrial landscapes (Mendenhall et al. 2014).
According to island biogeography theory (MacArthur & Wilson, 1967) islands close to the mainland will likely receive more colonists from the mainland compared to islands further away, and the probability of colonization of large islands will be higher compared to smaller islands. Species will also be more sensitive to go extinct on small islands compared to larger islands, due to factors such as smaller population sizes and less available habitat on small islands. These parameters go hand in hand predicting that species richness will be higher on large islands near the mainland, and be lowest on small islands far away from the mainland. Bars represent relative species richness on the island. The island biogeography theory can be transferred to any other type of fragmented habitat in a hostile matrix, for example midfield islets in crop fields.

One recently suggested alternative hypothesis is the habitat amount hypothesis, stating that lower species richness in habitat fragments can be compensated by a larger amount of the same habitat type in the nearest surrounding (Fahrig 2013) (Fig. 3). This means that several small habitats, for example semi-natural grasslands, within a certain distance from each other would be as suitable for biodiversity as a single large habitat. Thus, it would be possible to compensate for the destruction of a large habitat by protecting several small ones. Fragmentation of or the reduction in habitat size increases species extinction risks as habitat size has been shown to affect speed of extinction and result in a quicker turnover (Fahrig 2001; Dobson et al. 2006; Kuussaari et al. 2009; Hylander & Ehrén 2013; Bommarco et al. 2014). The size of small remnant habitats, their spatial distribution and total amount in agricultural landscapes may therefore have major influence on ecosystem functions as well as biodiversity.
Figure 3 According to the habitat amount hypothesis (Fahrig, 2013) species richness will increase in a focal patch (red dots) if the amount of surrounding habitat increases (yellow dots) (a). Thus, species richness in a smaller local area will be compensated by a larger amount of surrounding habitat and have as high species richness as a larger, isolated patch, under condition that the sampling area (black squares) are constant in all patches (b) (paper I).

1.5 Habitat openness (paper II, III and IV)

The sizes and spatial distribution of habitats affects the species that are present, as well as the ecosystem functions provided, but community composition is also influenced by other local factors. For example, soil pH, water and light availability all determine the establishment of a dispersed seed (Bruun 2000) among other post-dispersal limiting processes such as seed predation (Bruun et al. 2010) and the presence of pesticides and fertilizers from surrounding crop field. As small habitats have a high edge to interior ratio, or no interior at all, light availability promotes light demanding species but is not suitable environment for species favored by interior habitats, for example forest specialist species (Honnay et al. 1998).

1.6 Traits and ecosystem functions (paper II and IV)

Several studies have pointed out that richness of plant traits in a community is important to multiple ecosystem functions, and plant communities’ resilience to and survival after disturbance (de la Riva et al. 2017; Gross et al. 2017). Functions in a trait-poor community are more sensitive to threats from the surroundings or environmental change than a trait-rich community, where several species can share the same ecosystem functions (redundancy). Large natural or semi-natural habitats, where the functional connectivity between populations is sufficient to uphold stable populations, are often more species rich, and the species present are generally also more genetically diverse (Aavik et al. 2017). Hence, they are more adaptable to changes in the environment, such as to climate or management (Vogel et al. 2012). A larger area of monoculture is e.g. more susceptible to pests (Woodcock et al. 2016) as species richness of predatory insect species is correlated with species richness of plants (Ramsden et al. 2015). Furthermore, in a monoculture, all plants flower at the same time. This provides a lot of pollen and nectar at this point, but only for a limited time-period and for groups of pollinators that are attracted by and able to feed from that type of flower. Many crop-plants are wind-pollinated. Species-rich habitats embedded within the monocultures, such as in midfield islets, can offer a diverse set of flowers during a longer period of time, and are hence important resources for pollinators when crops are not flowering.

One way to estimate diversity is by measuring trait diversity in a community (Mayfield et al. 2010). Traits are characters of a species e.g. mean height, specific leaf area or flower shape (Box 3), which strongly enhance specific interactions with other species and the environment (Hooper et al. 2005).
Trait richness can provide information about the community response to environmental changes, and a higher species richness seems to have a greater possibility to stabilize the functional diversity in the community and make it more resilient to changes in the environment (Sakschewski et al. 2016). Today, functional traits are commonly used to link plant species traits to how species respond to the environment and provide links to other organisms e.g. dispersal propagules, specific leaf area and morphology of flowers (Kattge et al. 2011). The trait assembly of a plant community in a habitat determines the functions provided by the ecosystem, as different traits can contribute to different functions. In smaller habitats, connectivity to nearby habitats becomes exceedingly important, as dispersal between habitats can rescue declining populations (Hanski 1999). In this network of isolated habitats, the functional connectivity depends on dispersal vectors to disperse pollen between plants and seeds (Auffret et al. 2017). Thus, habitat quality includes the available food resource for the dispersal vectors. A weakening in ecosystem functions like pollination and biological pest control in crops has been observed in many agricultural landscapes, and the reason for the decline is argued to be agricultural intensification (Kremen et al. 2007).

Table 1 Study parameters used to evaluate the functions of small remnant habitats.

<table>
<thead>
<tr>
<th>Description</th>
<th>Used in</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of plant species in the field layer, including woody species with a height &lt; 50 cm.</td>
<td>Paper I, Paper IV</td>
</tr>
<tr>
<td>No. of plant species in the field layer, excluding woody species.</td>
<td>Paper III</td>
</tr>
<tr>
<td>No. of grassland specialist species and forest specialist species.</td>
<td>Paper I, Paper III</td>
</tr>
<tr>
<td>No. of woody species in field, shrub and tree layer.</td>
<td>Paper III</td>
</tr>
<tr>
<td>Flower shapes of all plant species in field, shrub and tree layer</td>
<td>Paper IV</td>
</tr>
<tr>
<td>Fleshy fruits of all plant species in field, shrub and tree layer</td>
<td>Paper IV</td>
</tr>
<tr>
<td>No. of seed settings in 48 plants</td>
<td>Paper II</td>
</tr>
<tr>
<td>Number of predated <em>Rhopalosiphum padi</em> aphids. In total 288 self-adhesive labels x 4 aphids</td>
<td>Paper II</td>
</tr>
<tr>
<td>Percentage of predated sheets with <em>Helianthus annuus</em> seeds. In total 192 sheets x 10 seeds</td>
<td>Paper II</td>
</tr>
</tbody>
</table>
1.7 Aim of the thesis

The aim of this thesis is to quantify the plant diversity present in small remnant habitats and investigate how landscape and local parameters affect plant diversity patterns and related ecological functions. This knowledge will shed light on the importance and buffering capacity of small remnant habitats in relation to the decrease of species associated to open/semi-open semi-natural and deciduous forests. I focus on two small remnant habitats; midfield islets and forest borders, located in agricultural landscapes of different levels of management intensity and with few semi-natural grassland or semi-open habitats left. My goal is to use this knowledge to discuss possible management strategies of small remnant habitats in the future.

I have surveyed and analysed the plant community (species richness, richness of specialist species, richness of species with fleshy fruits and different flower shapes) in small two small habitats. The ecological functions investigated in this thesis are, pollination, biological pest control, and seed predation and the provision of food for pollinators and frugivores (Table 1).

Specific aims of the thesis are to:

1. Identify the differences and similarities between plant species richness, composition and traits in small remnant habitats and semi-natural grasslands (paper I, III, IV).
2. Investigate the influence of landscape, distance between and size of remnant habitats on species richness (paper I and II).
3. Investigate the influence of canopy cover (paper II, III, IV) and the complexity of woody plants (paper III) on species richness and composition
2. Study area

The study area was chosen as it is one of the most intensively managed agricultural regions in Sweden (Fig. 4). It is located in south-central Sweden (central point coordinates 59°35′09″N and 17°37′15″ E).

Forestry is common in the region and the forest consists mainly of coniferous and mixed forest. Besides forests, there is a large area of arable land and lakes, where arable land occurs in valleys on finer soils and forest occurs on coarser soils higher up in the terrain. The dominant tree species are Norway spruce (*Picea abies* ((L.) H. Karst)), Scots pine (*Pinus sylvestris* L.), birch (*Betula pendula* and *pubescens* L.) and European aspen (*Populus tremula* L.). Most forests are managed coniferous forests with a species-poor vascular plant field layer (Cousins & Eriksson 2001). The growing season, which starts when the temperature reaches above 5°C and ends when the temperature is below 5°C for four consecutive days) generally occurs from late April to October-November. Mean annual temperature is 5-6°C and mean annual precipitation in the region is 500-600 mm (SMHI 2017).

The long historical continuity of livestock grazing and haymaking has had a large positive impact on the plant species pool in the region (Eriksson & Cousins 2014). Since the late 19th century however, a predominant part of the open/semi-open pastures or meadows has turned into
forest or crop field, and the landscape is now more homogeneous compared to 150 years ago (Cousins et al. 2015).

2.1 Midfield islets and forest borders

Midfield islets are dry habitats with a core of bedrock or boulders. The size of a midfield islet varies from a few square meters to a maximum of 0.5 ha and they are surrounded by crop field. Often, this is where farmers gathered the stones that obstructed ploughing the fields. Midfield islets were within the infield system and mowed for hay, and also grazed when fields were in fallow. Thus they were open grass-dominated habitats (Fig. 3). The high species richness on midfield islets means that they are potential sources for species favored by open or semi-open habitats. Another reason to study midfield islets is that their island-like positions in a species-poor crop field, which makes them excellent models for studying processes (e.g. the effect of fragmentation and isolation) occurring also in larger fragments such as semi-natural grasslands. Midfield islets are protected by Swedish law (Miljöbalken 1998) which means that they should not be destroyed. However, management to maintain their conservation value, for grassland species at least, it is sometimes necessary to remove stands of younger trees.

Both midfield islets and forest borders were included in the grazing system less than 100 years ago (Cousins and Eriksson, 2001). Forest borders (forest edges in paper III) were historically mostly open or semi-open grassland, mown or grazed (Cousins et al. 2015). Today there is often a strip of natural established mixed or deciduous forest at the forest edge that is not included in forest production. Therefore grassland specialist species can still be growing in forest borders as remnant populations and act as additional habitats to semi-natural grasslands for light demanding plant species. Forest borders create a large area of linear deciduous forests in landscapes, where light demanding shrubs and trees, otherwise rare in dense managed forests, may occur. Forest borders are often situated at the transition between clay soil and moraine with open crop fields on the finer soils and dense, often managed, coniferous forest on the coarser soils. Forest borders can have very varying soil moisture whereas midfield islets are usually extremely dry.

Many studies conducted by forest ecologists have focused on measuring the edge effect or the ecotone of the border into the forest, to analyse the way in which plant species composition changes with increasing distance from the adjacent land use (Barlow et al. 2007; Chabrerie et al. 2013; Hardt et al. 2013). True forest specialist species are negatively affected by the open edge and prefer to grow in the forest interior where there is no effect from adjacent crop fields (Chabrerie et al. 2013). In this thesis, I consider the borders as a specific habitat type, a remnant grassland habitat, separated from managed forests. In such ecotones, transition zones between two habitat types, species richness is often high because a mixture of species from both habitat types are found. However, few studies in forest edges are conducted from a “conservation of grassland species” perspective (Cousins & Eriksson 2001).

In anthropogenic landscapes there are often high intensive land uses and sharp boundaries. In total, there are 148 836 km of anthropogenic borders in central Sweden (Esseen et al. 2016). Only a fraction of these borders are complex in their structure and species composition (Esseen et al. 2016). A complex border acts as a less abrupt transition zone between crop-fields and forest. It should have a mix of trees species (deciduous trees are actively promoted by some land managers) and shrubs in a gradual transition zone (Fig. 5). A more complex border is considered a better environment for birds and other animals because it can provide more food, shelter and nesting places than less complex borders. Hence, this provides an opportunity to increase species richness in agricultural landscapes by changing the way in which forest borders are managed. This argument has made forest borders a key target for hunters, land managers and policy makers. Forest borders are interesting model habitat as they are the dividing line between forestry and agriculture, handled by different authorities, and not least within different scientific disciplines. This fact can cause disagreement about the management objectives. Some species can be regarded as important for grassland conservation but these are often not desirable or of interest for forest conservation.
However, there are few empirical studies supporting the management recommendations. Management to create a more complex border will affect the composition of plants in the border (Sottile et al. 2015), and may increase diversity of more light demanding species (e.g. grassland specialist species) in the border, as long as there are dispersal sources, spatial or in the seed bank, in the nearby landscape.

Figure 5 (Adapted from paper III) The left side of the figure illustrates a simple border with few species of deciduous trees and shrubs between crop field and managed production forest. The right side illustrates a complex border including gaps, with a diversity of deciduous trees and shrubs in different sizes.
3. Methods

3.1 Extracting landscape variables and identifying study objects

The size of small habitat remnants means that they are not always included in existing maps. I used infra-red aerial photographs (from 2010-2013) to interpret and digitize land cover, including midfield islets, for Paper I, II and IV. This was performed using Stereo Analyst for ArcGIS. To increases the generality of the models, several landscapes in intensively managed landscapes (agriculture and forestry) were chosen. Ten larger landscapes (circle shaped with radii 10 km) were chosen (Fig. 4) and for paper I, twenty-seven smaller landscapes (circles with radii of 500 m) were placed where there were midfield islets in crop fields within the larger landscape circles. In Paper IV, I used midfield islets, forest borders and semi-natural grasslands from five of landscapes used in Paper I and all border used in paper III (Fig. 7).

For Paper I and II distances, area and amount of midfield islets were calculated in ArcGIS 9.2-10.2. I used the Swedish Board of Agriculture’s database of valuable grasslands (TUVA, http://www.siv.se/tuva) to identify and calculate distance to the nearest semi-grassland.

For Paper III I used ArcGIS to randomize points on the border between forest and crop field according to the terrain map (Terrängkartan in Swedish). I then used infra-red aerial photographs (from 2013) with the Stereo Analyst for ArcGIS to identify borders of varying vegetation compared to adjacent forest for Paper III and IV. Sharp borders, those with coniferous managed forests directly adjacent to crop fields and lacking the differentiation in the border vegetation from the managed forest, were excluded.

3.2 Vegetation surveys (paper I, III, IV)

The vegetation surveys of plant communities were conducted during the summers of 2012-2014. Midfield islets and semi-natural grassland was expected to have a high density of species in the field layer (Wilson et al. 2012). Hence these were surveyed using relatively small quadrats (0.5 x 0.5 m) (Table 2).

Plant surveys in forests are usually sampled in larger quadrats (Plue et al. 2017), because forest species are not as densely packed as grasslands communities. Therefor the field layer in forest borders was surveyed using 2x2 m quadrats (Table 2). The openness of semi-natural grasslands, midfield islets and forest edge transects was visually classified in the field into four categories: 1) >50 % canopy cover; 2) 25≤50 %; 3) 10<25 %; and 4) < 10 % canopy cover. Complexity of forest borders was estimated by openness (percentage of gaps <25%, 25-50%, ≥50 %), species richness of trees and shrubs and the diameters of all tree trunks at breast height (130 cm, dbh).

In total I sampled the vegetation from 205 midfield islets, 50 forest borders and 13 semi-natural grasslands in this thesis.
Table 2 Number and sizes of measured parameters on midfield islets, forest borders and semi-natural grasslands.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Midfield islet</th>
<th>Forest border</th>
<th>Semi-natural grassland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness in the field layer, height&lt;50cm (I,IV)</td>
<td>0.5x0.5 m</td>
<td>2x2 m</td>
<td>0.5x0.5 m</td>
</tr>
<tr>
<td>Species richness of non-woody species in the field layer (III)</td>
<td>2x2 m</td>
<td></td>
<td>250</td>
</tr>
<tr>
<td>Species richness of specialist species (I, III)</td>
<td>0.5x0.5 m</td>
<td>2x2 m</td>
<td>250</td>
</tr>
<tr>
<td>Species richness of woody species (III)</td>
<td>10x10 m</td>
<td></td>
<td>250</td>
</tr>
<tr>
<td>Species richness of flower shapes (IV)</td>
<td>0.5x0.5 m</td>
<td>2x2 m</td>
<td>250</td>
</tr>
<tr>
<td>Species richness of plants with fleshy fruits (IV)</td>
<td>The whole midfield islet</td>
<td>131</td>
<td>50x the border depth</td>
</tr>
</tbody>
</table>

3.3 Multifunction experiment set-up when testing pollination, biologic pest control and seed predation (paper II)

In Paper II three ecological functions; pollination, biologic pest control and seed predation were tested using an experiment on midfield islets of similar size (Table 1). These ecosystem functions are of major economic interest for farmers as the potential spillover from the remnant habitats could benefit crop production (Alignier et al. 2014; Kammerer et al. 2016; Woodcock et al. 2016). The novelty of this study is the approach of a multifunctional field experiment to analyze the way in which local factors and surrounding landscape variables affect three different ecosystem functions during the same time period and over the same spatial extent. Three common species in Swedish agricultural landscape were used as study objects; Primula veris (Cowslip), Rhopalosiphum padi (Bird cherry-oat aphids) and Helianthus annuus (Common sunflower) seeds to evaluate the effect of local openness and distance to key habitats, semi-natural grassland and forest on pollination, pest and seed predation.

I first chose 12 midfield islets of similar size, which differed in their distance to semi-natural grasslands and forest habitats. Pollination was quantified using 48 pots containing Primula veris (Cowslip, Fig. 6). P. veris is a perennial primrose and a heterostylos species that rarely achieve successful pollination without an interaction with an insect. Plants were chosen carefully to balance the number of inflorescences and morph ratio (thrum: pin morph). The pots were placed out in May 2015 in two pairs on each midfield islets. After five weeks the pots were collected and each inflorescence protected from further pollination by a thin fabric. The plants were kept outdoors and number of seeds per flower and plant was recorded later in July.
3.4 Traits (paper IV)

In the final study (IV) I used species data from all inventoried habitats (130 midfield islets, 50 forest borders and 13 semi-natural grasslands). I chose to analyse traits related to ecological functions of attracting pollinators and frugivores during different time-periods of the growing season. I analyzed trait richness to assess whether the composition of flower shapes present differed among habitat types and season, i.e. habitat complementary. I also analyzed the richness of species with fleshy fruits as it is energy-rich food important for frugivores. By fleshy fruits I
mean a fruit containing a fleshy tissue, e.g. berries, drupes, rosehips and apples (Eriksson & Ehrlén 1991; Bolmgren & Lönnberg 2005) and the classification of flower morphology was derived from the Biolflor database (Klotz et al. 2002).

Flowering season of the plants was according to the Swedish flora “Den nya nordiska floran” (Mossberg & Stenberg 2010) and classified as early (April-May), mid (June-July) and late (August-October).

3.5 Data analysis

In all four studies there were several factors that influenced plant species richness (I, III), pollination and predation (II) and trait richness of flower morphology and fleshy fruits (IV). These were related to habitat size, isolation and the local environmental conditions. Therefore, multivariate analysis was used in all four papers. Multivariate analysis makes it possible to compare the effects of different factors and to identify the most important factors. Generalized linear models (GLM) was used in paper I, II and IV, multiple linear models (LM) in paper II and III. GLMs allow modelling of data where the residual variation is not normally distributed; i.e. where this key assumption of LMs is violated (Zuur et al. 2007). Non-metric multidimensional scaling (NMDS) was used in paper VI to analyse plant communities dissimilarly (Oksanen 2015). NMDS uses rank information and can therefore handle nonlinear responses (Oksanen 2015). All numerical analyses in this thesis were carried out in R 2.14.1-3.3.0.
5. Major findings and discussion

5.1 Species composition comparisons

This thesis demonstrates the importance of small remnant habitats, in particularly for maintaining plant diversity. Small remnant habitats were, in many cases, the main habitats for species favoured by open/semi-open habitats in intensively managed agricultural landscapes. Both midfield islets and complex forest borders were clearly remnants of former grassland management. There was a higher plant species richness in midfield islets compared to forest borders and the species composition on midfield islets had an overlap with semi-natural grassland of 60% (Fig. 7).

Figure 7 A visualisation showing overlap in plant species composition. Out of all plant species found in 13 semi-natural grassland (n=352), 63% were also found in either midfield islets (60%) or forest borders (4%) in the same regions (n=5). (The visualisation includes only occurrence of species and not abundance.)

Forest borders had a 40% overlap with species in semi-natural grassland, although it should be noted that this analysis does not include species abundance in the different habitats. Twenty percent of the species in semi-natural grassland were not found in midfield islets or forest borders. In Paper IV, the difference of the communities is shown by the analyses of similarity of the plant communities, including abundance (Fig. 8).
One explanation for the difference in species composition in forest borders compared to semi-natural grassland and midfield islets may be time since land use change which affect species richness, in particularly specialist species. Another explanation, tested in this thesis, is openness in the habitat. In forest borders, light availability decreases with succession as tree density increases. This in turn will negatively affect populations of light demanding species (paper III). Succession is faster in forest borders, compared to midfield islets, as the soil conditions are more favourable. Midfield islets have thin soils on top of bedrock prone to drought, which can slow down succession.

When plant species richness declines in the landscape, it is likely also that the number of flower morphologies also decreases, which may in turn affect richness or abundance of pollinators. Even though fluctuation of abundance of common pollinators, and not species richness of pollinators, are major drivers of pollination services in crops (Genung et al. 2017), a positive relationship between species richness and stability of ecosystem functions has been identified (Hooper et al. 2005; Mace et al. 2012; Sakschewski et al. 2016). However, the presence of a high species richness of flower shapes may affect the richness of pollinators, as one out of several factors. A greater diversity of functional traits present within the ecosystem, usually increases resilience towards environmental changes (Tilman et al. 1996; Tscharntke et al. 2012). Fleshy fruits are energy-rich food for frugivores and the dispersal of plants with fleshy fruits depends on animals eating and dispersing seeds. This plant-animal interaction links habitats together, with the dispersal pattern of plants reflecting the movement pattern of frugivores in the landscapes (McConkey et al. 2012). My results show that, even though forest edges are less species-rich, they are important in providing a diversity of fleshy fruits to frugivores and as a source for flowering species providing nectar and pollen to pollinators in spring and early summer (paper IV). The value of remnant habitats are complementary in importance for different groups of organisms which may change over the season. Thus, small remnant habitats are not only important for many plant species but also for other groups of organisms in homogenous agricultural landscapes.
5.2 Connectivity in the landscape

The ability of the habitats to have a high diversity of plants depends on several landscape factors. Despite previous suggestions that habitat amount is the main driver for species richness, and that isolation is of minor importance (Fahrig 2013), the result show that connectivity between habitats is of great importance to maintain both overall species richness and grassland specialist species richness in this system (Paper I). In paper I, the habitat amount hypothesis was shown to be less effective in predicting species richness than habitat area and distance to similar habitats. The results indicate therefore that it is not possible to compensate the reduction of the habitat size by many surrounding habitats, although a higher proportion of semi-natural habitats results in higher plant species richness in the landscape (paper I). This result is consistent with a contemporary study from Norway (Evju & Sverdrup-Thygeson 2016). Populations within a functional distance increase pollination success (paper II) and reduce extinctions due to genetic drift. In other words, the more locations a plant species occurs in the landscape, the better chance it has to maintain a diverse species gene bank, and therefore to persist (Aavik et al. 2014; Aavik et al. 2017).

Small remnant habitats can also affect ecosystem functions in agricultural landscapes, which increases their importance when there are no or little natural and semi-natural habitats left. One function that may be effected is pollination, as a high proportion of semi-natural habitats have a positive effect on the richness and abundance of bees (Carrié et al. 2017). Plant species composition in small remnant habitats determined food supply (Paper IV), shelter and nesting possibilities for many organisms. However, successful dispersal and establishment of plants depends on the distance between suitable habitats. My results in paper II show that more forest surrounding a midfield islet, which means less crop field and shorter distances from the midfield islet to other species-rich habitats like road verges or forest borders, was positive for all tested functions (pollination success, biological pest control and seed predation). This supports the findings that the success of crops needing pollination, is higher closer to habitats with high plant species-richness (Woodcock et al. 2016) and that structural connectivity is determined by the spatial arrangement of the remnant habitats and affects the interaction between plants and their pollinators and seed dispersers (Auffret et al. 2017). Further, increased plant diversity, e.g. in small remnant habitats, near crop-fields, has been shown to control the efficiency of both pollination and biological pest control (Woodcock et al. 2016; Hatt et al. 2017). Thus, more heterogeneous landscapes, including species-rich small remnant habitats will promote several vital ecosystem functions at the landscape scale (Fig. 9). But to maximize the species-richness in small remnant habitats they may need managements (paper II, III and IV).
5.3 Canopy cover or not?

I have estimated openness of the tree canopy as a proxy for light availability for the field layer (paper II, III, IV) and all studies showed its positive effect on plant diversity, particularly species associated to semi-natural grasslands. High habitat openness increased plant species richness (Fig. 10 a) (paper III), richness of grassland specialist plant species (Fig. 10 c) (paper III), richness of flower shapes (paper IV), and pollination success (paper II). On the other hand, the occurrence of most plants with fleshy fruits, seed predation and biological pest control, declined with openness. Not surprisingly, richness of forest specialist plant species is higher in forest borders with denser canopy cover (Fig. 10 b).
If midfield islets and forest borders are not managed they will be encroached by trees and shrubs, where the soil depth allows it. Small remnant habitats with local spatial variability can serve as connections between different patches and increase the chance of survival of species preferring semi-open habitats, which are rare in our modern landscape. This is important in landscapes where connectivity between semi-natural grasslands has decreased and there are remnant populations of grassland specialist species left in small habitats. The range of a species is partly limited by environmental factors e.g. the local climate (Holt 2003) but to counteract species loss due to limited ability to range shifts during climate change, a network of heterogeneous habitats is needed to meet different environmental requirements of species (Donaldson et al. 2017).

Figure 10 (Adapted from paper III) Boxplots (showing median, interquartile range and outliers) of the effect of amount of gaps in the forest border on plant diversity of the field layer. The percentages of gaps in the forest/field border (50 m) affect species richness of a) all plants in the field layer, b) deciduous forest specialist plant species and c) grassland specialists. The percentage of gaps are divided into categories: 1) < 25% (n=24), 2) 25% < 50% (n=16), 3) ≥50% (n=10). According to Wilcoxon rank sum tests, there were significant difference between the most open to the most closed border in richness of all species (p-value=0.001, w=35.5), forest specialist species (p-value=0.002, w=39) and of grassland specialist species (p-value=0.015, w=183.5).
6. The importance of management to improve green infrastructure

There is a concern in Sweden that forest encroachment will cause a decline in biodiversity in agricultural landscapes. Many species are threatened, and 33% of all red-listed species in Sweden are associated with agricultural landscapes (Sandström et al. 2015). Authorities in Sweden are working to develop management instructions to increase ecosystem functions of the forest border and to improve landscapes’ green infrastructure. The Swedish Environmental Objectives (the overall goal of Swedish environmental policy) aims to maintain a sustainable environment (Swedish Environmental Protection Agency 2016). A corporate list of actions suggested by several contractors, including the Board of agriculture and the Forestry commission, has been created to promote diversity, infrastructure of the landscape and ecosystem services (Swedish Environmental Protection Agency 2016). One of its goals is to provide proposals on the management of transition zones between agriculture and forest to create less abrupt transition zones. The directives advocate a complex forest border, containing a mix of trees species and shrubs in a gradual transition zone (Fig. 5). Some management plans suggest that gaps should be included so that light can reach the ground in some areas. Whether forest borders should be managed to promote forest specialist (less or no gaps) or grassland specialist species (more gaps) (paper III) should be decided by the landscape context. In my study area, semi-open areas are lacking and small remnant habitats, such as forest borders, could possibly increase the connectivity of habitats for light demanding plants species. Small remnant habitats can be important alternative habitats to semi-natural grasslands, if they are managed to promote grassland specialist species. The management would also improve the green infrastructure of semi-open habitats in the agricultural landscape. For example, small remnant habitats together with larger semi-natural grassland in the landscape has a combined positive effect on the abundance and species richness of birds that is higher than in landscape with only small remnant habitats or only semi-natural grasslands (Cunningham et al. 2008).

In a changing world, both in terms of land use and climate, a green infrastructure (a network of habitats which is expected to enhance biodiversity) with functional connectivity between habitats, where pollen and seeds can be dispersed in the landscape, is central for plant populations and communities to persist. Small habitats increase the landscape mosaic and acts as temporary habitats or as stepping stones to increase connectivity in a changing climate when species has to shift their range to meet up the environmental changes (Donaldson et al. 2017). My results confirm that landscape- and habitat heterogeneity have clear positive effects on biodiversity (Paper I, III, IV) (Benton et al. 2003; Honnay et al. 2003; Weibull et al. 2003b), a heterogeneity which has been found to even exceed the effects of management regimes in some cases (Weibull et al. 2000; Roschewitz et al. 2005; Gibson et al. 2007; Rader et al. 2014). Hence, a heterogeneity of openness in habitats will provide a diversity of theoretically suitable niches for plants with different environmental requirements and possibly increase species mobility and persistence as isolated small population grows with an increasingly threat of extinction because of global change (Nicol & Possingham 2010).

As only a fraction of the forest borders in Sweden are complex in their structure and species composition (Esseen et al. 2016), by managing forest borders to increase the percentage of gaps and complexity would (re)create a large area of semi-open habitats in the landscape and counteract the lack of heterogenic habitats in agricultural landscapes (Paper III). Increasing management by removing trees and shrubs in small remnant habitats can improve the functional dispersal network and green infrastructure, and decrease the number of threatened populations of plant species in the landscape (Hooftman et al. 2016; Auffret et al. 2017) as canopy cover is a strong governing factor on the structure and composition of grassland plant communities (Paper III and IV).

Including small remnant habitats in landscapes management plans would go in line with the policy European union resolved in 2013 to improve biodiversity and healthy networks of ecosystems, where the Natura 2000 network is the central part (European commission 2017-10-06). To embrace small remnant habitats in larger management units e.g. by free-range grazing is one way to increase functional connectivity. Although, this will not only aid the dispersal of specialist
species, but also more common species that are stronger competitors, in particular in intensively managed agricultural landscapes where the eutrophication which might result in an advantage for more competitive species (Smart et al. 2006). Therefore, it is of great importance to prevent propagation of nutritional supplements in the small remnant habitats. If it is not possible to graze the habitats, new management methods is needed to compensate the decline in grazing animals in these landscapes. Another issue is that small remnant habitats rely on human management to preserve their ecological value. Generally, they are not well protected by law in Europe (e.g. Poschlod & Braun-Reichert 2017). Directives on the best way to manage small remnant habitats in fragmented landscapes are required.

Concluding remarks

This thesis shows that both landscape composition and local condition are important for biodiversity and ecosystem functions in small remnant habitats in agricultural landscapes. A decline of plant diversity at the landscape scale could negatively affect essential ecosystem functions, and the diversity of other organisms that depend on structures or specific plants species growing in the small remnant habitats. Larger sizes and greater connectedness to other remnant habitats showed an increasing possibility to support a high species richness of plants, also in fragmented landscapes. Although small remnant habitats are not able to compensate for the decline in diversity or ecosystem functions, replacing the semi-natural grassland, they can act as compliments and stepping stones between semi-natural grasslands and should be included and managed as important green infrastructure in management plans. Understanding landscape heterogeneity and ecosystem functions in agricultural landscapes is a key part of working to achieve a sustainable environment in the future. Small remnant habitats will be even more important when climate change and species needs to shift range. The lost or degradation of each single small remnant habitat might be fateful for present and future functional connectivity and ecosystem functions. These small remnant habitats can also be used as a model system to be applied on larger systems e.g. fragmented forests or semi-natural grasslands.

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SMHI 2017. Swedish Meteorological and Hydrological Institute, Statistic information including mean monthly temperature and mean annual precipitation in Sweden.


4 Summary of papers

4.1 Paper I

*Is habitat amount in landscapes a better predictor of species richness of plants than isolation and size of the focal habitat patch?*


Fragmentation and isolation affect species richness of plants in different habitats. There is a need within conservation to find efficient and accurate estimates of fragmentation and isolation effects on biodiversity. The effects are even greater on small habitats, as illustrated by the steeper curve of the species area relationship of plants in small habitats. It has been argued that a larger amount of the habitat type in a local landscape around a focal patch (habitat) will buffer a decline in species caused by a smaller patch area, on the focal patch (the habitat amount hypothesis according to Fahrig 2013). In the classical island biogeography theory model (MacArthur & Wilson 1967), the area and the distance to the main land, or the same habitat type, will be the most important factors effecting species richness on islands. We tested which of the habitat amount hypothesis or the island biogeography theory that the most effective model of species richness and grassland specialist species of plants in the field layer on 131 midfield islets (each of an area > 150 m²) in 27 agricultural study areas in south-eastern Sweden. We also tested whether sampling area affects the prediction of landscape variables on total species richness.

The scale of the study makes the analysis a robust way to analyse the effects of patch size, isolation and habitat amount on plant species richness patterns. We found that the amount of habitat in the local landscape had a positive relationship with overall species richness and grassland specialist species, but this was not as effective a predictor as the classical island biogeography theory. We recommend that even in small habitat patches, it is important that sampling effort is scaled according to patch size for an optimal prediction of species richness from landscape variables. Understanding the pattern of biodiversity in fragmented landscapes is an important task future conservation management. The results are of broad interest for policy makers, conservationists and ecologists.

4.2 Paper II

*How does distance to key habitats and local openness affect pollination and predation of aphids and seeds?*

Lindgren, J., Lindborg, R. and Cousins, S.A.O. Local conditions in small habitats and surrounding landscape are important for pollination services, biological pest control and seed predation.

Large monotonous areas of crop fields can affect ecosystem functions e.g. pollination or susceptibility against pests in the landscape. However, different functions may respond differently to the same factor for example the connectivity between natural or semi-natural habitats. Habitat
connectivity improves, not only dispersal, but also the opportunity of organisms to forage or in-
teract with organisms in other habitats. Small semi-natural habitats are important structures to
maintain a high biodiversity in agricultural landscapes. Besides habitat size and connectivity also
local environmental conditions, such as light availability, will influence plant species composi-
tion. Few studies have investigated three ecosystem functions at the same time and in the same
landscape through a set-up of field experiments. Multifunctional experiments are unusual, partic-
ularly with field experiments. In this study we tested how the ecosystem functions pollination,
biological pest control and seed predation were affected by local factors: tree and grass cover,
and by landscape factors: isolation from and amount in the surrounding of key habitats (semi-
natural grassland and forest) on 12 midfield islets of nearly the same size. The study species were
Primula veris (pollination success), Rhopalosiphum padi (predation of aphids) and Helianthus
annuus (seed predation). Altogether, 7181 seeds were produced by 48 plants of Primula veris
after five weeks planted on the midfield islet. The plants were covered with fabric before and
after being planted and re-potted. Thirty-nine % of the placed aphids were eaten and 56 % of the
strips with glued seeds were predated.

Pollination success and seed predation were predicted by both local and landscape factors. Pollination success improved with more forest in the surrounding landscape. This also correlates
with short distances to habitats were wild populations of P. veris grows. Lower levels of canopy
cover on the midfield islet had a positive impact on pollination success and a negative impact on
seed predation, while biological pest control in trees increased with distance to forest. The results
indicate that connectivity between semi-natural habitats and a small-scale variation in habitat
openness, i.e. including both grassy areas and areas with trees and shrubs have a positive effect
on several functions in the landscape. Managing ecosystems to provide a range of different func-
tions is one of the main future goals within the EU agricultural policy services. Pollution ser-
vices, biological pest control and seed predation as weed control are three significant functions
to food production. By managing small non-crop habitats and creating more semi-open habitats
(more heterogeneity in canopy cover), pollination success and possibly also biological pest con-
trol, can be improved and reduce seed predation within the non-crop habitats. In this way the
amount of pesticides could decrease at the same time as pollination success of wild flowers and
insect pollinated crops would increase. Understanding the pattern of ecosystem functions in frag-
mented landscapes is an important task for future conservation management, particularly to dis-
entangle conflicting effects on different functions. This study is a contribution to the theoretical
framework of policy drivers in conservation biology by adding real landscape data into multi-
functional analysis.

4.3 Paper III

Does suggested management of borders affect the species composition of plants in the forest
border?

Lindgren, J., Kimberley, A. and Cousins, S.A.O. The complexity of forest borders determines the
understory vegetation

In agricultural landscapes small habitats can act as a habitats for many plants. Marginal habitats,
such as forest borders are one of only a few places in the modern landscape for more light de-
manding species of plants to exist e.g. deciduous trees, shrubs and grassland specialist species, as
well as many typical ancient deciduous forest specialist species. Managing borders to make them
more complex is therefore encouraged in landscape planning, to enhance and conserve biodiver-
sity in anthropogenic landscapes. The focus of the forestry commission is to increase flowering
and berry/fruit bearing trees and shrubs without any specific management objectives for the field
layer. Although there are many recommendations, the management effect on species composition
of plants in forest borders have not been systematically investigated. To study the effect of management we surveyed 50 borders between managed forests, primarily coniferous, and crop fields in 5 landscapes. Increasing complexity of the forest border had an effect on the species composition in the field layer. Plant species richness increased with more gaps in the tree canopy. Grassland specialist species increased and forest specialist species, not surprisingly, decreased with increasing proportion of gaps and was also positively affected by a high tree diversity. Therefore the creation of gaps is crucial to species composition and should be in line with landscape management plans. This study is the first, to our knowledge, that tests the effect of management of forest borders in agricultural landscapes, on plant species composition in the understory field layer. The results give empirical evidence to the suggested management to increase forest border complexity to actually increase species richness of plants. Thus, forest borders has a potential to increase biodiversity in agricultural landscapes with an appropriate management. As the forest borders are remnants from previous grassland management in the study area, it could be argued that forest borders should primarily be managed to be more open to make an effort to preserve grassland species in the landscape. However species associated to deciduous forest ecosystems are declining thus forest borders in some landscapes could be managed more towards increasing deciduous trees and shrubs. The study is a contribution to the framework of policy drivers in conservation biology and biodiversity restoration to test proposed management strategies with empirical data at a landscape scale.

4.4 Paper IV

*Can remnant habitats in fragmented agricultural landscape buffer the decline of semi-natural grassland as a food resource for pollinators and frugivores?*

Lindgren, J., Kimberley A., Eriksson, O. and Cousins, S.A.O.

When species-rich grasslands have declined by up to 90% in the study area, small remnant habitats may become increasingly important to uphold different ecological functions in intensively managed landscapes. Species richness sometimes correlates with functional richness although this is not always the case. It is not clear to what extent plant species composition in small remnant habitats may “buffer” the functions that semi-natural grasslands provided in the past. In this study we investigated the overlap in plant species composition between semi-natural grasslands, midfield islets and forest borders. Additively, we analyzed the proportion and richness of plant traits (flower morphology and flower season and fleshy fruits) chosen for their ecological importance as food resources and for supporting wildlife (pollinators and frugivores) in remnant habitats. We analyzed the effect of habitat type, habitat openness and surrounding agricultural management. Midfield islet had the most similar plant species composition to semi-natural grasslands. Not surprisingly, they also had the highest diversity of flower morphologies, whereas forest borders had the largest proportion of plants with fleshy fruits. Analysing the timing of flowering there was a difference between the habitats too, where forest borders peaked in spring/early summer whereas midfield islets are more important for pollinators in mid- and late summer. Thus, midfield islets and forest border differed as food resources for both pollinating insects and frugivores. Comparisons of ecological functions in different habitat types, during different times or seasons are an essential step in predicting their importance to other organismal groups than plants. It is also a prerequisite to understand where in the landscape important interactions occur between plants and other groups, to improve the resilience of the ecosystems. In landscapes with little other species-rich habitats left a diversity of small habitat types is needed to complement each other to support pollinators and frugivores. Well-connected habitats in the green infrastructure will also increase the potentials for diversity of other plant interacting organism groups.
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