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## Effective conservation of biodiversity and ecosystem services in agricultural landscapes

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# Effective conservation of biodiversity and ecosystem services in agricultural landscapes

WILLIAM SIDEMO HOLM

ENVIRONMENTAL SCIENCE | CEC | FACULTY OF SCIENCE | LUND UNIVERSITY

## Effective conservation of biodiversity and ecosystem services in agricultural landscapes

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- I. Sidemo-Holm, W., Ekroos, J., Smith, HG. Conceptualizations of land sharing vs. land sparing – a systematic overview. Submitted to Conservation Science and Practice.
- II. Sidemo-Holm, W., Seufert, V., Birkhofer, K., Ekroos, J., Tschumi, M., Smith, HG. Organic farming benefits both rare and common species: a global meta-analysis. Manuscript.
- III. Sidemo-Holm, W., Carrie, R., Ekroos, J., Lindström, SAM., Smith, HG. Reduced crop density increases floral resources to pollinators without affecting crop yield in organic and conventional fields. Submitted to Journal of Applied Ecology.
- IV. Sidemo-Holm, W., Brady, MV., Carrie, R., Ekroos, J., Smith, HG. Cost-effectiveness of organic farming for conserving biodiversity in different landscape contexts. Manuscript.
- V. Sidemo-Holm, W., Smith, HG., Brady, MV., 2018. Improving agricultural pollution abatement through result-based payment schemes. Land Use Policy 77, 209-219.

# Effective conservation of biodiversity and ecosystem services in agricultural landscapes

William Sidemo Holm



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DOCTORAL DISSERTATION

by due permission of the Faculty of Science, Lund University, Sweden.  
To be defended in the Blue Hall, Ecology building, Sölvegatan 37, Lund,  
on Friday 26<sup>th</sup> of March 2021 at 13.00,  
for the degree of Doctor of Philosophy in Environmental Science

*Faculty opponent*  
Professor William Sutherland  
University of Cambridge  
United Kingdom

<b>Organization</b> LUND UNIVERSITY Centre for Environmental and Climate Science <b>Author:</b> William Sidemo Holm		<b>Document name</b> DOCTORAL DISSERTATION
		<b>Date of issue</b> 26th March 2021
<b>Title</b> Effective conservation of biodiversity and ecosystem services in agricultural landscapes		
<b>Abstract</b> Agricultural land use is a major driver of biodiversity losses and changes in ecosystem services. Thus, for the sake of both humans and wild organism per se, effective strategies that enable both agricultural production and conservation of biodiversity and ecosystem services are urgently needed. Such strategies can be divided into those that reduce the intensity of farming in general (such as organic farming), and those that target specific habitats of key importance for farmland biodiversity (e.g., maintaining semi-natural, grazed grasslands). In this thesis, I used a combination of scientific methods in five different studies to assess and propose such strategies that promote biodiversity and ecosystem services, effectively and cost-effectively, in agricultural landscapes. This included reviewing the literature on land-sharing vs. land-sparing strategies, which explicitly compare the merits of spatially integrating (land sharing) or separating (land sparing) biodiversity conservation and agricultural production, respectively. I found that the literature has focused on a limited number of taxonomic groups, ecosystem services and economic factors (particularly birds, carbon storage and agricultural output), which impedes a more holistic understanding of the strategies' social and ecological consequences. In another study, I evaluated the potential of organic farming to preserve rare species, which includes species of high conservation concern. Using a meta-analysis on a global dataset, I showed that organic compared to conventional farming benefits both rare and common species of arthropods, birds, earthworms and plants. I also carried out an empirical study where I compared abundance and diversity of bumblebees and flowering weeds, as well as crop yields, across 19 organic and conventional farms. The study showed that organic farming benefits bumblebees by harboring more flowering weeds, but only when crop yields are low. This demonstrates the need for strategies to enhance yields in organic crop fields (which are typically lower than those in conventional fields) without degrading the benefits of organic farming to biodiversity. I found that one such strategy can be to reduce crop sowing density, which benefited flowering weeds and thus indirectly bumblebees, without significantly affecting crop yields. I subsequently used data from the same farms in a study where I modelled the influence of landscape complexity on the cost-effectiveness of organic farming in promoting plant species richness. The cost-effectiveness, in terms of achieving targets for increasing species richness at a landscape scale at the lowest possible cost, was highest in the least complex landscape. Lastly, I performed a study showing how a model can be used to predict environmental results in result-based payment schemes. The study demonstrated that result-based payments can promote substantially more cost-effective agricultural pollution abatement than action-based payments. In conclusion, this thesis has contributed with new knowledge about how existing conservation strategies affect biodiversity and ecosystem services, as well as proposed novel conservation strategies. The findings of this thesis can contribute to more effective and cost-effective conservation and promotion of biodiversity and ecosystem services in agricultural landscapes		
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William Sidemo Holm



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# List of papers I-V

The thesis is based on the following papers, referred to in the text by their Roman numeral.

- I. **Sidemo-Holm, W.**, Ekroos, J., Smith, HG. Conceptualizations of land sharing vs. land sparing – a systematic overview. Submitted to Conservation Science and Practice.
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# Author contributions

- I. WSH, HGS and JE conceived the idea. WSH designed the methodology, collected and analyzed the data and finally wrote the manuscript with input from HGS and JE.
- II. WSH, HGS and JE designed the study with input from VS, KB and MT. WSH and VS collected the data. WSH analyzed the data and wrote the manuscript with input from all authors.
- III. WSH, HGS, JE and SL conceived the idea and designed the methodology. WSH, RC and JE collected the data. WSH analyzed the data with input from HGS and JE. WSH wrote the manuscript. All authors contributed to the final manuscript.
- IV. WSH, MB and HGS conceived the idea and designed the methodology. WSH, JE and RC collected the data. RC developed the ecological model, and WSH and MB the ecological-economic model. MB calibrated the empirical economic model and ran the simulations. WSH analyzed the results with input from MB and RC. WSH wrote the manuscript. All authors contributed to the final manuscript.
- V. MB and HGS originally conceived the idea. WSH designed the models, performed the analyses and wrote the manuscript, all with input from MB. All authors contributed to the final manuscript.



# Populärvetenskaplig sammanfattning

Idag används mer än en tredjedel av jordens markyta till jordbruksproduktion. Till följd av jordbrukets expansion har ytan naturliga habitat minskat, liksom bestånd och mångfald av vilda arter. Med en alltjämt växande världsbefolkning och ökande efterfrågan på jordbruksprodukter kommer troligtvis efterfrågan och därmed jordbruksproduktionen att fortsätta expandera på bekostnad av naturliga habitat och bli alltmer intensiv under kommande decennier. Exempel på negativa effekter av intensifiering av jordbruket inkluderar direkta och indirekta effekter på biologisk mångfald från användning av växtskyddsmedel och näringsläckage till vattendrag, sjöar och hav som uppstår vid användning av gödningsmedel. För att minska jordbrukets negativa påverkan får jordbrukare bidrag för att utföra miljöåtgärder. Några av de vanligaste miljöåtgärderna är att upprätthålla skötsel av permanenta gräsmarker, odla ekologiskt och placera skyddszoner mellan åkrar och vattendrag eller sjöar för att fånga upp ytavrinning av jordbruksföroreningar (framförallt fosfor). Ofta varierar miljöåtgärders effektivitet beroende på olika omständigheter. Till exempel kan effekten av ekologisk odling på biologisk mångfald vara olika beroende på hur mycket naturliga eller seminaturliga miljöer det finns i det omkringliggande landskapet. Miljöåtgärder ger ofta upphov till direkta kostnader för skapande och skötsel, samt inkomstbortfall när jordbruksmark används mindre intensivt eller tas helt ur bruk. Därför är det viktigt att miljöåtgärder både är effektiva på att bevara biologisk mångfald och ekosystemtjänster (dvs. produkter och tjänster från naturen som människor har nytta av), och är kostnadseffektiva så att värdeförlusten från jordbruksproduktionen minimeras.

I denna avhandling har jag analyserat befintliga, samt utvecklat nya, strategier för att möjliggöra effektivare och kostnadseffektivare bevarande av biologisk mångfald och ekosystemtjänster i jordbrukslandskap. Med jordbrukslandskap åsyftar jag sammanhängande områden med jordbruksproduktion som den huvudsakliga markanvändningen och vars yta sträcker sig över flera gårdar.

Jag har funnit att studier som har utvärderat alternativa markanvändningsstrategier som syftar till att kombinera jordbruksproduktion och bevarande av biologisk mångfald har fokuserat på ett fåtal organismgrupper (främst fåglar) och ekosystemtjänster (främst



kolbindning). Dessutom har bara ett fåtal studier mätt hur sådana markanvändningsstrategier påverkar jordbrukares nettoinkomst. Istället har studier rapporterat den totala jordbruksproduktionen, vilken inte behöver korrelera med nettoinkomsten då kostnader och intäkter kan variera beroende på strategi och gröda. Ett resultat av detta relativt snäva fokus är att det inte går att veta hur undersökta strategier påverkar biologisk mångfald eller ekosystemtjänster i allmänhet, eller hur ekonomiska värden påverkas. För att bättre kunna tillgodose olika behov och mål gällande bevarande av biologisk mångfald, ekosystemtjänster och jordbruksproduktion, finns det ett behov av studier som med ett bredare fokus utvärderar markanvändningsstrategier för jordbruksproduktion och biologisk mångfald. Resultat från sådana studier kan sedan användas som informationsunderlag för att möjliggöra implementering av strategier med högre potential att generera ekologiska och ekonomiska värden.

Vid bevarande av biologisk mångfald är det viktigt att miljöåtgärder gynnar både vanliga arter som kan vara viktiga för ekosystemtjänster och ovanliga arter som riskerar att utrotas regionalt eller globalt. Ofta är ovanliga arter särskilt känsliga för jordbruksexpansion och -intensifiering, och därför i större behov av miljöåtgärder för att inte regional försvinna. Ekologisk odling är en miljöåtgärd som generellt gynnar biologisk mångfald jämfört med konventionell odling på grund av minskad användning av jordbrukskemikalier och mer komplexa växtföljder. Det har dock ifrågasatts om ekologisk odling har någon effekt på ovanliga arter, eller om det huvudsakligen är vanliga arter som gynnas. I en studie undersökte jag hur ekologisk odling påverkar leddjur, fåglar, dagmaskar och växter. Jag fann att ekologisk odling gynnar både ovanliga och vanliga arter av alla de undersökta organismgrupperna, och att ovanliga arter dessutom gynnas mest. Studien visar därför att ekologisk odling fungerar som en bevarandeåtgärd för ovanliga arter i jordbrukslandskap.

Ekologisk odling genererar generellt mindre skördar än konventionell odling, bland annat eftersom det utan växtskyddsmedel är svårare att bekämpa ogräs som konkurrerar med grödorna om näring, sol och vatten. Med hjälp av nya metoder, till exempel effektivare mekanisk ogräsbekämpning, finns det dock möjlighet att minska det så kallade skördegapet mellan ekologisk och konventionell odling. I en studie där jag undersökte biologisk mångfald i ekologiskt och konventionellt odlade fält med varierande skördar, fann jag att ekologiskt odlade fält med låga, men inte höga, skördar gynnade mångfalden av och mängden blommande växter. Samtidigt fann jag att mängden blommande växter i fälten gynnade individ- och artantalet humlor. Detta tyder på att jordbruksmetoder som åstadkommer högre skörd även leder till att fördelarna med ekologisk odling för biologisk mångfald försvinner. Därför är det viktigt att utveckla strategier som möjliggör att egenskaperna som leder till att ekologisk odling gynnar biologisk mångfald bevaras när skördehöjande jordbruksmetoder införs. Jag visade att en sådan metod kan vara att minska utsädesmängden så att avståndet mellan

varje frö av den sådda grödan ökar med ett antal centimeter. Jag fann att detta ökade mängden blommande vilda växter, vilket gynnar pollinatörer som utnyttjar dem som en födoresurs, utan att det påverkade skörden negativt. Denna typ av åtgärd är viktig för att bevara den positiva effekten av ekologisk odling vid införandet av skördehöjande åtgärder.

Genom att använda så kallad ekologisk-ekonomisk modellering, visade jag även att mängden permanenta gräsmarker i landskapet som omger jordbruksfälten kan påverka potentialen av ekologisk odling att gynna biologisk mångfald kostnadseffektivt. Jag fann att omvandlingen av konventionell till ekologisk odling för att gynna mångfalden av vilda växtarter är mer kostnadseffektiv i jordbrukslandskap utan eller med en låg andel permanenta gräsmarker. Detta betyder att det går att få större ekologisk nytta från ekologisk odling givet kostnaden om policyer rumsligt inriktar sig på landskap med få permanenta gräsmarker. Studien visade även att det är en stor skillnad på antalet växtarter i landskap med och utan permanenta gräsmarker och påvisade därigenom vikten av att bevara existerande permanenta gräsmarker i jordbrukslandskap.

Det är vanligtvis frivilligt att utföra miljöåtgärder såsom ekologisk odling på sin jordbruksmark. Jordbrukare som väljer att göra det får i utbyte en miljöersättning som ska kompensera för kostnader och inkomstbortfall. Ersättningar är traditionellt sett åtgärdsbaserade, vilket betyder att deras omfattning beräknas beroende på typ av miljöåtgärd och dess storlek. Detta kan dock leda till att de inte blir kostnadseffektiva, eftersom jordbrukare har ett ekonomiskt incitament att placera miljöåtgärder på den jordbruksmark som är minst lönsam, samtidigt som potentialen för att gynna biologisk mångfald och ekosystemtjänster kan vara betydligt större på en annan del av jordbruksmarken. Detta har lett till ett ökat intresse för resultatbaserade miljöersättningar. Med resultatbaserade miljöersättningar beror jordbrukares ersättning på hur utförda miljöåtgärder påverkar biologisk mångfald eller ekosystemtjänster. Det vill säga, ju effektivare åtgärderna är, desto mer får jordbrukarna betalt. Det har tidigare bevisats att resultatbaserade ersättningar är ett lovande policy-verktyg för att rumsligt rikta miljöåtgärder dit de gynnar biologisk mångfald mest kostnadseffektivt. Jag visade i en studie att resultatbaserade ersättningar även kan ge incitament för att kostnadseffektivt minska förorenande näringsläckage med hjälp av miljöåtgärden skyddszoner. Jag använde modeller för att uppskatta mängden fosforavrinning som skyddszoner kan minska beroende på deras placering. Mina resultat visade att relativt åtgärdsbaserade ersättningar kan resultatbaserade ersättningar öka jordbrukares vinst och minska förorenande näringsläckage till en lägre kostnad, både gällande betalda bidrag och förlorade värden från jordbruksproduktionen. Ett problem när det gäller resultatbaserade ersättningar är att det ibland är svårt att uppskatta vilken nytta en åtgärd genererat. I denna studie visade jag för första gången hur ett ersättningsystem kan baseras på uppskattningar av miljönyttan med hjälp av modeller. I Sverige liksom i många andra EU-länder finns det rumsligt explicit data som möjliggör modellering

av hur åtgärder såsom skyddszoner minskar näringsläckage. Implementering av resultatbaserade bidrag för att minska näringsläckage skulle drastiskt kunna öka kostnadseffektiviteten av åtgärder såsom skyddszoner och bidra till hälsosammare och renare vattendrag, sjöar och hav.

Sammanfattningsvis så kan upptäckterna som har gjorts i denna doktorsavhandling bidra med att öka effektiviteten och kostnadseffektiviteten av bevarande och gynnande av biologisk mångfald och ekosystemtjänster, vilket är viktigt både för människor och naturen.

# Introduction

## Nature and people

Humans depend on nature. Nature produces the air we breathe, the food we eat, and purifies the water we drink. The great diversity of nature, and the actions and interactions of living organisms, are central for making the Earth habitable. Without nature, the Earth wouldn't be more livable than the moon.

The benefits that organisms provide to humans are commonly referred to as “ecosystem services” (MEA, 2005), or with a slightly more general term “nature’s contributions to people” (IPBES, 2019). For producing ecosystem services that provide direct use values, e.g., an apple, there are typically several other underpinning ecosystem services involved (Fisher and Turner, 2008). For instance, for an apple tree to produce an apple, insect pollinators need to pollinate its flowers and the soil where it stands needs to be nutritious, which typically involves decomposing soil organisms. Other ecosystem services that benefit apple production include biological pest control (e.g., from arthropods and birds that feed on apple pests), water purification and erosion control. These and other ecosystem services are natural processes occurring as organisms strive to persist and thrive.

To maintain ecosystem functioning and provisioning of ecosystem services in different environments and over time, a diversity among living organisms (biodiversity) is fundamental (IPBES, 2019). Evolution has led to the origin of millions of species, where *“every species is a masterpiece, exquisitely adapted to the particular environment in which it has survived”* (Wilson, 2016). As species have adapted to different environments, they have evolved different functional traits, consisting of a wealth of adaptations in terms of their morphology, life-histories, diets etc. Species with different traits can contribute to particular ecosystem functions and services. For instance, insects with a short tongue are often more efficient pollinators of flowers with short corolla tubes, such as flowers of apple trees, while a long tongue is preferable for flowers with long corolla tubes, such as honeysuckle (cf. Klumpers et al., 2019).

Even in cases when a limited number of species currently provide the majority of a particular ecosystem service (e.g., crop pollination, Kleijn et al., 2015), a rich biodiversity with accompanying variation in traits can significantly increase the benefits (e.g., crop pollination and biological pest control, Dainese et al., 2019). Because

different species are important for different functions at different places and times, biodiversity is needed for resilient provisioning of ecosystem services across different spatial and temporal scales (MEA, 2005). Furthermore, because species can respond differently to environmental changes, e.g., climate change and pollution, those that currently appear functionally redundant could in the future provide key ecosystem functions and services (Dee et al., 2019; Hooper et al., 2002).

In addition to materially important ecosystem services, such as those involved in food production, biodiversity contributes to less tangible values, including physical and mental health benefits from recreation, aesthetic enjoyment and spiritual experiences (IPBES, 2019). Ultimately, as with humans, other organisms have intrinsic value, i.e., they have a value for their own sake, and we therefore have a moral obligation towards them (Callicott, 1995).

In spite of our moral obligation towards nonhuman organisms, and their fundamental values to humans, there is currently an ongoing loss of biodiversity, both in terms of variation, such as extinction of species, and in numbers of individuals, that is faster than at any other time in human history (IPBES, 2019). The main drivers of this unprecedented decline include land-use change, climate change, invasive species, wildlife poaching and pollution (IPBES, 2019). Among the many human activities that fuel these drivers, none has arguably had a larger impact than the expansion and intensification of agriculture (IPBES, 2019; Maxwell et al., 2016).

## The impact of agriculture on nature

More than a third of the land on Earth is used for agriculture (World Bank Group, 2018). Over the past 50 years, agriculture has become increasingly intensive due to technological advances and increasing demands for agricultural products from a growing and wealthier human population (FAO, 2017). Agricultural intensification has via increased production per unit area contributed to making food cheaper relative to disposable income (USDA, 2020), reduced the prevalence of undernourishment in the world (FAO et al., 2015) and will remain important in achieving Zero Hunger by 2030, one of United Nation's 17 Sustainable Development Goals (United Nations, 2015). At the same time, agricultural intensification is causing declines in biodiversity (Foley et al., 2005; Kehoe et al., 2017; Newbold et al., 2015; Tilman et al., 2001) and essential ecosystem services, including pollination (IPBES, 2016), biological pest control (Bianchi et al., 2006; Geiger et al., 2010), soil formation, nutrient cycling, and water regulation and purification (Rasmussen et al., 2018). The decline in ecosystem services that are important for agricultural production can to some extent be compensated. However, such solutions often exacerbate the negative impact on biodiversity and ecosystem services and are in the long run less resilient and sustainable

than naturally occurring ecosystem services. For instance, increased use of mineral fertilizers and pesticides to compensate for degraded nutrient cycling and biological pest control respectively, leads to increased nutrient leaching, accelerated depletion of non-renewable phosphorus resources and further declines in biological control agents (Matson et al., 1997; Scholz et al., 2013).

Agricultural intensification involves both changes in field management and expansion into semi-natural habitats (Lüscher et al., 2016). Every second species found in agricultural landscapes exclusively occurs in semi-natural habitats such as semi-natural grasslands, field margins, hedgerows and forest remnants. The majority of the other half occurs in both semi-natural habitats and crop fields, while a smaller share exclusively occurs in crop fields (Lüscher et al., 2016). Therefore, impact of agricultural intensification on either of crop fields or semi-natural habitats can lead to local species loss.

Agricultural intensification involves increased use of synthetic pesticides and mineral fertilizers which negatively impact both target organisms, e.g., weeds and insect pests (Oerke, 2006), and non-target organisms, e.g., birds (Mineau and Whiteside, 2013) and bees (Rundlöf et al., 2015), in crop fields and nearby habitats (Egan Franklin et al., 2014; Geiger et al., 2010; Gonthier et al., 2014; Kleijn et al., 2009; Kleijn and Snoeiijing, 1997). Pesticides and fertilizers also disperse and pollute ground and surface waters, giving rise to water purification costs and degraded fishery and loss of recreational values (Tilman et al., 2002). The dispersion of pesticides and fertilizers has also affected irrigation water quality, with the consequence that 15-35% of all withdrawals have become unsuitable for agricultural purposes (MEA, 2005). Furthermore, agricultural intensification has entailed increased meat production and use of fossil fuels to run heavy equipment and machinery (Willett et al., 2019), two of the main contributors to greenhouse gas emissions from the agricultural sector, which account for 10-13% of the world's total emissions (IPCC, 2015; Tubiello et al., 2014).

Another consequence of agricultural intensification is that agricultural landscapes are becoming increasingly simplified across multiple spatial and temporal scales. At the regional level, simplification occurs as regions become more specialized in particular production systems, e.g., livestock or crop production (Eurostat, 2021a). Likewise, individual farms are becoming increasingly specialized by focusing on either livestock or crop production (Eurostat, 2021a), and use increasingly simplified crop rotations involving a few high-yielding crop varieties (Aguilar et al., 2015). Such specialization has largely been enabled by greater accessibility to, and use of, external inputs. Fertilizers and livestock feed can be acquired from outside the farm, relaxing the need for farmers to produce their own manure for fertilizing crops and feed for livestock, while pesticide application relaxes the need for complex crop rotations as a remedy for pest control (Abson, 2019). Temporally, there is less variation in the growing period between and within fields, because farm management has become more synchronized

as a result of fewer crop types and more efficient land management (Robinson and Sutherland, 2002). There is also less within-field ecological heterogeneity because of weed control with herbicides, and fewer farmers practicing intercropping and polyculture (Abson, 2019; Benton et al., 2003). The heterogeneity of the environment beyond crop fields has decreased as fields have become larger (White and Roy, 2015) and farms fewer but larger (Ciaian et al., 2010), as a result of transformation of semi-natural habitats, such as field margins, hedgerows and semi-natural grasslands (Benton et al., 2003).

Agricultural landscape simplification is affecting biodiversity negatively in various ways. Loss or degradation of semi-natural habitats leads to losses in the organisms residing there. It also reduces the connectivity among remaining semi-natural habitats, making it more difficult for species to recolonize habitats following stochastic extinctions (Hanski and Ovaskainen, 2000). Species living in semi-natural habitats frequently disperse to crop fields, where they stay, pass through, or use for collecting resources (Smith et al., 2014). Consequently, loss or degradation of semi-natural habitats also impacts the biodiversity in crop fields (Tschardt et al., 2005). At the same time, within-field heterogeneity can benefit biodiversity in both crop fields and semi-natural habitats, by providing resources to mobile species inhabiting these habitats and making the matrix between semi-natural habitats more permeable (Sirami et al., 2019; Smith et al., 2014).

Agricultural landscape simplification can affect species differently depending on their traits. Species that have very specific needs, typically in terms of diet or habitat condition, are often affected more negatively by landscape simplification than species able to thrive in a broader variety of environmental conditions (Devictor et al., 2008; Gámez-Virués et al., 2015). Species with low dispersal ability and low fecundity have also been identified as being at higher risk of population declines or extinction because of landscape simplification (Börschig et al., 2013; Smith et al., 2014).

To sum up, the effects of agricultural intensification on usage of pesticides and fertilizers, and landscape simplification are the main drivers of the severe decline in biodiversity in agricultural landscapes (Benton et al., 2003; IPBES, 2019; Stoate et al., 2009).

# Biodiversity conservation in agricultural landscapes

With the global population projected to reach 9.7 billion by 2050 (United Nations, 2019), it will be a huge challenge to meet the food demand without severely degrading nature, and thereby threatening the existence of species and long-term supply of ecosystem services that are essential for agriculture and human welfare at large (Kehoe et al., 2017; Tilman et al., 2011).

Payments for agri-environmental measures are a key policy instrument to mitigate the negative effects of agriculture on biodiversity and ecosystem services (Baylis et al., 2008). In the European Union (EU), agri-environmental measures are implemented by farmers to protect or enhance biodiversity, water, soil, landscape quality, air quality and climate change adaptation and mitigation (European Commission, 2017). Agri-environmental measures may for instance entail not using synthetic pesticides or fertilizers, or creating and maintaining semi-natural habitats. Organic farming is one of the most common agri-environmental measures in the EU, accounting for more than 8.5% of all farmland (Eurostat, 2021b). Organic farming involves farming without synthetic pesticides or mineral fertilizers and typically more complex crop rotation schemes compared to conventional farming. As a result, organic farms have higher species richness and abundance of wild organism than conventional farms (Bengtsson et al., 2005; Tuck et al., 2014). Other examples of agri-environmental measures include sowing flower strips along field margins (Haaland et al., 2011), restoring and maintaining semi-natural grasslands with required grazing pressure (Metera et al., 2010), and reducing agricultural pollution by growing cover crops and/or vegetated buffer strips that prevent fertilizers and pesticides from dissipating from crop fields and polluting surrounding environments (Abdalla et al., 2019; Haddaway et al., 2018). Agri-environmental measures can also benefit ecosystem services that enhance agricultural production, such as crop pollination (Garibaldi et al., 2014), pest control (Tschumi et al., 2016) and soil fertility (Busari et al., 2015).

The effectiveness of agri-environmental measures in benefiting biodiversity and ecosystem services often depends on spatial context, such as landscape complexity (Batáry et al., 2011; Kleijn et al., 2011; Tschardt et al., 2005) and may differ between taxonomic and functional groups (Tuck et al., 2014). Therefore, a better understanding of the influence of context, such as that organic farming benefits biodiversity more effectively in simpler than in more complex landscapes (Tuck et al., 2014), is important to guide implementation of agri-environmental measures to where they are most effective.

Implementing agri-environmental measures usually entails management and opportunity costs, i.e., direct costs associated with carrying out measures and foregone



income from not optimizing the land use for agricultural production. Therefore, out of fairness and to encourage their implementation, policy schemes typically incentivize agri-environmental measures with payments that compensate for farmers' management and opportunity costs. It is important from a food security and welfare perspective that policy schemes incentivize cost-effective implementation of agri-environmental measures, i.e., high gains in biodiversity and ecosystem services relative to the management, opportunity and transaction costs (e.g., costs of controlling, monitoring and searching information). When measures are implemented cost-effectively, the loss in the value of agricultural production is minimized relative to the achieved conservation benefit (Wätzold and Schwerdtner, 2005). Since agri-environmental measures are typically funded by government subsidies, cost-effectiveness is also critical for high leverage with the available public funds (Boyd et al., 2015; Joseph et al., 2009), which are modest compared to what is required to reach global biodiversity targets (McCarthy et al., 2012). Furthermore, greater leverage of the public funds used for conservation is urgently needed as restoring biodiversity lost from agricultural landscapes is becoming increasingly expensive as land rent prices increase (Phelps et al., 2013) and more species become threatened (Drechsler et al., 2011).

Despite its importance, the cost-effectiveness of agri-environmental measures is often considerably lower than what is achievable (e.g., Batáry et al., 2015; Burton and Schwarz, 2013; Ferraro and Pattanayak, 2006; Fisher et al., 2014; Smith et al., 2016; Wätzold and Schwerdtner, 2005). Further, only a small share of the literature evaluating agri-environmental measures have analyzed cost-effectiveness (Ansell et al., 2016; Wätzold and Schwerdtner, 2005). Therefore, there is a pressing need for more research investigating the factors that impact the cost-effectiveness of agri-environmental measures; so that these can be designed to maximize the conservation benefits given the limited conservation budgets.

In addition to understanding what influences the cost-effectiveness of agri-environmental measures, there is a need for policies that incentivize such implementation (Armsworth et al., 2012). Existing incentives to preserve biodiversity are by and large designed so that farmers receive payments depending on the type of agri-environmental measures and their extent, while the effects on biodiversity or ecosystem services do not impact the payment size. Consequently, farmers have a financial incentive to implement agri-environmental measures when the payments are greater than the opportunity and management costs. Conversely, the payments do not provide farmers with an incentive to optimize implementation of agri-environmental measures to preserve and promote biodiversity or ecosystem services. What is more, the potential benefits to biodiversity and ecosystem services can vary considerably depending on the type of agri-environmental measure as well as when and where it is implemented (Wätzold et al., 2015). However, without any incentive to achieve high benefits, farmers will likely implement agri-environmental measures to minimize their

costs rather than maximizing the benefits given the payment. In this respect, studies have shown that the cost-effectiveness of agri-environmental measures can increase considerably if payments are instead connected with environmental results (e.g., Barraquand and Martinet, 2011; Fleury et al., 2015; Klimek et al., 2008).

Within the EU, there is increasing awareness about the importance of better connecting payments with the outcomes of agri-environmental measures via result-based payment schemes (e.g., Herzon et al., 2018; Keenleyside et al., 2014). However, in-practice application has been limited, and generally restricted to ecological results that can be easily measured by proxies, such as specific plant species indicating high species richness in grasslands (e.g., Kaiser et al., 2010; Klimek et al., 2008; Wittig, 2006). Accordingly, outcomes that are difficult (costly) to measure have received less attention, e.g., abatement of nutrient emissions to water. However, when measuring pollution abatement at source is infeasible, it can instead be modelled (Rekolainen et al., 1999). Modelling rather than measuring the results of agri-environmental measures has the potential to expand the application of result-based payments and lead to more cost-effective conservation of biodiversity and ecosystem services (Bartkowski et al., 2021).

To conclude, the increasing demand for agricultural products and unprecedented decline in biodiversity present an urgent and grand challenge for humanity, to develop and implement land use management that can meet the demands from a growing population while simultaneously protecting biodiversity and ecosystem services. I have devoted my thesis to increasing our knowledge of how agri-environmental measures impact agriculture and biodiversity conservation, and how to ensure that these measures are carried out cost-effectively.



# Thesis Aim

The aim of my thesis was to better understand how to preserve biodiversity and ecosystem services effectively and cost-effectively in agricultural landscapes. To this end, I used an array of different scientific approaches, including a systematic literature overview, a meta-analysis, an empirical field study, ecological-economic modelling and policy evaluation. Below follow motivations for the five individual papers of this thesis and the main research questions they address:

- I. With a high and increasing global demand for agricultural products, and a generally negative impact from agricultural land use on biodiversity, it is crucial to develop and implement land-use strategies that reconcile agricultural production with biodiversity conservation. This has been explicitly studied by comparing the merits of the land-use strategies known as land sharing and land sparing. Land sharing is defined as low intensive agricultural production on a large area, which results in few remaining non-cropped habitats, and land sparing as high intensive agriculture on a smaller area, resulting in more remaining non-cropped habitats (Green et al., 2005). Comparisons are typically done when the agricultural production is equalized between the two strategies. In practice, land sharing is typically exemplified as wildlife-friendly agriculture, such as organic farming or agroforestry, and land sparing as conventional agriculture in combination with conservation of larger nature areas (Kremen, 2015). Ever since the dichotomy between land sharing and land sparing was introduced, there has been a vivid debate regarding which of the strategies is generally preferable to reconcile agricultural production with biodiversity conservation (Fischer et al., 2014). However, there is no systematic overview of what different taxonomic groups (e.g., birds and plants) or ecosystem services that the literature has considered. Importantly, it is also not known to what degree studies have measured different economic factors, such as opportunity costs. In this study, we address these matters by assessing which metrics of economic factors, biodiversity and potentially other

ecosystem services have been used. This study thus shows potential knowledge gaps in what we know about land sharing and sparing.

- II. Organic farming is generally beneficial for biodiversity in comparison to conventional farming (Bengtsson et al., 2005). However, it is unknown if differences in biodiversity between the farming systems are mainly driven by common species, or if rare species of different taxonomic groups also benefit from organic farming (but see Lichtenberg et al., 2017). Because rare species are generally at higher risk of extinction, there is a need to analyze the impact of organic farming on rare species to better understand its conservation potential. In this study we performed a meta-analysis to investigate the impact of organic relative to conventional farming on rare and common arthropods, birds, earthworms and plants.
- III. Bumblebees are important pollinators of wild and cultivated plants (Ollerton, 2017). Although bumblebees utilize plants in flowering crops and semi-natural habitats, also flowering weeds that occur in low densities but over vast areas in agricultural fields, may provide important food resources, especially in landscapes devoid of other flower resources (Bretagnolle and Gaba, 2015). One of the reasons as to why organic farming is more beneficial to pollinators than conventional farming, is the higher abundance of flowering weeds in organic fields (Holzschuh et al., 2007). However, as new techniques are implemented to increase organic crop yields to approach those of conventional farms (e.g., effective mechanical weed control), there is a risk that flowering weeds will decline and hence their benefits to pollinators (cf. Rösös et al., 2018). Therefore, to preserve viable pollinator communities in high-productive fields, there is a need for more evidence on how crop yields relate to pollinators and flowering weeds. If there is a trade-off between crop yield and flowering weeds, there may be a need for novel practices that enable larger organic crop yields without negatively affecting flowering weeds, to prevent the loss of the biodiversity benefits of organic farming. Here we address the question whether there is a trade-off between crop yield and flowering weeds and bumblebees in organic and conventional fields. We also investigate whether adjustments in crop sowing density has the potential to benefit flowering weeds, and thus indirectly bumblebees, without affecting crop yields.
- IV. Within the EU, farmers are offered payments to adopt agri-environmental measures. Such measures often entail taking land out of

production, e.g., not cultivating field borders, or reducing farming intensity, e.g., organic farming, both of which result in less agricultural production (Zimmermann and Britz, 2016). From a societal perspective, it is desirable that agri-environmental measures achieve biodiversity conservation at the lowest possible loss in benefits from agricultural production, i.e., that they are cost-effective. One aspect that is known to typically have an impact on how well agri-environmental measures succeed in preserving biodiversity is landscape complexity, i.e., how much semi-natural habitat there is in the surrounding landscape (Batáry et al., 2011; Tschardt et al., 2005). However, it is not known to what extent it might affect cost-effectiveness. Here, we assessed the influence of landscape complexity on the cost-effectiveness of organic farming for promoting flowering plant species richness.

- V. Eutrophication caused by agriculture is a global ecological and economic problem that is degrading aquatic ecosystems as well as water quality (Tilman et al., 2002). To reduce eutrophication, governments often pay farmers to implement agri-environmental measures on their farmland that have the potential to reduce nutrient emissions from farmland, e.g., buffer strips along field borders adjacent to surface water to retain phosphorus runoff. These payment schemes are by tradition action-based, which means that they are fixed depending on the type of measure and its area. For instance, Swedish farmers can receive 3000 SEK for each hectare of created and maintained buffer strip. This leads to farmers being financially incentivized to implement this measure where it has the lowest cost for the farmer, such as on land with low agricultural productivity. Conversely, farmers have no financial incentive to implement measures to maximize the environmental results, i.e., reducing nutrient emissions. The lack of connection between the payment and environmental results is the major reason why environmental payments to farmers have low effectiveness in achieving desired outcomes (Reed et al., 2014). An alternative approach, that promises higher effectiveness, is paying farmers for the actual results of their measures (Burton and Schwarz, 2013). Such result-based schemes provide incentives to farmers to implement measures such that the potential reduction of nutrient emissions is high relative to the management cost and foregone income from not farming the land. However, the feasibility of result-based schemes for reducing nutrient emissions has been questioned due to the difficulties and high costs associated with measuring the results (Schwarz et al., 2008).

Here we investigate if it is possible to design a result-based payment scheme for reducing nutrient emissions by modelling the results of implemented measures (actions). We also analyze the difference in cost-effectiveness between a current action-based scheme and a proposed modelled result-based payment scheme for reducing nutrient emissions from arable land.

# Methods

Below I describe how we designed the studies, and collected and analyzed the data, for each of the five papers in this thesis.

## Study design and data collection

In **Paper I**, we reviewed the scientific literature, which empirically compares land-sharing and land-sparing strategies. We used a systematic approach to avoid bias in the selection of articles. We searched for articles in several databases, including Scopus and Web of Science Core Collection, for articles that had “land sharing” and “land sparing”, or other synonym terms, in their titles, keywords or abstracts. The articles that matched the search string were then screened on titles and abstracts to remove those that did not meet our two conditions i) had studied land-use strategies that they defined as land sharing and land sparing (or synonyms), and ii) had reported empirical results. We then read the full texts of the remaining articles, removed additional articles that turned out not to match the criteria, and extracted data from a final set of 51 studies on the taxonomic groups, ecosystem services and economic factors they had studied.

In **Paper II**, we collected data from published articles to perform a meta-analysis of the impacts of organic and conventional farming on rare and common species. We searched through databases, including the Web of Science Core Collection, for articles that compared the abundance of species from four taxonomic groups (arthropods, birds, earthworms and plants) on organic and conventional farms. We screened articles that had used a matched pairs design to reduce the influence of confounding factors. We downloaded the data on species abundances when available on data repositories. When data was not available online, we contacted the authors and asked if they would share the data with us. We extracted additional data from the articles regarding where the study had taken place, where on the farms the data was collected (field center, field edge or field margin) and what crops were grown in the sampled fields. In the end, we extracted data on abundances and the additional factors from 83 studies that were performed in 22 different countries on five continents.

In **Paper III**, we carried out a field-based study in southern Sweden to compare biodiversity, crop yield and crop sowing distances across organic and conventional



farms. The study was carried out on 19 farms in total, ten organic and nine conventional. Farms were selected to control for confounding factors that did not relate to management type, such as landscape complexity (measured as the proportion of semi-natural grasslands within 1 km radius of each field). We sampled two fields on each farm. Bumblebees and flowering weeds were surveyed along 1m × 100m transects within the central parts of the fields five times between May and August 2017. During each visit, we counted and identified bumblebees at the species level when walking along the transect for 10 minutes. We also estimated the flower cover (as a proxy for floral resources) and recorded the species of flowering weeds in the transects. Separately from the visits above, we visited each field at the end of June to measure the sowing distances between crop plants. This was done by placing a 0.5m × 0.5m frame five times along a 100m transect within the central parts of each field. Within the frame, we measured the distance between the stem at the bottom of crop plants within the same sown row (sowing distance within rows) and that between crop plants in parallel rows (sowing distance between rows). At the end of the season, the farmers provided us with estimates of the crop yield of each field. We assessed relationships between data on the collected variables using linear regressions.

In **Paper IV**, we develop a theoretical ecological-economic model to derive the optimal combination of agricultural land use (among conventional arable land use, organic arable land use and semi-natural grassland) to maximize profit given a biodiversity target. We then developed an empirical ecological-economic model to simulate how different proportions of the three land uses affect profit and flowering plant species richness. We used Positive Mathematical Programming (Howitt, 1995) to calibrate the economic optimization sub-model automatically and objectively to regional agricultural data and observed proportions of the three land uses. The ecological sub-model is a modified countryside biodiversity model (Pereira and Daily, 2006), which was calibrated using ecological data collected from an earlier field study (Carrié et al., 2018) involving the same farms as in **Paper III**.

In **Paper V**, we first developed a theoretical ecological-economic optimization model to derive farmers' optimal combination of arable land use to maximize profit given a pollution abatement target. In our model, farmers had the option to use arable land for production or measures that abate pollution. We included both action-based payments for measures that abate pollution and result-based payments for achieved pollution abatement in the model. We then compared the cost-effectiveness of action-based payments compared to result-based payments for achieving particular levels of pollution abatement.

We applied our theoretical model in **Paper V** in a case study with an existing farm of ca. 1500 ha of arable land located in southern Sweden. We assumed that the farmer could use arable land for crop production or implementing buffer strips to abate phosphorus runoff (a main contributor to pollution of surface water in Sweden). We

used ICECREAM, a process-based nutrient emissions model (Rekolainen and Posch, 1993), to calculate the phosphorus runoff from crop fields and potential pollution abatement from implementing buffer strips. We limited the potential widths of buffer strips to 6-20 meters and placement on arable land bordering surface water. This corresponded with the requirements to receive action-based payments for implementing buffer strips in Sweden at the time of the study.

To calculate phosphorus runoff and potential abatement by buffer strips, ICECREAM uses a combination of parameters that characterize the spatial context. The parameters are determined by the variables: geographical region, crop type, catchment area, soil texture, phosphorus in the soil and slope. We collected data on these variables to make our predictions with ICECREAM. We used a map to determine the geographical region according to the classification used in ICECREAM. We measured the slope and catchment area in each field using a digital elevation model with 2m × 2m cell size from Lantmäteriet that was processed in ArcGIS. The amount of phosphorus in the soil was classified using Eriksson et al. (1997), which was verified by results from soil analyses by the farmer. We determined the soil texture according to FAO's international soil taxonomy using Eriksson et al. (1999) and the WebbGIS tool from the County Administrative Boards of Sweden.

The farmer provided details of the crops that had been grown on the different fields over the previous five years. We also collected data for the same period to calculate the opportunity cost (foregone profit) of using arable land for buffer strips instead of agricultural production. This data consisted of average yields for each field, average crop prices (retrieved from Lantmännen and Nordic Sugar, the main local buyers in the region), and variable production costs based on regional enterprise budgets from a main advisory service (Hushållningsällskapet, 2013). The farmer supplied us with data about the location and width of buffer strips, as well as received agri-environmental payments, that were currently implemented on the farm.

## Analyses

In **Paper I**, we compiled the extracted data and quantitatively assessed if there were any tendencies and research gaps regarding studied taxonomic groups and ecosystem services, and how often studies had measured production quantity and profit.

In **Paper II**, we classified species in each of the included 83 studies as rare or common. Species were classified as common if they were among the most common species that together comprised 80% of the total abundance of their taxonomic group. The less common species that comprised the remaining 20% of the total abundance were regarded as rare. Following this ratio, we classified species as rare or common using two

different methods, one is a study-based classification where we classified species based on their relative abundance in each analyzed dataset, while the other is based on the number of records of a particular species in the Global Biodiversity Information Facility database (GBIF) relative to the other species of the same taxonomic group in the same study. GBIF is an open-access database of spatially explicit records of species that have been collected by private persons and institutions from around the world. The GBIF-based classification was done based on records from the same country in which each study was performed, except for European studies where we used records from the whole of Europe, because there were no GBIF records for many of the species identified in European countries. The GBIF records were retrieved in August 2017 from [www.gbif.org](http://www.gbif.org) using the R library `rgbif` (Chamberlain et al., 2014).

We compared the abundance and species richness of rare and common species in organic and conventional fields using log response ratios (Hedges et al., 1999). We calculated log response ratios for each taxonomic group, as well as across all organisms, where species rareness was classified according to both the study-based and the GBIF-based methods respectively. We analyzed differences in abundance and species richness in organic and conventional fields by testing if the log response ratios were significantly different from zero based on one-sample t-tests. We also analyzed if there was a difference between how rare and common species were affected by organic vs. conventional farming, by testing whether their log response ratios differed based on independent-sample t-tests. We investigated the relationship between abundance and species richness with Pearson's correlation coefficient. Ultimately, we compared the similarity between the two rarity classification methods using the Jaccard similarity coefficient.

In **Paper III**, we used statistical models to analyze the relationships between biodiversity and different farm management practices. We used generalized linear mixed effect models (GLMM) to analyze the associations between the response variables, bumblebee species richness and bumblebee abundance, and the predictors: flower cover, farming system (organic or conventional) and crop yield. We also used GLMMs to analyze the associations between the response variables, flower cover and flowering weed species richness, and the predictors: sowing distance within rows, sowing distance between rows, farming system and crop yield. We used a general linear mixed effect model (LMM) to analyze the association between the response variable crop yield and the predictors: sowing distance within rows, sowing distance between rows and farming system. All GLMMs were fitted with maximum likelihood, and the LMM with restricted maximum likelihood. We controlled for the influence of landscape complexity (proportion of semi-natural grasslands in the surrounding landscape) and crop type in all models. We accounted for the non-independence between fields belonging to the same farm by including a random intercept term for farm identity. The significance of the relationships between predictors and response variables was

tested with likelihood-ratio tests. Models were fitted with the R-packages `glmmTMB` (Brooks et al., 2017) and `lme4` (Bates et al., 2015) using R ([www.r-project.org](http://www.r-project.org)).

In **Paper IV**, we integrated the statistical ecological model with the economic optimization model to create an empirical ecological-economic model. We applied the empirical model to determine the cost-effectiveness of promoting plant species richness in a representative agricultural landscape. We set the landscape size at 1000 ha, which was the maximum area for which the ecological model could make predictions that were supported by the field data it was estimated with. We evaluated five different landscape scenarios, where 0%, 5%, 10%, 15% or 20% of the 1000 ha was assumed to be semi-natural grasslands. After solving the calibrated economic model without a biodiversity target, approximately 94% of the arable land area was managed conventionally and 6% organically to maximize total profit in the landscape. This baseline, in other words, corresponds to what the proportion of organic farming would be in the landscape if no policy payments were given to produce organically or manage semi-natural grasslands. Converting additional land from conventional to organic would therefore entail an opportunity cost but would on the other hand increase the species richness of flowering plants (according to the ecological model). We used the ecological-economic model to compare the marginal conservation cost (i.e., marginal opportunity cost for increasing species richness) for converting conventional arable land into organic in the different landscape scenarios.

In **Paper V**, we analyzed the cost effectiveness of action- vs. result-based payments to incentivize abatement of phosphorus runoff from arable land with buffer strips on a real farm. We first used the ICECREAM model to estimate the amount of phosphorus runoff that buffer strips of different widths would abate if placed at any of the possible locations on the farm. We then used an economic model based on opportunity costs to analyze where it would be profitable for the farmer to implement buffer strips given the action-based payment for buffer strips that existed at the time of the study (3000 SEK/ha). Since the action-based payment is area-based, the farmer would have maximized their profit by implementing the widest allowed buffer strips (20 m) at any profitable location. We then calculated the total budget needed to remunerate the farmer for implementing the buffer strips. Then we analyzed where the farmer would have implemented buffer strips, and at which widths, if payments would instead have been result-based. We used the same total payment budget as was required in the action-based scheme. We set the result-based payment (i.e., payment per unit abated phosphorus runoff) to maximize the total phosphorus abatement calculated with ICECREAM, given that the farmer would only implement profitable buffer strips. We repeated the analysis with result-based payments based on a budget corresponding to how much the farmer actually received for their implemented buffer strips. We used ICECREAM to calculate the amount of phosphorus runoff that would be abated by the profitable buffer strips under the different payment schemes, as well as the actually

implemented buffer strips. We analyzed the opportunity cost per abated unit of phosphorus to compare the cost-effectiveness, and payment per abated unit of phosphorus to compare the budget efficiency, between the different schemes and budgets (including the existing scheme). We also assessed the impact of the different schemes on farm profit.

# Results and discussion

In this thesis, I have explored how different conservation strategies can contribute to preserving and promoting biodiversity and ecosystem services in agricultural landscapes. I have particularly investigated aspects relating to the effectiveness and cost-effectiveness of such strategies. My main results include that few of the published studies comparing land-use strategies that combine agricultural production and biodiversity conservation (framed as land sharing vs. sparing) have considered profit or ecosystem services, and that most studies have focused on a limited range of taxonomic groups (**Paper I**). I have also found that organic farming benefits both rare and common species (**Paper II**), and only increases floral resources to pollinators in crop fields when the yield is low (**Paper III**). However, reducing sowing density increased floral resources in crop fields without affecting yields (**Paper III**). I also found that the cost-effectiveness of organic farming for preserving biodiversity is influenced by landscape complexity (**Paper IV**). In the last paper (**Paper V**) I showed that a process-based model can be used to predict results in terms of reduced nutrient emissions, and that result-based payment schemes can increase the cost-effectiveness of nutrient emissions abatement by several times compared to action-based payment schemes. Below I report and discuss the results of the five papers comprising this thesis in more detail.

In **Paper I** we show that the studies comparing land-use strategies to achieve both biodiversity conservation and agricultural production (framed as land sharing vs. land sparing) have usually assessed the impacts of the strategies on a single taxonomic group, most commonly birds. Less than half as many studies assessed plants, arthropods or mammals. Two studies had assessed amphibians and one had assessed reptiles. Species richness between taxonomic groups often correlates poorly at taxonomic ranks corresponding to those specified above (Wolters et al., 2006). Within agricultural landscape, the low correlation in species richness between taxonomic groups can depend on varying species' traits, such that species respond differently to environmental changes (Smith et al., 2014). Thus, specific taxonomic groups cannot be used to draw conclusions about overall biodiversity without high uncertainty. Our study therefore shows that there is a need for more studies of the less studied taxonomic groups to better understand how they are affected by land-sharing and -sparing strategies. Ideally, these should study multiple taxonomic groups to understand the impact of the land-use strategies in the studied context.

In **Paper II** we performed a meta-analysis of 83 studies from 22 different countries to assess how rare and common species within different taxonomic groups were affected by organic and conventional farming. We found that the species richness and abundance of both rare and common species were higher on organic than conventional farms. The total abundance and species richness of rare species increased respectively by 77% and 20%, in contrast to the abundance and species richness of common species (56% and 4%). Thus, rare species benefited more than common species from organic farming, however, only significantly so for species richness. Similarly, when analyzing taxonomic groups individually, organic farming generally benefited rare species more than common species, and significantly so for plant species richness.

The positive biodiversity effects of organic compared to conventional farming has previously been shown in global syntheses that did not distinguish between rare and common species (Bengtsson et al., 2005; Tuck et al., 2014). This has also been shown by a global synthesis analyzing rare arthropods (Lichtenberg et al., 2017). However, **Paper II** is the first study to use a global dataset to analyze the effect of organic farming on rare species across several taxonomic groups (arthropods, birds, earthworms and plants). Furthermore, while Lichtenberg et al. (2017) and case studies (e.g., Kleijn et al., 2006; Kolářová et al., 2013) classified species rarity based on their relative abundance within studies, **Paper II** in addition used a rarity estimate independent of the analyzed data, which was based on relative differences between species in GBIF records within the country of each study (or within Europe if a European country). Our results were similar regardless of the rarity classification method, which increases our confidence in the robustness of our results.

Rare species are in general disproportionately threatened by human activities (cf. Pimm and Jenkins, 2010; Purvis et al., 2000). Therefore, for the sake of species' existence (UNEP, 1992), it is important that agri-environmental measures effectively benefit rare species. Promoting rare species is also important for their role in sustaining ecosystem functioning and services (Dainese et al., 2019). Rare species often possess less common or unique traits that influence, and increase the diversity of, ecosystem functioning and services despite their low abundances (Jain et al., 2014; Mouillot et al., 2013; Soliveres et al., 2016). Furthermore, rare species that currently have a limited functional role in ecosystems may depending on response traits contribute with essential ecosystem functions and services under future environmental conditions (Dee et al., 2019; Säterberg et al., 2019).

In **Paper I** we found that only a quarter of the literature comparing land sharing and sparing had measured effects on ecosystem services beyond agricultural production and biodiversity per se. While the initial framework only included agricultural production and biodiversity (Green et al., 2005), considering other ecosystem services enables more holistic assessments of how land-use strategies impact nature and people. However, studies measuring ecosystem services had almost exclusively only considered carbon

storage and only one study had assessed the impact of biodiversity via intermediate ecosystem services on agricultural production (Railsback and Johnson, 2014). Studies that do not account for ecosystem services may fail to acknowledge the importance of biodiversity for agricultural production in both the short and long terms (Ekroos et al., 2014). While other strands of the agri-ecological literature have investigated a wider spectra of ecosystem services, and their impact on agricultural production (Ricketts et al., 2016), there is a need for a better understanding of how large scale land-use strategies, such as land sharing and sparing, impact different ecosystem services (Grass et al., 2019). Thus, an increased focus from the land-sharing vs. -sparing literature on ecosystem services could both contribute to a more comprehensive understanding of their relative merits and increase the factual basis for land-use policies that strive to achieve welfare and conservation objectives.

In **Paper III** we compared cereal crop yields of organic and conventional farms, and analyzed how the type of farming system affects flowering weeds and bumblebees. We found that crop yields were on average 36% lower in organic compared to conventional fields. This is in line with what has been shown previously, and is usually caused by higher weed density, pathogen attack rates and nutrient limitation (Seufert et al., 2012). In contrast, organic fields had more bumblebee species as well as more species and floral resources of flowering weeds compared to conventional fields. The positive effect of organic farming on bumblebees was driven by floral resources. While cereal fields are not insect-pollinated, flowering weeds in cereal fields can be important to supply floral resources to maintain viable communities of bumblebees and other insect pollinators in agricultural landscapes (Bretagnolle and Gaba, 2015). Therefore, the increased floral resources in organic cereal fields can benefit the pollination of wild plants and crops that are insect-pollinated and grown in the same landscape (Bretagnolle and Gaba, 2015; Ollerton, 2017), such as field beans and oilseed rape (Free, 1993). However, our results showed that organic fields only had more floral resources than conventional ones in fields where organic crop yields were relatively low. In the more high-yielding organic fields, the abundance of floral resources was similar to that in conventional fields. There was no correlation between floral resources and crop yield in conventional fields, which may be due to herbicides maintaining a low density of weeds regardless of crop yield. The negative correlation between organic crop yield and floral resources is likely caused partly by yield-enhancing strategies involving weed removal (Röös et al., 2018) and partly by that crops and weeds compete for light, water and nutrients (Gaba et al., 2017; Oerke, 2006).

In **Paper III** we also demonstrated that it is possible to increase flowering weed species richness and floral resources without affecting crop yield by adjusting sowing distances. Typically, sowing distances are adjusted to maximize crop yield and suppress weeds. However, such relationships are usually demonstrated when comparing relatively high differences in sowing distances (Boström et al., 2012; De Vita et al., 2017; Kolb et al.,



2012). Here we instead showed that when using the standard row distance in Sweden (ca. 12.5 cm) in combination with an increase in the distance between crop plants within the same rows from 5 to 10 cm, floral resources and flowering weeds species richness both more than doubled, regardless of the type of farming system, while crop yield was unaffected. The positive effect on flowering weeds may be explained by reduced competition with crops. Meanwhile, crop yield may have been unaffected by a lower sowing density and more flowering weeds due to intra-crop compensation, i.e., grain weight and tiller capacity increases (Weiner et al., 2010). Thus, our results suggest that adjusting the sowing distance within rows can be a strategy to benefit flowering weeds, and indirectly bumblebees, without affecting crop yield. This could be an important strategy to avoid losing biodiversity benefits of organic farming when implementing yield-enhancing management.

When conducting field studies to assess how farming systems affect biodiversity, there is a risk that the results may be affected by confounding factors. A majority of studies that were included in the meta-analysis in **Paper II** had used a matched pairs design to reduce the impact of confounding factors, such as landscape complexity. A matched pairs design also controls for that farms within studies are from the same region and have comparable species pools, reducing the potential confounding impact from systematic differences in regional species pools between organic and conventional farms. In **Paper III**, it was infeasible to use a paired design (due to the scarcity of organic farms in some areas), so we instead carefully selected farms in a balanced manner along gradients of landscape complexity. Thus, although there in both studies is some risk that non-measured variables influence the results, we find it likely that the differences between organic and conventional farms in both **Paper II** and **Paper III** to a large extent can be attributed to the farming systems per se.

A large part of the literature compares the effect of conservation measures on biodiversity in agricultural landscape, but not values from agricultural production (Ansell et al., 2016). However, the strand of the literature that uses the land-sharing vs. -sparing framework explicitly focuses on alternative land-use strategies to reconcile biodiversity conservation with agricultural production (Green et al., 2005). We found that most studies comparing land sharing vs. sparing had measured the impact of the land-use strategies on agricultural or other commodity production, but less than 10% had measured the impact on farm profit (**Paper I**). Measuring the impact on production quantity is interesting, but it does not as such reflect the value of agricultural production. For that the costs of inputs, such as labor and capital, need to be accounted for as well. Only by measuring the profit (i.e., benefits after subtracting costs) is it possible to assess the welfare effects, as well as cost-effectiveness, of a particular land-use strategy.

In **Paper IV** we assessed the cost-effectiveness of increasing the proportion of organic farming in an agricultural landscape as a land-use strategy to promote flowering plant

species richness. We found that the cost-effectiveness of converting conventional into organic farmed land depends on landscape complexity. In general, organic farming increased species richness, both in absolute numbers and proportionally, most cost-effectively in less complex landscapes. While it is well established that landscape complexity influences the effectiveness of organic farming in preserving biodiversity (e.g., Lichtenberg et al., 2017; Tuck et al., 2014), by showing the influence on cost-effectiveness, our study can contribute to enabling the conservation of more biodiversity given limited conservation budgets.

The ecological model used in **Paper IV** was calibrated with a relatively small data set (19 farms), all located in Scania in southern Sweden. Therefore, more research is warranted, with data from different regions, before the results can be extrapolated to other contexts. Furthermore, relative to conventional farming, both organic farming and semi-natural grasslands generate multiple benefits that were not assessed in our study, such as improved water quality, carbon storage, aesthetic values and enhanced biodiversity beyond plant species richness (Bengtsson et al., 2019; Kremen, 2020). Thus, from a holistic perspective, the relative merits of conventional farming, organic farming and semi-natural grasslands may be different when considering a broader range of values than agricultural production and biodiversity conservation. Furthermore, there are also other land-use options to consider, e.g., planting flower strips along field edges or hedgerows along field margins, which may be better options depending on the objectives, costs and environmental context (Kremen, 2020).

Strategies that preserve biodiversity most cost-effectively from society's perspective may still cause opportunity costs for farmers. Therefore, incentives that compensate for management costs and foregone income are often needed to encourage socially desirable land use and management. In **Paper V** we showed that modeling can be used to predict environmental results that are remunerated by result-based payments. We compared how a farmer would have maximized their profit by optimizing their arable land use for either agricultural production or agri-environmental measures when offered payments based on actions (area of buffer strips) or results (achieved phosphorus abatement). The farmers (through higher profit) and taxpayers (through more abatement and lower cost) both benefited from result-based payments relative to action-based payments. The cost-effectiveness, i.e., achieved abatement divided by opportunity cost, was approximately ten times higher with result-based payments compared to action-based payments.

Our results indicate that result-based payments can considerably contribute to reducing eutrophication by incentivizing the most cost-effective placements and widths of buffer strips. This is an important result, given that the agricultural sector is a major contributor to eutrophication in Sweden and Europe (Östersjöcentrum, 2017). The high gain in cost-effectiveness from paying for results rather than actions is mainly due to the high spatial variability in phosphorus runoff. According to the models, some

optional locations for buffer strips (i.e., arable land bordering surface water), had no runoff, while others received a relatively high share of the total farm runoff. Thus, it is crucial that farmers have strong incentives to place buffer strips where they are most effective, which in our dataset correlated with high opportunity costs (i.e., where action-based payments were least likely profitable). We only assessed the effect of buffer strips, but given the spatial heterogeneity of nutrient emissions, result-based incentives for locations of other spatially explicit measures, e.g., wetlands, cover crops and reduced usage of fertilizers, could also be expected to be more cost-effective than their action-based equivalent. While our study was confined to a single farm, the input data to run ICECREAM is available and can be used to inform a result-based payments scheme for the whole of Sweden.

It is not necessary to know about farmers' opportunity costs beforehand. Ideally, the payment level should be set to the social value of phosphorus abatement. However, as this is difficult to estimate, a general estimation of opportunity costs can be made to approximately set the payment at a level that is attractive enough to encourage phosphorus abatement to reach policy goals. Employing a result-based payments scheme to abate phosphorus with buffer strips, or in addition other pollutants by means of a menu of different measures, may entail higher transaction costs (e.g., administration and instructing farmers) than current action-based payment schemes (Bartkowski et al., 2021). However, these are likely outweighed by the advantages in terms of cost-effectiveness and in budget efficiency (Armsworth et al., 2012).

While we assumed that the farmer would make land-use choices to maximize profit, the farmer mentioned that he also implemented buffer strips to hedge farm income. Furthermore, he owned a large part of a lake that received much of the nutrient emissions from the farm, which could be expected to increase his preference to reduce nutrient emissions. These types of preferences that go beyond profit maximization are difficult to model and likely vary amongst farmers. However, an increased preference to reduce nutrient emissions will likely only impact the outcome from result-based payments in that farmers will allocate buffer strips as if the payment per abated unit nutrient emission was higher, and still prioritize the most cost-effective locations (while adding some less cost-effective ones). To evaluate the potential of result-based payments in the presence of such preferences, we also compared the results between the currently implemented buffer strips and those that would have been implemented if the farmer optimized for profit with the same budget used for result-based payments. As before, the farmer and taxpayers both benefited from result-based payments relative to action-based payments. Result-based payments were shown to increase the cost-effectiveness almost three-fold.

As when measuring results, accuracy is crucial to ensure that modeled results are actually attained. The model we used to predict phosphorus emissions and retention, ICECREAM, is considered one of the most accurate for Scandinavian conditions

(Larsson et al., 2007). However, the modelled and the real-world outcomes will never be identical due to the impact of variables that are not or cannot be modelled, such as heavy rain events. However, given the extreme benefits of using results-based over action-based payments, the uncertainty accompanying the modelling should still not impede using models to predict results (Bartkowski et al., 2021).



# Conclusions and future perspectives

In my thesis, I have evaluated and developed new strategies to more effectively, and cost-effectively, preserve and promote biodiversity and ecosystem services in agricultural landscapes. I have found that within the land-sharing vs. land-sparing literature, there is a need for greater focus on less studied taxonomic groups, economic factors such as profit, and ecosystem services to gain a more holistic understanding about the social and ecological consequences of different land-use strategies.

To preserve biodiversity as such, it is critical that conservation efforts benefit rare species, which are often comparatively susceptible to human activities, including intensive agricultural land use (cf. Allan et al., 2014; Kleijn et al., 2009; Suding et al., 2005). Therefore, our results, showing that organic farming relative to conventional farming can contribute to preserving abundances and species richness of rare species, provide important support for organic farming as a strategy to preserve biodiversity. This result is conditional on that organic farming would not cause unintended off-site biodiversity loss if reduced yields are compensated by production moving elsewhere on the globe (Phalan et al., 2011). Further research will be needed to better understand the mechanistic links between benefits to rare species and specific management actions associated with organic farming. Such understanding can help to predict potential trade-offs between preserving rare species and agricultural production. Nevertheless, our results, based on data from 83 studies, which were consistent for two classifications of rarity, strongly suggest that organic management leads to more abundant and diverse communities of both rare and common arthropods, birds, earthworms and plants.

My thesis also shows that yield-enhancing management on organic farms (e.g., increased fertilization and weed removal, cf. Rööös et al., 2018) risks degrading the benefits to biodiversity and associated ecosystem services. This indicates a need for strategies that retain aspects of organic farming that benefit biodiversity when implementing yield-enhancing management. We showed that one such strategy may be decreasing sowing density by increasing the sowing distance within rows, which had a clear positive impact on flowering weeds and the resources these provide to pollinators, without causing yield losses.

My thesis also showed that landscape complexity influences the trade-off between benefits of organic farming to biodiversity and agricultural production. More precisely, the conversion of conventional to organic farmland to benefit flowering plant species richness could be done with a lower net loss in value from agricultural production in less complex landscapes.

Result-based payments is a promising policy instrument to spatially target measures to preserve biodiversity where they are the most cost-effective (e.g., Matzdorf and Lorenz, 2010; Wittig, 2006). We demonstrate that result-based payments can also incentivize cost-effective measures and placements of such to reduce nutrient pollution by modelling the results. Compared to traditional action-based payments, results-based payments can increase the farmer's profit and achieve higher pollution abatement at a lower cost. In Sweden, and likely other EU Member States, there are spatially explicit data available to apply our approach. This could dramatically improve the cost-effectiveness of agricultural pollution abatement and thereby contribute to healthier and cleaner waters. Buffer strips and other measures that reduce pollution can also benefit biodiversity (Cole et al., 2020; Underwood and Tucker, 2016), and a potential development for future result-based payment schemes could be to incentivize implementation of AEMs to promote multiple benefits.

Looking forward, there are clear benefits of accounting for factors influencing the effectiveness and cost-effectiveness of environmental measures and conservation strategies. Because resources are limited, it is essential that conservation strategies are as effective and cost-effective as possible. My thesis contributes to this cause by discovering new benefits of existing strategies (e.g., organic farming benefits rare species), entirely new strategies (e.g., adjusting sowing distances to benefit biodiversity without affecting crop yield), impact of contexts (e.g., landscape complexity's impact on how cost-effectively organic farming promotes biodiversity) and new applications of incentives to encourage optimal implementation of conservation strategies (e.g., result-based payments for modelled results).

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