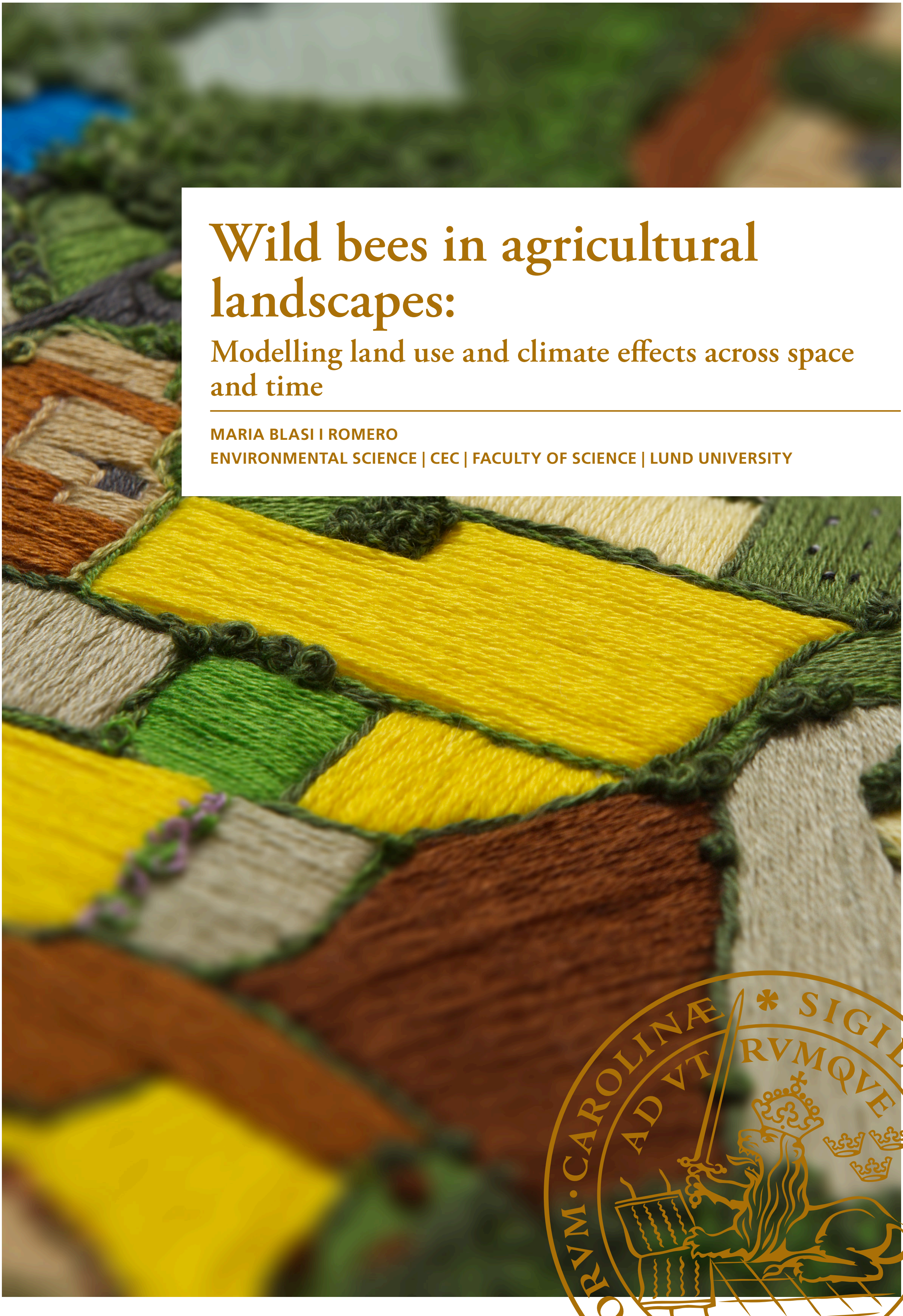
Wild bees in agricultural landscapes:

Modelling land use and climate effects across space and time

MARIA BLASI I ROMERO
ENVIRONMENTAL SCIENCE | CEC | FACULTY OF SCIENCE | LUND UNIVERSITY



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Maria Blasi i Romero

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Abstract

Wild bees are declining in many parts of the world, which poses a risk for crop pollination and ecosystem health. Land use and climate change are two of the main drivers of the decline, and understanding the interactive effects of these two drivers and wild bees is very important to be able to develop proper responses and mitigate future negative effects. In this thesis I have investigated the effects of land use and climate on pollinators and pollination in agricultural landscapes, to increase our understanding of how the variability and interaction between these drivers. To do so, I have used both empirical and ecological modelling approaches, including estimation of effects and prediction on data collected in multiple European regions in multiple years, hypothesis testing on long-term citizen observations of bumblebees, and simulation studies based on a newly developed theoretical model. I demonstrate the limits of transferring statistical models to novel contexts, which is in part due to the quality and type of data and variables used in these models (paper I). I have also improved methods for studying climate-land use interactions by developing a spatially explicit model of population dynamics that captures how bee populations respond to land use and weather at a landscape scale during their active season (paper II, III). The model captures realistic patterns of bee population dynamics. We used the model to investigate the effect of drought-induced reductions in floral resources on population dynamics (paper II), and projected bee population responses to different RCP climate scenarios in multiple types of agricultural landscapes (paper III). Finally, we studied bumblebee queen phenology shifts in Sweden in the last 120 years, and show how some common species keep track of global changes while rare and declining species might not (paper IV).

Altogether, the thesis contributes to a growing body of knowledge providing evidence of organisms tracking changes in land use and climate, expands the modelling opportunities for exploring interactions between land use and climate change, and provides recommendations for how to improve transferability of results in pollination ecology.

Key words wild bees, pollination, ecological models, model transferability, phenology, land-use, climate change, agricultural landscape

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MADE IN SWEDEN

To my family and friends

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Author contributions

I. **MB** and YC formulated and developed the idea, **MB** performed the analysis with support from YC, and wrote the first draft of the manuscript. PO generated the land-use data used in the analysis, together with **MB** and YC. The remaining co-authors contributed with the data used in the analyses. All authors contributed to revisions of the manuscript.

II. **MB** and US developed the model, designed the simulation experiment and methods for sensitivity analysis, with input from AMJ and YC. **MB** and US wrote the first draft of the manuscript with contributions from all the authors. All authors contributed to revisions of the manuscript.

III. **MB** developed the idea with input from US, AMJ and YC. YC simulated the landscape maps, ZC collected the remote sensing data and AMJ collected the climate data. **MB** and US modified the model and processed the remote sensing and climate data to include it in the model. **MB** performed the analysis with input from AMJ, US and YC. **MB** wrote the first draft. All authors contributed to revisions of the manuscript.

IV. **MB**, RC, and ASP formulated and developed the idea. ES and CF collected and processed the data. RC developed the methodology. **MB** analysed the data with input from RC and ASP. **MB** wrote the first draft with contributions from all the authors. All authors contributed to revisions of the manuscript.

Popular Summary

Pollination is key in maintaining healthy ecosystems and agricultural production. Insect pollination is especially important, as 3 out of 4 crops benefit from insect pollination to increase the quality or quantity of the crop, including coffee, nuts, and many fruits that humans consume. In Europe, the economical benefits of insect pollination are estimated to be several billion euros per year. However, pollinators are declining in many parts of the world, posing an important negative ecological and economic impact that could significantly affect the maintenance of wild plant diversity, ecosystem stability, food security, and human welfare.

Bees are probably the best-known and very important group of pollinators. There are many species (~20 000 species worldwide – around 10% of them in Europe) and groups like bumblebees (250 species, 68 in Europe), solitary bees, and the well-known domesticated honeybee (which is just one species).

Research has identified which things cause bee declines, and these range from diseases, invasive species, climate change, to the way we change land for urbanization and the way we manage agriculture. Current agricultural management relies on a lot of pesticides, herbicides, monocultures, and causes the loss of natural habitats that provide bees with nesting habitats and flowers that they feed off throughout the season. However, the effects of the interactions between these drivers on bees are not completely well understood. In my thesis, I have studied how interactions between land use and climate change affect wild bees like bumblebees and solitary bees. Both climate and land-use change influence the availability of flowers for food and locations for nests for bees. For example, with climate change, temperatures are predicted to increase gradually which affects when and for how long plants flower, when bees are active. Further, climate change is also associated with extreme events like droughts, hurricanes, wildfires, which are predicted to occur more often.

Oilseed rape or Canola oil or (*Brassica napus*) is an example of a common crop grown as monoculture in Europe. The crop is used to produce oil for cooking and to use as biofuel. When oilseed rape is in full bloom, an extensive area in the landscape will turn to bright yellow during a few weeks, and many people enjoy taking pictures of it. This crop, however, has a bitter-sweet story for pollinators: pollinators can profit from the crop like an all-you-can-eat buffet since the crop provides a large amount of food. However, the crop flowers only for some weeks, and after that, an incredibly large area in the landscape is left without any flowers for the bees, meaning that they will starve if there isn't another flowering crop or a flower meadow nearby. Bees are called central place foragers, which means that they go looking for food from a nest, and always come back to the nest, where leave the resources are gathered, after which leave again. Depending on the bee species and their size, the maximum travel distance will range between 500 m and 1.5 km. Since oilseed rape fields are very large and do not flower for long, it is not strange that when you go looking for pollinators in these crops, you might not find many of them.

In paper I of this thesis, I looked at how the number of bees during the peak of oilseed rape flowering is affected by how much other oilseed rape and semi-natural habitats, like forest and meadows, there is in the surrounding landscape. I wanted to know if the results that we would find in one year or region would be the same in another year or region. To do that, I gathered observations of bumblebees and solitary bees from 2011, 2012, and 2013 from five different European regions in Sweden, Germany, Netherlands, and the United Kingdom. We found that increasing oilseed rape in the landscape had a generally negative effect on wild bees in all regions. However, we also saw that the effect of semi-natural habitats was more variable between the regions, especially for solitary bees.

We also checked how well our statistical model could be used to predict the number of bees from one region to another, and from one year to another, the so-called statistical transferability. It is common in ecology to transfer the knowledge derived from statistical analysis, but it is not so common to test how well the models used to obtain these results can perform in other areas. We tested that and showed that the transferability was limited, both across the regions and across years. We discussed that this might be because the characteristics of semi-natural habitats are quite different between regions. That is, the same name for a habitat on a map can look very different in different regions. For example, what we consider a pasture in Sweden might look very different compared to the UK or The Netherlands, or even within the same country.

To understand the relation between climate-land use and bees, the use of models is necessary to be able to project future scenarios. For example, what can happen to wild bees and pollination if we don’t limit climate change to 1.5 degrees warming and if we, on top of that, create landscapes with only a few meadows and trees? What if we go above 2 degrees? And what happens if we have a 2-week drought versus an extreme 4-week drought? It is possible to study all these combinations with models, and in paper II I developed one of these models with which we have asked some of these questions. The model imitates the life cycle of bumblebees and how they live in their colony. A bumblebee queen emerges in spring, after spending the winter hibernating underground, starts looking for places to nest and to start her colony (for example in old mouse burrows, field borders, or grass areas). The queen will also collect floral resources and start laying eggs, the workers. Once there are some foragers out foraging, the queen will stop going out of the nest and will spend the rest of her days in the nest producing eggs. Sometime at the end of the summer, there will be a moment when the queen stops producing workers to start producing daughter queens and males. The males and queens will leave the nest, and mate with other queens and males from other nests, and the old queen will die. The daughter queen will overwinter, and the cycle starts again next spring. In the model developed in paper II we capture this cycle from the moment when the queen emerges during spring, until the moment when daughter queens are produced in the nest. We also simulate what happens in the agricultural landscape: the flowering of grasslands, early flowering crops, and late flowering crops. We developed the model so that the different stages of the colony and the start and end of flowering will be influenced by temperature, and thus climate change. In paper III we use the model to project bee population dynamics under future climate scenarios that are also used by the IPCC (RCP 2.6 and 8.5).

In paper IV of the thesis, we studied if overwintering queens are active nowadays at the same time in the year as they did in the past in Sweden (phenological shifts). Several studies show that bumblebees are flying earlier or later than they used to in many places in Europe and North America, likely because of climate change. We also know that some bumblebees are better adapted to the consequences of how we manage the landscape for agriculture than others.

To study phenological shifts in Sweden we needed to compile a lot of data from many years, and records from museum specimens and observations from citizen science platforms are great to compile this information. We studied ten species of bumblebees that we know differ on different times to emerge in the spring (some are very early, and some are late in the spring/early summer) and we found that they are flying earlier than they used to. In Scania, the southernmost part of Sweden, we found that bumblebees are active earlier in areas where agriculture is very intense and there are few semi-natural habitats, and within these habitats, the early emergent species are even active earlier.

The use of models is necessary when we make projections about pollinators and pollination in the future, but there are inherent uncertainties: from the model system (the model is always a simplification of reality) to the uncertainties from future climate projections, and the quality of land cover maps. To monitor landscape quality for pollinators, land cover data are generally accessible and easy to use, as there are associations between the categories and resources for pollinators. The Paper I shows, however, that these associations differ from region to region and from year to year, and that it is important to consider more detailed characteristics of what we consider semi-natural habitats of each region (i.e., the grasslands in Sweden may not be the same as in Germany, or in the Netherlands).

The production of more systematic and refined data through pollinator monitoring systems would offer a better classification of the different types of semi-natural habitats where individuals were collected or observed, and potentially improving the transferability of the models. Monitoring schemes would also help to keep track of the risks and benefits of conservation actions, which is extremely important for developing good policies for pollinators.

The presence of natural habitats, pastures and forests in agricultural landscapes, as well as ensuring the continuity of flowers in the landscape during the life cycle of bees, is essential for their conservation. The presence of natural habitats, in addition to providing places to make nests and flowers, can provide important shelters in less favourable times such as drought events.

Bumblebee (*Bombus terrestris*) pollinating oilseed rape flowers.

Resum popular

La pol·linització és clau per mantenir els ecosistemes saludables i la viabilitat de la producció agrícola. La pol·linització d'insectes és especialment important, ja que 3 de cada 4 cultius es beneficien d'aquest tipus de pol·linització per augmentar la qualitat o la quantitat de cultiu, inclosos el cafè, els fruits secs i moltes fruites que consumim. A Europa, s'estima que els beneficis econòmics de la pol·linització d'insectes són de bilions d'euros a l'any. No obstant això, les poblacions de pol·linitzadors estan disminuint a moltes parts del món, presentant un important impacte ecològic i econòmic que podria afectar significativament el manteniment de la diversitat de plantes silvestres, l'estabilitat dels ecosistemes, la seguretat alimentària i el benestar humà.

Les abelles són probablement el grup de pol·linitzadors més conegut i important. Hi ha 20.000 espècies descrites/conegudes a tot el món - al voltant del 10% a Europa que inclouen grups com borinots (250 espècies, 68 a Europa), abelles solitàries i les popularment conegudes abelles de la mel (que són només una espècie).

Els experts han identificat quines són les amenaces que provoquen la davallada de les abelles: des de malalties, espècies invasores, el canvi climàtic, la pèrdua d'hàbitat a causa dela urbanització i els canvis en els tipus de cultius, fins la actual forma de gestió agrícola. Avui dia, l'agricultura es veu afectada per l'ús de molts pesticides, herbicides, tendència a cultivar en monocultius, i la conseqüent pèrdua d'hàbitats naturals, que proporcionen a les abelles llocs de nidificació i flors que s'alimenten durant tota la temporada. Tot i això, la interacció d'aquestes amenaces amb la proliferció de les abelles no està del tot clara.

A la meva tesi, titulada "Abelles silvestres en paisatges agrícoles: models de l'ús del sòl i dels efectes climàtics a través de l'espai i el temps" he estudiat com les interaccions entre l'ús del sòl i el canvi climàtic afecten a les abelles silvestres com els borinots i les abelles solitaries, ja que aquests dos factors influeixen la disponibilitat de flors i llocs adients per a nidificar. Per exemple, amb el canvi climàtic, es preveu que les temperatures augmentin gradualment, i això afecti el temps i quantitat de floració. A més, degut al el canvi climàtic s'espera un increment d'esdeveniments extrems com sequeres, huracans, incendis forestals, que afecten directament i indirectament a les abelles.

L'oli de colza (*Brassica napus*) és un exemple de cultiu que es cultiva com a monocultiu a Europa. La collita s'utilitza per produir oli per cuinar i com a biocombustible. Quan la colza floreix, una gran zona del paisatge es converteix en groc durant unes setmanes i molta gent en gaudeix fent-ne fotografies. Aquest cultiu, però, té una història agre-dolça per a les abelles: elles se'n poden beneficiar com si fos un restaurant de menja tant com vulguis, ja que el cultiu proporciona una gran quantitat d'aliments, pero no per molt de temps. El cultiu floreix durant poques setmanes i després d'això, allà on hi havia una gran quantitat d'aliment, ara ja no hi ha res, cosa que significa que moriran de gana si no hi ha un altre cultiu florit o un prat de flors a prop (penseu que des del punt de vista d'una abella, la seva distància màxima de recorregut oscil·la entre els 500 m i els 1.5 km, depènent de les espècies).

A l'Article I d'aquesta tesi vaig estudiar com, durant el pic de floració de la colza, el nombre d'abelles) es veu afectada per la quantitat d'altres hàbitats de colza i hàbitats seminaturals, com els boscos i prats, al paisatge circumdant. Volia saber si els resultats que trobaríem en un any o regió serien els mateixos en un altre any o regió. Per fer-ho, vaig reunir observacions d'abellots i abelles solitàries durant els anys 2011, 2012 i 2013 en cinc regions europees diferents a Suècia, Alemanya, Països Baixos i el Regne Unit. Els resultats de l'Article I indiquen que tant la coberta a escala paisatgística dels cultius de floració massiva i hàbitats semi-naturals permanents, incloses les pastures i els boscos, són importants conductors d'abundància d'abelles salvatges a totes les regions estudiades. Vam trobar que l'augment de la colza en el paisatge tenia un efecte generalment negatiu sobre les abelles salvatges de totes les regions. Tanmateix, també vam veure que l'efecte dels hàbitats seminaturals era més variable entre les regions, especialment per a les abelles solitàries. També vam comprovar fins a quin punt es podria utilitzar el nostre model estadístic per predir els resultats d'una regió a una altra i, d'un any a un altre, l'anomenada transferibilitat estadística. És habitual en ecologia transferir el coneixement derivat de l'anàlisi estadística, però no és tan habitual provar el rendiment dels models utilitzats per obtenir aquests resultats en altres àrees. Ho hem provat i hem demostrat que la transferibilitat era limitada a tota la regió i a través del temps. Vam argumentar que això podria ser degut a que les característiques dels hàbitats semi-naturals són força diferents entre regions. És a dir, el mateix nom d'un hàbitat en un mapa pot tenir un aspecte molt diferent en diferents regions. Per exemple, un "prat seminatural" pot tenir un aspecte molt diferent a Suècia en comparació amb el Regne Unit o els Països Baixos, o fins i tot dins del mateix país.

Per entendre la relació entre l'ús climàtic del sòl i les abelles, és necessari l'ús de models que projecten què pot passar en el futur. Per exemple, què pot passar amb les abelles silvestres i la pol·linització si no limitem l'escalfament global a 1.5 graus i si, a més, creem paisatges amb només uns pocs prats i arbres? I si superem els 2 graus? I què passa si tenim una sequera de 2 setmanes, o una sequera extrema de 4 setmanes? Totes aquestes combinacions es poden estudiar amb models.

A l’article II, he desenvolupat un d’aquests models amb el qual ens hem preguntat algunes d’aquestes preguntes. El model imita el cicle de vida dels borinots i com viuen a la seva colònia. De forma simple, el cicle dels borninots és així: després de passar l’hivern sota terra, una reina de borinots surt a la primavera i comença a buscar llocs per niar i començar la seva colònia (per exemple, en caus vells de ratolins, vores de camp o zones d’herba). La reina també recollirà recursos florals i començarà a posar ous, d’on sortiràn les treballadores. Un cop hi hagi unes quantes treballadores, la reina deixarà de sortir del niu i passarà la resta dels seus dies produint ous. En algun moment del final de l’estiu, la reina començarà a produir noves reines i mascles. Els mascles i les reines abandonaran el niu, s’aparellaran amb altres reines i mascles d’altres nius i la vella reina morirà. La filla de la reina hivernarà i el cicle començarà de nou la primavera següent. En el model desenvolupat a l’articleII, capturem aquest cicle des del moment en què la reina emergeix durant la primavera, fins al moment en què es produeixen princeses al niu. També simulem el que passa al paisatge agrícola: la floració de les praderies, els cultius de floració primerenca i els cultius de floració tardana, i fem que les diferents etapes de la colònia i l'inici i final de la floració estiguin influïdes per la temperatura. A l’Article III fem servir aquest model per projectar la dinàmica de la població d'abelles en els escenaris futurs del IPCC (RCP 2.6 i RCP 8.5).

A l’Article IV de la tesi, hem estudiat si les reines de borinot que surten a la primavera avui dia són actives a la mateixa època de l'any que en el passat a Suècia (canvis fenològics). Diversos estudis demostren que els borinots volen abans o després del que solien fer en molts llocs d’Europa i Amèrica del Nord, probablement a causa del canvi climàtic. També sabem que alguns borinots s’adapten millor a les conseqüències de com gestionem el paisatge per a l’agricultura que d’altres espècies d'abelles. Per estudiar els canvis fenològics a Suècia, vam recopilar moltes dades de molts anys, i els registres d’espècimens de museus i observacions de plataformes de ciència ciutadana per aconseguir aquestes dades. Hem estudiat deu espècies de borinots que sabem que surten de la hivernació en moments diferents (algunes són molt primerenques i altres surten al final de la primavera o principis d’estiu). Els resultats indiquen que, efectivament, els borinots estudiats volen més aviat ara del que feien fa anys. A més, a Scània, la part més el sud de Suècia, vam trobar que els borinots són especialment actius abans en zones on l’agricultura és molt intensa, comparat amb zones on hi ha molts més hàbitats naturals i, dins d’aquests hàbitats, les espècies més primaverenques són les que són més actives abans, possiblement responent a la pressió del paisatge.

L’ús de models és necessari quan fem projeccions sobre els pol·linitzadors i la pol·linització durant el futur, però hi ha incerteses inherents: des del sistema de models (el model sempre és una simplificació de la realitat) a les dades utilitzades, que inclouen futures projeccions climàtiques i la qualitat dels mapes de la coberta de la terra.

Per controlar la qualitat dels paisatges per als pol·linitzadors, les dades de coberta de cultiu de la terra són generalment accessibles i fàcils d'utilitzar, ja que hi ha associacions entre les categories en aquestes dades i recursos per als pol·linitzadors. El paper mostra, però, que aquestes associacions difereixen de la regió a la regió i de l'any a l'any, i que és important considerar característiques més detallades del que considerem hàbitats semi-naturals de cada regió (és a dir, les pastures de Suècia poden no ser les mateixes que a Alemanya, o als Països Baixos).

La producció de dades de forma més sistemàtiques i refinades a través de sistemes de seguiment de pol·linitzadors oferirien una millor classificació dels diferents tipus d'hàbitats semi-naturals on es van recollir o observar els individus, i potencialment millorant la transferibilitat dels models. Els esquemes de seguiment també ajudarien a fer un seguiment dels riscos i beneficis de les accions de conservació, que és extremadament important per desenvolupar bones polítiques per als pol·linitzadors.

La presència d’hàbitats naturals, de pastures i boscos als paisatges agrícoles, aixi com assegurar la continuitat de flors al paisatge durant el cicle de vida de les abelles és essencial per la seva conservació. La presencia d’hàbitats naturals, a més de proporcionar llocs per fer nius i flors, proporcionen refugis importants quan hi ha sequeres.

Abellot (*Bombus pascuroum*) en trèvol de prat.

List of Abbreviations

GDD growing degree days

IPBES Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IPCC Intergovernmental Panel on Climate Change

MFC Mass-flowering crop

NDVI Normalized Difference Vegetation Index

NDYI Normalized Difference Yellowness Index

RCPs Representative Concentration Pathways

SNH Semi-natural habitat

Introduction

Agroecosystems: balance between food production and biodiversity conservation

A core challenge for achieving the United Nations Sustainable Development Goals (SDG) for 2030 is to meet the increasing demands for food, feed, and fibre for a growing world population (Godfray et al. 2010, Tilman et al. 2011), while reaching a more sustainable way of production. Agriculture plays a crucial role providing those needs: from crop production for human consumption, to feeding livestock and producing biofuel. However, crop production faces constant pressures: confronts a more degraded environment with associated loss of biodiversity, and uncertainties arising from climate change (IPBES 2016, 2019, IPCC 2021).

In many arable-dominated areas, current agricultural management has been intensified over the last 100 years to enhance food productivity (FAO 2017). Nowadays, agricultural management relies heavily on short crop rotations, inorganic fertilizers, and pesticides. These dependencies, combined with maximal use of land for crop production, too often results in the destruction and fragmentation of biodiversity-rich semi-natural habitat. Agricultural intensification has led towards biodiversity declines worldwide including well-documented taxa such as European farmland bird populations (Donald et al. 2001), plant species richness (Kleijn et al. 2009), and pollinators (Williams and Osborne 2009, Bommarco et al. 2012, Raven and Wagner 2021).

To resolve the negative trade-off involved in agricultural intensification, ecological intensification has been put forward as a way to reach a safe operating space that provides adequate food and nutrition for everyone without crossing critical environmental thresholds (Doré et al. 2011, Bommarco et al. 2013, Pywell et al. 2015). Ecological intensification entails maximizing the options for crop production by managing biodiversity and multiple ecosystem services, and is one of the three complementary approaches suggested to safeguard pollinators in agricultural ecosystems, together with diversified farming systems, and ecological infrastructure (Potts et al. 2016). The goal is to increase human benefits by harnessing ecosystem services and optimizing trade-offs among these. However, there are several obstacles to the uptake of ecological intensification, including the lack of knowledge on the type of most effective practices and the scale (i.e., field, farm, landscape) at which such practices need to be implemented (Potts et al. 2016). For example, pollinators are affected by local management, but also by land use at the landscape scale, and much effort is being dedicated to finding common patterns of landscape-scale land-use effects on crop pollination services (Ricketts et al. 2008). Understanding the interactions of insects underlying these services with the landscape, also in the light of uncertainties arising from climate change, is crucial for developing better agricultural management strategies (Dicks et al. 2016). In this thesis, I focused on the effects of landscape management and climate on pollination and wild bees as pollinators.

Wild bees and the need for landscape management

Pollination by wild animals is a key ecosystem service. A large part of the global crop production depends highly on insect pollination (Klein et al. 2007), with wild insects playing an especially important role in sustaining yields of many crops (Garibaldi et al. 2014, Rader et al. 2016). However, pollination may be in danger given evidence from several regions that pollinators (wild and domestic) are declining (Carvell et al. 2006, Potts et al. 2010, Bommarco et al. 2012). This decline of pollinators is a source of economic vulnerability for agriculture (Gallai et al. 2009, Lippert et al. 2021).

Worldwide, the most common and most important threats to pollinators are related to land cover and configuration, and land management (Dicks et al. 2021). Intensive agricultural management reduces spatial heterogeneity through large field sizes, increases the propensity for monocultures, and reduces crop diversity at the landscape scale (Aizen et al. 2019), which also induces temporal uniformity (e.g., same flowering crop blooming and finishing blooming at the same time in the landscape). This is the bittersweet case of mass flowering crops (MFC) such as oilseed rape (*Brassica napus*). These crops are pollinated by bees and provide important foraging resources when flowering (Westphal et al. 2003; Holzschuh et al. 2016), but it is usually the case that the flowering period of these crops is shorter than the flying period of their pollinators. Thus, these beneficial insects that can pollinate the early-flowering oilseed rape may not have food available at the end of the season, if they are not able to find late-flowering crops in their foraging range.

It is possible to reverse the process of land homogenization by combining ecological intensification with strengthening diversified farming systems and focusing on the composition and configuration of the landscape. Mosaic landscapes effective in supporting ecosystems consist of patches of land with different functional cover types (i.e. semi-natural habitats, unmanaged field margins, and flower strips near crop-pollinated fields) that provide different feeding and nesting resources (Fahrig et al. 2011), to secure habitat components within seasonal or daily movement distances (Smith et al. 2014). Especially for central-place foragers (i.e., birds and nest-building insects), the availability of multiple habitat patches is important to sustain populations through landscape supplementation processes and/or landscape complementation (Olsson and Bolin 2014).

The effectiveness of solutions for improving the delivery of pollination and other ecosystem services can be region- and context-dependent. First, the efficacy depends on the proportion of the landscape under agri-environmental measures and the landscape complexity (Smith et al. 2010, Concepcion et al. 2012), as these measures are most effective when they are implemented in structurally simple arable land, with poor resources (Scheper et al. 2013). Second, providing additional food (such as flower strips) next to cropland can be complicated because it will benefit pollinators in the long term but might move pollinators out from the cropland in the short term (Nicholson et al. 2019), distracting them and reducing visitation of crops, so-called Circe principle (see Bartomeus and Winfree 2011). Third, there is a concern about which kind of pollinators are reinforced with these measures. For conservation goals, these schemes need to consider habitat connectivity and availability for specialist species and those with low dispersion (Ekroos et al. 2010). However, common pollinators are the ones enhanced, and rare species are not benefited. These measures thus may might increase the abundance of ES providers without enhancing biodiversity (Scheper et al. 2013) thus falling short of conservation goals (Kleijn et al. 2015).

Wild bees and climate

Another important driver for bee decline is climate change (Potts et al. 2010, IPBES 2016, Soroye et al. 2020), which acts simultaneously with land use change (Kammerer et al. 2021, Zaragoza-Trello et al. 2021). The combined effects of climate and land use change can be difficult to disentangle and predict and may differ between bee species (Kammerer et al. 2021). While one may expect them to be cumulative, in some cases they have been shown to have opposing effects (Kelemen and Rehan 2021).

The impacts of ongoing climate change on pollinators, pollination services, and agriculture may not be entirely apparent for several decades due to delayed response times in ecological systems (IPBES 2016). However, there is growing evidence that bees are already responding to climate change, and that variations in climatic conditions affect bumblebee species differently. While some species change morphology, move their geographical ranges, shift their phenology towards earlier emergence, others do not, indicating that there are adaptive limits to the capacity of this pollinator group to track climate change (Kerr et al. 2015, Martinet et al. 2020). The asynchrony of phenological shifts between plants and pollinators leads to plant-pollinator mismatches, with consequences for pollinators, crop pollination, and wild plants pollination (Settele et al. 2016). For this reason, estimating trends and abundance of wild pollinators is even more urgent and quantifying their phenological patterns is increasingly of interest in ecology.

Simulations of future climate show an increase in the frequency of extreme events such as droughts and heatwaves as a part of ongoing gradual changes, according to the IPCC (2018,2021). These events will also have consequences on bee populations (Settele et al. 2016). Droughts for example, have consequences for both plant physiology and bee survival, with the threat of both direct and indirect effect to pollinators and crop pollination. Land-use-driven changes to landscape structure, combined with climate changes, might thus lead to increasingly species-poor plant-pollinator communities dominated by highly mobile (i.e. species that can disperse or migrate large distances), habitat generalist species (Potts et al. 2010).

In this thesis, I explore the interaction between climate and land use on bee population dynamics and pollination services, ranging from the effects of drought (paper II), as an example of extreme events, to gradual changes in flower phenology (III), and phenology of bumblebee queen flight period (paper IV).

Ecological models for decision making

Understanding how spatial and temporal variability interact at the landscape level and affect pollinator populations driven by land use and climate is crucial. This applies not only at the landscape level but also at the regional scales, where evidence is needed to inform policies for building resilient food production systems to ensure the demand and supply of pollination services well-matched (Settele et al. 2016, Perennes et al. 2021) and to guarantee pollinator-crop-dependent nutritious food production (Hoiss et al. 2015, Nicholson and Egan 2020).

Decisions are made based on beliefs and values, and scientific knowledge can inform these beliefs by providing facts, opinions, and uncertainties (von Winterfeldt 2013). The decisions around pollination involve society (economics and benefits from pollination services), and nature (pollinator health, conservation).

In pollination ecology, some of the questions decision makers want answers to develop environmental policies are “How can farmers increase their yield and help pollinators at the same time?”, “How much habitat is needed for pollinators?”, “How will pollinators be affected by future climate change, and hence the crop?". Mapping and assessing ecosystem services is a way to identify priorities and problems in dealing with both ecosystem services promotion and biodiversity conservation. By mapping ecosystems and assessing ecosystem service flows, science can assist different actors in need of ecosystem services maps: policymakers and administration from EU to local level, and farmers (e.g. mapping and quantifying pollination services in the European Union (Schulp et al. 2014).

Valuing ecosystem services and natural resources results in better decisions and actions to the use and management of these. However, mapping ecosystem services deals with multiple uncertainties coming from the limited ability to capture important processes as well as translating and scaling mapped information (Hou et al. 2013). How certain we can be about the results? How good is a model at making predictions? Therefore, how reliable is? Which model will be the best to address these issues? Quantifying the values and levels of ecosystem services for management decisions is often difficult. For this reason, it is important that stakeholders get the information they need, and scientists can communicate those results and implications, including uncertainties (Fischhoff and Davis 2014).

Ecological models have great potential for supporting environmental policy and decision-making (Addison et al. 2013, IPBES 2016). Ecological modelling refers to the use of mathematical models and system analysis for the description of ecological processes and for the sustainable management of resources. Often, models are used to answer specific questions about interactions among model components or about the present or future behaviour of the system under analysis. Facing a strong demand for ecological predictions on ecosystem services demand and supply, ecosystem services modelling, and its specific application of mapping, is a useful input for policy (Maes et al. 2012, Polce et al. 2016, Costanza et al. 2017).

There is a need for models that can consider the interactions between climate and land use, occurring at a smaller scale, to quantify at least the relative impact of climate change under different scenarios and land use conditions. Modelling the demographic responses at the landscape-scale gives a proximal indication of how pressures affect pollinator population size, viability, and extinction risk (Selwood et al. 2015).

Spatially explicit models of pollinators and pollination are used as a basis for mapping pollination services and are essential to predict effects of land-use change in the future (e.g. Polce et al. 2013, Häussler et al. 2017, Gardner et al. 2020, Perennes et al. 2021). These models use estimates of bee abundance as a proxy for the supply of pollination (e.g. InVEST pollination module using Lonsdorf et al. 2009). Pollination models are often based on central place foraging founded on the foraging theory model (Olsson et al. 2015), and like Lonsdorf et al. (2009), assume that the number of bees produced (i.e. fitness) is entirely dependent on nesting quality and floral resources. However, these models need further developments since they capture limited sources of variability, coming from the fluctuations of resources through the season due to management activities to weather induced variability. In this thesis, I used the foraging function of a central place forager model (Häussler et al. 2017) and developed a mechanistic model to capture weekly variability in the resources in the landscape and explore the effects of climate and land use on bee populations and pollination (papers II and III).

Model transferability in space and time

How well models generalize to new contexts (e.g. different times, places, or taxa) is a central question in ecology (Houlahan et al. 2017). The creation and parametrisation of a model, and the assessment of its predictive performance, are often conducted on the same dataset, alternatively with different subset of data from the same study system. Even when models are clearly described in scientific publications, allowing onward use, they seem to be rarely used by other research groups. While the knowledge created with these models is easily transferred from region to region (e.g., effects of semi-natural habitats, flower strips), the same results do not hold when empirical data is gathered and shows that transferability may be weak. There are several potential constraints on model transferability. One can be the differences in the range of the predictor variables used in the model construction, calibration, and validation phase, compared to the ranges encountered in model application. A second constraint is that the predictor variables may only be proxies (explored in Paper I), and the relationship between the actual quantities of interest and the proxies might differ between cases. A third constraint includes the differences in species composition, and species traits, that may be ignored yet undermine transferability.

Within ecology, there has been much interest in transferability of species distribution models (SDM) (e.g. Barbosa et al. 2009, Acevedo et al. 2014, Duque-Lazo et al. 2016) but this issue has received less attention in the field of biodiversity-based ecosystem service modelling (Yates et al. 2018). Much can be gained by reducing the knowledge gap on how processes and patterns are transferable in space and time, on the impact of temporal variability on the relationship between landscape-scale land-use and ecosystem services, and on how climate change will affect the ecosystem service delivery in contrasting landscapes. Achieving these goals requires a combination of empirical and predictive science using existing methods to quantify and model variability in space and time; and to account for uncertainty when making predictions of future states. In this thesis I addressed transferability of statistical models in paper I, using bumblebees in oilseed rape fields in contrasting landscapes as study system across Europe, and I explore in paper II and III further methods to improve predictability by integrating weather and climate drivers within in spatial-explicit models of pollination.

Aims

In this thesis, I explore the effects of land use and climate on pollinators and pollination in the context of agro-ecosystems. This thesis aims to increase the knowledge on how the variability of these effects can be considered to increase predictability in ecology.

I divided my thesis into different aims according to the papers that form the thesis: Paper I estimates the effects of landscape-scale land-use on wild bee abundance in fields of a common mass-flowering crop across Europe using statistical models, and assesses the transferability of these models across regions and years.

Paper II develops a theoretical spatially-explicit population model that considers the impact of variability in resources in space and time resulting from changes in land use and weather. The model contains a plant phenology submodel that simulates the flowering season for mass-flowering crops and semi-natural habitats at the resolution of weeks. The model is applied in a simulation study to explore drought effects on bumblebee population dynamics and pollination services delivery.

Paper III combines the model developed in Paper II with remote-sensing and climate data to investigate the phenology-mediated effects of future climate. Future climate is considered as projections of growing degree-days from the IPCC scenarios RCP 2.6 (low-end emissions) and RCP8.5 (high-end emissions). The impact of variability in resources in space are considered by simulating the model under different combinations of land-use in the southernmost part of Sweden, for bumblebee population dynamics and pollination services delivery.

Paper IV uses historical and citizen science-reported data to test the interactive effects of climate and land-use through the investigation of shifts in bumblebee queen flight period over the last century in Sweden, and whether such shifts depended on latitude, agricultural-induced landscape simplification, or temperature. In addition, the paper aims to explore if phenology shifts may predict bumblebees' sensitivity to long-term changes in climate and landscape structure.

Methods

This thesis uses a multidisciplinary approach to capture the effects of land use and climate on wild bees and pollinators. The general approach of the thesis is ecological modelling and uses a wide range of data sources: from wild bee observations in focal oilseed rape fields (paper I), citizen observations and historical collections of museum specimens (paper IV), to model simulations (papers II, III). This thesis also uses different sources of land use maps (Fig. 1), climate model simulations (paper III) and remote sensing data (paper III).

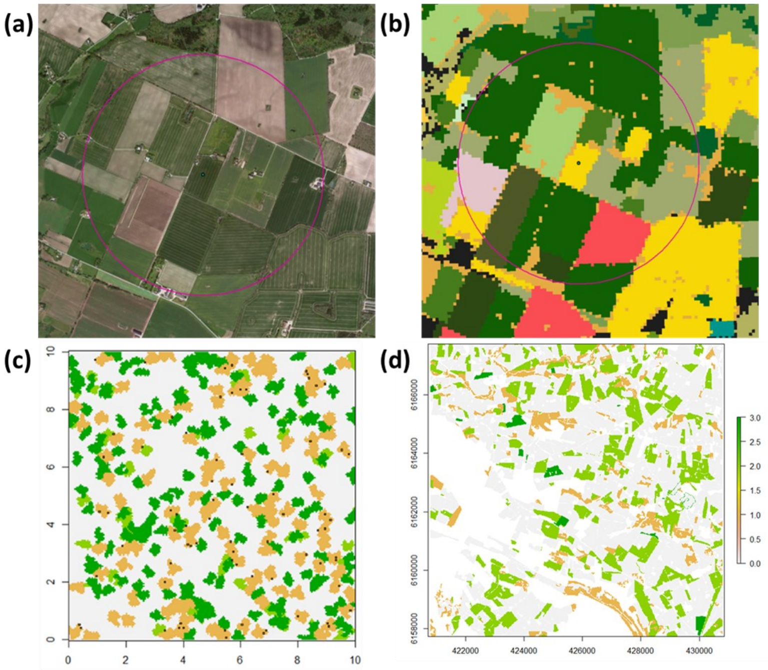

Figure 1. Representation of different land-use maps used in this thesis. (a) Aerial view in Google maps for a field in Scania used in paper I; (b) same field as shown in (a) including detailed vegetation classes using agricultural crop cover data from Integrated Administration and Control System (IACS) and Svenska Marktäckedata (SMD) for Sweden, and translated it into a common code for all EU locations used in the study; (c) simulated landscapes used in paper II using the R package *landscapemetrics (Hesselbarth et al. 2019)* for four land use cover categories; and (d) Scania landscape used in paper III with simplified vegetation classes using the Swedish National Land Cover Database (Nationella Marktäckedata) (NMD) with the agricultural crop cover data from the 2019 Integrated Administration and Control System database and Land Parcel Information System (IACS-LPIS). (c) and (d) use the same colour coding for the land use cover (0 for non-bee habitat, 1 for semi-natural habitats, 2 for early flowering crop, 3 for late flowering crop).

In this section the datasets and analysis used in each paper are described in more detail:

In **Paper I**, we studied the temporal and spatial transferability of statistical models linking landscape-scale land-use composition to empirical observations of bumblebee and solitary bee abundance in a mass-flowering crop, winter oilseed rape fields (*Brassica napus*) from studies conducted in five different regions located in four countries (Sweden, Germany, Netherlands, and the United Kingdom), in three different years (2011, 2012, 2013) (see Fig. 2 for the overview of the dataset used in the study). The focal landscape variables were the proportion of oilseed rape and proportion semi-natural habitat, derived from high-resolution land-use crop-cover and data. These land-use metrics were extracted in a 500 m and 1000m buffer around the centroid of each field for solitary bees and bumblebees respectively, based on their common foraging distances (Osborne et al. 2008, Zurbuchen et al. 2010). We developed a hierarchical model combining all studies using linear mixed-effects models and evaluated the transferability of the statistical model using three different types of non-random cross-validation approaches. The linear mixed model contained a random intercept for each individual combination of country, study and year and in addition, to assess the importance of spatial and temporal differences in the responses across the studies, the model also contained random slopes for both oilseed rape and semi-natural habitat. The cross-validation methods differed in the partitioning of the data between the training and evaluation dataset: a balanced stratification of the data where all-region and year combinations are in both the training and evaluation set; temporal extrapolation (i.e., for the same region, testing from one year to another); and spatial extrapolation (i.e., for the same year, testing from one region to another). Data partitioning was done using the R package *Groupdata2* (Olsen 2017). Model fit evaluation was done using three complementary quantitative goodness-of-fit measures: the mean absolute error (MAE), the root mean squared error (RMSE) and the coefficients of determination R2.

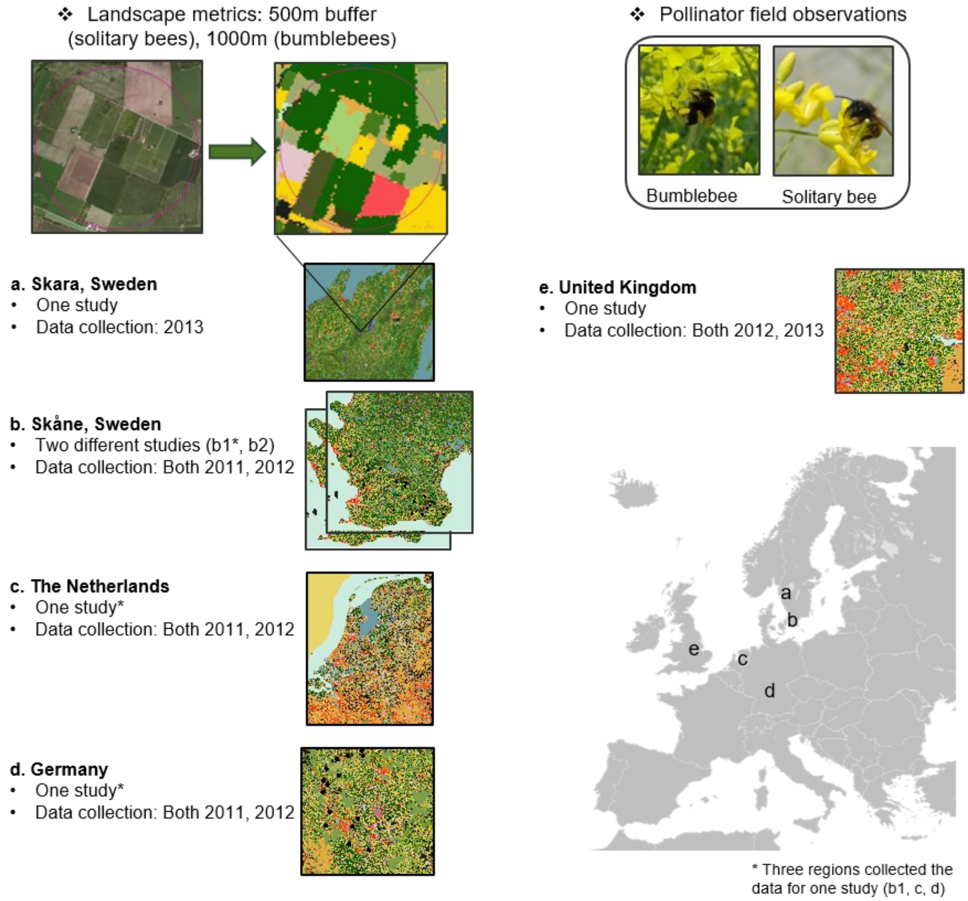

Figure 2. Representation of the dataset used in paper I. Figure adapted from paper I.

In **paper II,** we developed a theoretical model that considers land use and climate variables as inputs and models pollination dynamics and pollination services (Fig. 2). The motivation to develop this type of model is that changes in land use and climate influence the availability of nesting and floral resources and are major threats to bee populations. The model describes empirical patterns of bee foraging at the colony level and temporal population dynamics for an average colony at the landscape level. The model describes the dynamics of *Bombus sp*. during one season, from overwintering queen emergence during the spring, to the production of daughter queens during late summer. The model allows the foragers to collect and bring back resources to the colony that will trigger, together with time and temperature, the change to different colony key stages. The model outputs are population size (number of workers), population viability (queen daughters), and ecosystem services (pollination potential in flowering crops). We applied the model in simulated landscapes with different habitat patches including semi-natural habitats, an early and late flowering crop, and non-bee habitats created using the *landscapemetrics* package in R. We used the model to simulate populations and pollination services in different landscapes and to detect the impacts from extreme drought events, introduced in the model as effects in the shortage of food resources.

To evaluate the sensitivity of the model outputs to the model parameters we performed a local sensitivity analysis. To evaluate the effects of drought and landscape composition and configuration on the maximum number of workers in the season, the number of queens produced, and the pollination potential in crops we used linear mixed-effects models. For each of these models, our model predictors included the proportion of semi-natural habitats, the proportion of early crop, with the interaction of drought. We also included landscape identity as a random factor (to be able to evaluate drought with a case-control setup).

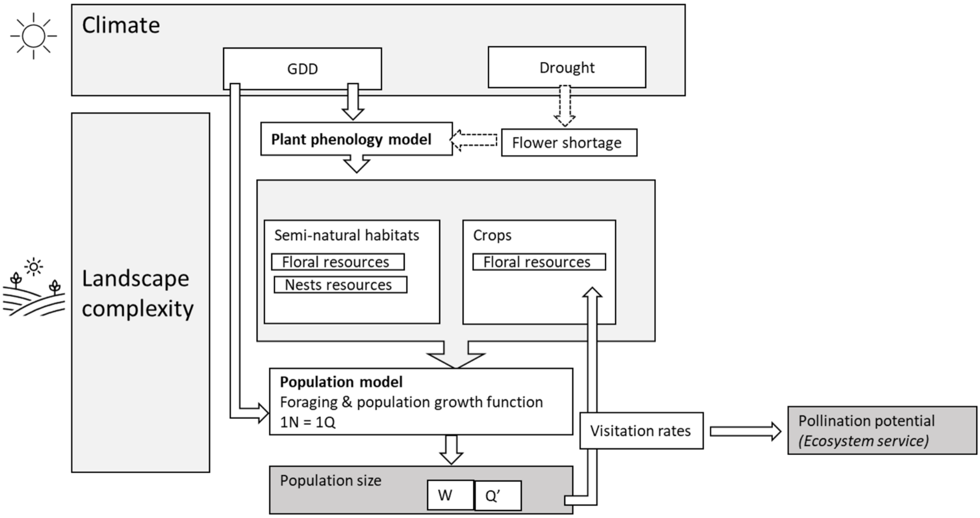

Figure 3. Graphical representation of the model workflow developed in paper II and used in paper III.

In **paper III**, we used the spatially explicit model for pollination developed in paper II, to study the effects of climate future simulations for the IPCC scenarios RCP 2.6 and RCP8.5, in landscapes contrasting in their land-use composition – with varying proportions semi-natural habitats, early-mass-flowering crops, and late-mass-flowering crops - on bee populations and pollination services in Scania (southern Sweden). To simulate more realistic crop growth and flowering phenology in the landscape we used remote sensing data to determine the start and end of the season and translated the peak of flowering to an assigned value. We used as a baseline the climate normal between 1990-2019, together with simulated climate data (temperature daily average) from 2021-2050 (representing near future) and 2071-2100 (representing far future) from the CMIP5 (Coupled Model Intercomparison Project, phase 5) runs with a regional climate model. I used the climate data to calculate yearly growing degree days (GDD), averaged over a selection of agricultural parcels, from 1990 to 2100 for all climate simulations to use it as input for the plant phenology model in the pollination model developed in paper II. For each of 30 pastures, 95 fields of oilseed rape and 115 clover fields known to be flowering in 2017, 2018 or 2019, I determined their flowering season using normalized vegetation index (NDVI) for pastures and clover, and normalized yellow index (NDYI) for oilseed rape, as it is shown to be a good phenology indicator for oilseed rape (d'Andrimont et al. 2020) processed with the program TIMESAT4 (Eklundh and Jönsson 2017, Jönsson et al. 2018). See Fig. 4 for the representation of the process of the satellite data.

To run the pollination model in Scania, I used 80 (10 x 10km, 10m resolution) raster maps covering eight different combinations of high and low proportion of early and late mass-flowering crops, and semi-natural habitats, with ten replicates per combination. We used linear mixed-effects models to evaluate the outcomes of climate and landscape in bee populations and pollination services. The models were built for each climate period, and in each model the independent variables included the interaction of climate scenario and landscape type. We used landscape identity as a random factor to control the different climate effects for the same type of landscape and added year as a random factor.

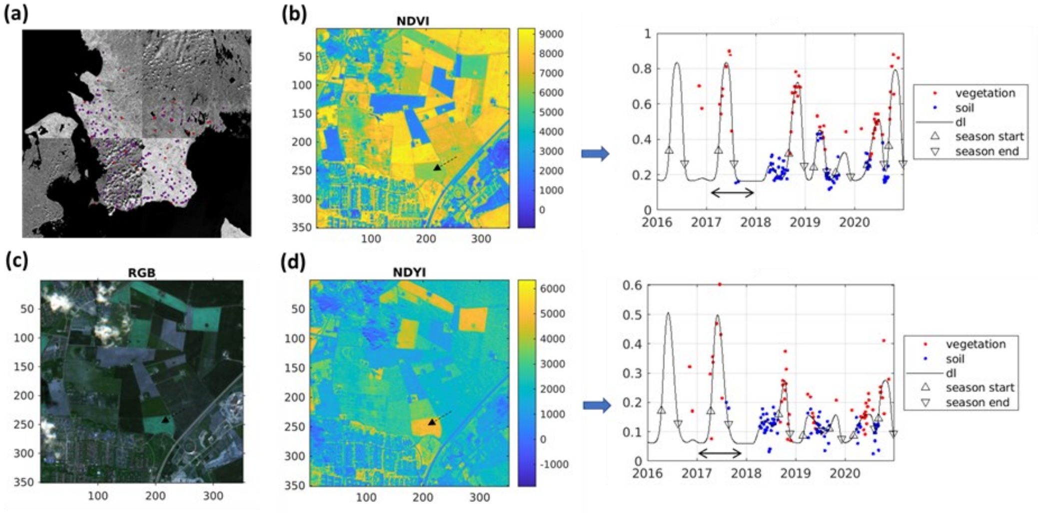

Figure 4. (a) Scania is covered by four tiles of the Satellite Sentinel-2 (33VVC, T33VUC, T33UVB, T33UUB). (b) NDVI image representation and time series representation produced in TIMESAT4. (c) RGB image of some fields in Scania. (d) NDYI image representation and time series representation produced in TIMESAT4. Figure adapted from paper III.

In **paper IV**, we used data collected from museum specimens from the Biology Museum at Lund University, and citizen science observations from The Swedish Species Observation System – Artportalen (SLU Artdatabanken 2020). We analysed overwintering queens from museum specimens collected between 1899 and 2016 in Scania (Fig. 5), and citizen science observations from Artportalen collected between 2000 to 2019 for all Sweden. We studied 10 different bumblebee species selected according to the representation of the phenological trait queen emergence. We included *B. lapidarius, B. lucorum, B. pascuorum, B. pratorum,* and *B. terrestris* as early emergent species, and included *B. distinguendus, B. hortorum, B. ruderarius, B. subterraneus* and *B. sylvarum* as late-emerging species, based on (Benton 2006, Persson et al. 2015, Cederberg and Mossberg 2012). To study differences in active flight period driven by land-use change in Scania, we used the large agricultural production areas (Stora Produktionsområde (PO) in Swedish) that divide Sweden into eight farming levels (1 is the most productive, and 8 the least productive one), defined by The Swedish Board of Agriculture (Statistics Sweden, 2014). These are suitable as a proxy for agricultural intensity and landscape heterogeneity, since they consider large-scale conditions for farming, comprising climate, topography, and soil. In Scania, three production areas are found: simplified landscape structure dominated by arable fields (area 1), mixed landscapes (area 2), and forested mixed landscapes (area 5). For the study in paper IV, I merged 2 and 5 to consider complex landscapes, as they are known to contain permanent pastures, smaller fields, clover leys).

As a proxy for the extent of climate change over the observation period of the dataset, we collected the mean spring annual temperature (March, April, May) at the national scale in Sweden from 1899 to 2019 from the Swedish Meteorological and Hydrological Institute (SMHI 2021). We used linear mixed-effects models to evaluate how the interaction of time and land use, spring temperature or latitude explained if bumblebee queen flight period shifted over time, or which phenological traits were more sensitive to land-use or climate change. We draw a 10 x 10 km grid over Sweden (for the Artportalen dataset), and a 5 x 5 km grid over Scania (for the museum dataset) and extracted the median observation of queen activity flight and used it as a response variable in our model. To control for the sampling bias of the nature of these non-systematic datasets, we weighed each grid cells by its yearly sampling effort per each species. We added the grid cell identity as a random effect, to consider the spatial and temporal dependency in the data, as grid cells were revisited across years, and neighbouring grid cells are spatially dependant.

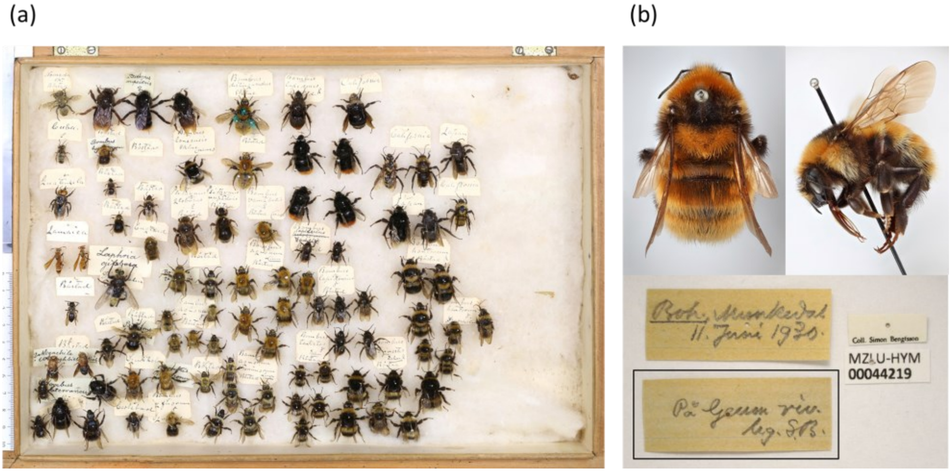

Figure 5. Representation of museum specimens used in the study. (a) Original drawer with specimens collected during late 1800s. (b) *B. distinguendus* (now extinct in Scania, and a red list status of vulnerable in Europe (Nieto et al. 2014)) pinned with its corresponding identification label. Each label contains information on the collection day, location and the name of the collector. The location of the specimen was later translated into coordinates to use in the study. (Photo: Christoffer Fägerström)

Results and discussion

The results in paper I indicate that both the landscape-scale cover of mass-flowering crops and permanent semi-natural habitats, including grasslands and forests, are important drivers of wild bee abundance in all regions studied. However, while the negative effect of increasing mass-flowering crops on the density of the pollinators is consistent between studies, the direction of the effect of semi-natural habitat is variable between studies. In addition, the results also show that the transferability of statistical models is limited, both across regions and across time. The results of paper I demonstrate the limits of using statistical models in combination with widely available land-use crop-cover classes for extrapolating pollinator density across years and regions, likely in part because input variables such as the cover of semi-natural habitats poorly capture the variability in pollinator resources between regions and years.

In paper II, we developed a spatially explicit bee pollination model by adding resource variability and climate variables. We tested the model to assess the effects of drought, by means of reduction in floral resources, in pollination dynamics and pollination services. The results in paper II indicate that drought and the amount of semi-natural habitats in the landscape are the main factors affecting population dynamics. The model also predicts that under drought conditions semi-natural habitats offer the possibility to stabilise populations.

In paper III, we used the model that we developed in paper II to assess impacts of climate change on crop phenology and bee dynamics in eight different types of landscapes. We found that changes in temperature induced phenological changes that may have contrasting effects on the number of workers and queens produced within bumblebee colonies: in the future scenarios (2071-2100) the maximum number of workers increases while the number of queens is reduced compared to the baseline (1990-2020). For the far future we also found significant interactive effects between land-use and climate scenarios, indicating that temperature increases in high-emissions scenarios may cancel differences between landscape types.

The results of paper IV, indicate that bumblebee spring queens in Sweden show shifts in the time they start flying, most probably due to climate change during past decades. We also found that in the southernmost part of Sweden, Scania, the phenology of bees is shifting caused by land-use changes. Importantly, we found that in agriculture-dominated areas, early-emerging species (most common species) are flying significantly earlier compared to landscapes with a high share of semi-natural habitats. In contrast, late-emerging species (mostly declining species) do not show significant differences in emergence date between landscape types.

Challenges and uncertainties when projecting pollinators and pollination for the future

When modelling future projections for pollinators and pollination there are inherent uncertainties involved, from the model system (the model is always a simplification of the reality), to the data used, including future climate projections, and the quality of land use-land cover maps.

To monitor the quality of landscapes for pollinators, land-use crop-cover data is generally accessible and easy to use, since there are associations between the categories in these data and resources for pollinators. Paper I shows, however, that these associations differ from region to region and from year to year. In paper I, while there was a shared positive relationship between bumblebee abundance and semi-natural habitat across the regions, we did not find the same effect for solitary bees. These results were contrary to what Steffan-Dewenter et al. (2002) found. In our study, there was a high variability of semi-natural habitats across regions and years, which could be explained by differences in the quality and quantity of these habitats. Part of this variability could be explained as we included grasslands and forests as semi-natural habitats since they are known to provide resources for wild bees (Svensson et al. 2000, Persson et al. 2018, Donkersley 2019). However, the effect of heterogeneity in forest and grassland management and composition on pollinators is less well understood. These results of paper I emphasize that it is important to consider more detailed characteristics of what we regard as semi-natural habitats in each region (i.e., grasslands in Sweden might not be the same as in Germany, or the Netherlands), and which target group we aim to benefit in conservation actions.

The results of paper I also show that the statistical model we used had overall low predictive power, which might be as well due to the simplicity of the model and the noise in the ecological data, as explained above. To improve the power and transferability of these models, not only additional data should be collected from the regions where the models are to be applied, but we also argue that more refined data describing the quality of the different habitats would increase the explanatory and predictive power of this type of models. The downside in more refined input data is that it is less likely to be widely available, compared to the data that we used as inputs to our model. In our study, we used homogenized maps of land cover across Europe. However, the aggregation into broad categories could have masked the interregional variation in semi-natural habitat quality and reduced model quality for the sake of wider applicability.

Compiling better datasets with a high thematic resolution of land use change is crucial to refining future biodiversity scenarios (Marshall et al. 2021). A way to improve this would be with a standardised system with robust yet detailed monitoring, which is also in the European Commission agenda for the EU Biodiversity Strategy (2020), and new research programs (see EuropaBON and Safeguard). In addition, remote sensing can also be used for mapping detailed land cover data, such as the very recent crop map based on Sentinel 1 (d'Andrimont et al. 2021). Remote sensing also have the potential to provide crucial information on phenology monitoring, as we explored in paper III, and to assess management intensity, and potentially availability of resources for pollinators (Abdi et al. 2021).

Mechanistic and spatially explicit models such as the one developed and used in paper II and paper III (LandscapeGDDBee), simulate pollinator abundance based on nesting and flower resources in the landscape. An interesting follow-up question would be to which extent mechanistic models can overcome the lack of transferability to predict bumblebee or solitary bee abundance based on underlying ecological processes, compared to statistical models. LandscapeGDDBee is constructed to capture weather-induced variability in food resources and climate stressors, but this needs to be tested with empirical data, which is a remaining challenge (Gardner et al. 2020).

Direct and indirect drivers of wild pollinator decline

The impacts of direct and indirect drivers of wild pollinator decline, and their interactions, are complex and far from completely clear (IPBES 2016). This is both due to the incomplete assessment of the status and trends of all pollinators, but also due to the lack of information on the drivers. Two of these drivers are climate and land-use change, which influence the variability of nesting and floral resources for pollinators. To help solve the need for pollinator models to capture the variability of these resources, we developed LandscapeGDDBee in this thesis, and demonstrated the model's ability to qualitatively reproduce realistic patterns of population dynamics, also during simulated drought conditions.

In this thesis, we also explored the addition of climate and remote sensing data to make a GDD informed phenological growth model, which is a new addition to pollination models and has significant potential for further exploration and to improve colony dynamics simulations. The advantage of the hierarchical structure of LandscapeGDDBee is the possibility for it to be used for other insects and land use types, by simply adapting the model inputs including temperature and maps of the region, and the corresponding GDDs to capture the phenology of the insect or plant development. The results of papers II and III show the importance of the spatial and temporal distribution of pollinator habitats for their population dynamics in a changing climate. The presence of semi-natural habitats and late resources in agricultural landscapes (explored in this thesis in the form of late-flowering crops) are examples of measures to promote heterogeneous landscapes and counteract seasonal resource gaps which is key for pollinators (Schellhorn et al. 2015, Hass et al. 2018, Timberlake et al. 2019, Nicholson et al. 2021).

Concerning bumblebees, special attention is needed for late-emerging species with queens that are active during summer flowering. They are often rare species, with long tongues, with strong preference for long corolla flowers, such as red clover (*Trifolium pratense L.*). The red clover is one example of a late-mass flowering crop of which the cultivation area has dramatically decreased, drastically affecting the bumblebee community composition (Bommarco et al. 2012). The use of long-term datasets (including museum specimens and citizen observed data used in paper IV) provide the potential for necessary understanding of the temporal trends in life-history traits (Bartomeus et al. 2013, Scheper et al. 2014, Kharouba et al. 2019, Pawlikowski et al. 2020). The datasets can help improve predictions of bumblebee viability or projections of their distributions under future climate change. However, these datasets usually involve arbitrary and non-systematic observations (i.e. sampling bias), which might lead to the data not consistently reflecting the occurrence or abundance of specific species, especially less abundant species which might be not detected by the observer. It is necessary and possible to correct this sampling bias (Carvalheiro et al. 2013, Bird et al. 2014, Rollin et al. 2020). Producing more systematic and refined data through systematic pollinator monitoring schemes would potentially allow a better classification of the different types of semi-natural habitats where the individuals were collected or observed (Carvell et al. 2017, Bartomeus and Dicks 2019, Garratt et al. 2019), and potentially improve transferability achieved by stratifying latitude, biogeographic region. Monitoring schemes would also help to keep track of the risks and benefits of conservation actions, which is extremely important for developing good policies for pollinators (Dicks et al. 2016, Cole et al. 2020).

The need for a multidisciplinary approach

In this environmental science thesis, I explore a range of methods from landscape and theoretical ecology, climate science, and remote sensing to increase the knowledge on pollinators population dynamics and guide future research. Although the approach taken in the thesis can be considered multidisciplinary, it is still fully within the natural sciences. To reverse the pollinator (and biodiversity) crisis, integrated changes in policy and behaviour are needed across all sectors, calling for a strong multidisciplinary approach of not only natural scientists but also social scientists. It is internationally recognised that it is urgent to strengthen the links between the climate crisis and biodiversity crisis we are currently facing, as exemplified by the workshop between IPBES and IPCC (Pörtner et al. 2021). Some of the necessary challenges to address are, for example, the socio-cultural viewpoint of the relation between society and economy and pollinators (Dicks et al. 2021), and to understand people's engagement in the conservation of pollinators (Knapp et al. 2021). Further, it is important to recognise the co-benefits of restoring wild pollinator conservation habitats not only for pollinator and ecosystems health, but also to address the benefits of environmental quality for human well-being.

As discussed in papers II, III, and IV, climate change effects on bees include gradual temperature changes that shift phenology. A mismatch between plants and pollinators occurs due to asynchronous phenology shifts, but also due to range shifts of pollinators, or that these floral resources are not there anymore. Potential ways to mitigate climate change effects can include adjusting different planting schedules, managing the landscape configuration, adopting crops more resistant to drought, and developing decision support tools (see examples at beescape.org or the BeeSteward (Twiston-Davies et al. 2021)).

Conclusion

Future research needs to increase our understanding of the drivers (direct and indirect) of pollinator decline as well as how these operate and interact in different contexts, so that management responses to protect pollinators can be targeted. There are effective policy and management responses that can be implemented to safeguard pollinators and sustain pollination services, but those can only be established by sharing knowledge and coordinated action (Potts et al. 2016). This thesis adds to the growing body of knowledge with the findings on the effects of gradual climate change and drought on pollinators and how these drivers interact with land use, as well as with the findings on the limited applicability of statistical pollinator models in novel contexts.

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Wild bees in agricultural landscapes:

Modelling land use and climate effects across space and time

I. Blasi, M., Bartomeus, I., Bommarco, R., Gagic, V., Garratt, M., Holzschuh, A., Kleijn, D., Lindström, S.A.M., Olsson, P., Polce, C., Potts, S.G., Rundlöf, M., Scheper, J., Smith, H G., Steffan-Dewenter, I., Clough, Y. (2021). Evaluating predictive performance of statistical models explaining wild bee abundance in a mass-flowering crop.

II. Blasi, M., Clough, Y., Jönsson, AM., Sahlin, U. A landscape population model of population dynamics and pollination services in agricultural landscapes with different land use and weather-induced variability in food resources for wild bees.

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Lund University
Faculty of Science
Central for Environmental and Climate Science

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