Mapping and assessing ecosystem services in an agricultural landscape following a tiered approach

Von der Naturwissenschaftlichen Fakultät der Gottfried Wilhelm
Leibniz Universität Hannover

zur Erlangung des Grades

Doktorin der Naturwissenschaften (Dr. rer. nat.)

genehmigte Dissertation

von

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Diplôme d´ingénieur (École nationale des travaux publics de l’État)

2022

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Tag der Promotion: 20.10.2022

Summary

Agricultural ecosystems are anthropogenically highly transformed ecosystems, mainly designed to maximise the delivery of provisioning ecosystem services (ES) such as food, material and fuel, often at the expense of other ES. Especially, conventional agriculture and agricultural landscape simplification have become major causes of climate change, ecosystem degradation and biodiversity loss. At the same time, the production of provisioning services depends on other, mainly regulating, ES. In the long-term, the viability of agricultural ecosystems and the delivery of provisioning ES rely on more sustainable farming practices and the conservation of ES and biodiversity. This calls for a shift in the agricultural production paradigm, towards more multifunctional and sustainable agricultural landscapes. Spatially explicit assessments of ES are key components in supporting the shift towards sustainable land use management: they inform on how and where land use decisions can affect ecosystems, on potential trade-offs between the delivery of different ES and help to design targeted ES conservation measures. Understanding the distribution patterns and the main drivers influencing the delivery of ES is needed to determine where land use management measures can be improved to maximise the delivery of (specific) ES. Specifically, spatial information on ES can assist economical decisions underlying agricultural practices: for instance, higher pollination and natural pest control ES potentials can increase crop yields and save resources.

The central question of this thesis is to assess how different ES assessment methods influence the predictions of ES supply potential, aiming to find the adapted level of information needed for an ES assessment at the local scale, in an agricultural landscape. To address this research question, several ES mapping and assessment methods, using simple (tier 1) to more complex (tiers 2 and 3) approaches, were developed and applied to a case study area in northern Germany. Additionally, this work aims at informing land use planners and decision-makers on the capacity of the landscape to deliver multiple ES. First, the ES matrix approach (tier 1) was used to assess the importance of spatial resolution and of accounting for ecosystem condition (tier 2). The two following studies developed and implemented more complex methods (tier 3) based on species distribution models (SDMs). SDMs were used to model the relationships between ES providers (ESP) (here wild bees and natural enemies of pests) and a combination of abiotic and biotic factors at different scales.

The results of this thesis show that designing multifunctional landscapes ideally requires a rather comprehensive assessment. For most regulation and cultural ES, simple proxies are not suitable for a local quantitative assessment of ES, as they cannot sufficiently cover the spatial heterogeneity of ES capacities and functions that arise from different ecosystem properties and conditions. This is particularly the case of ES delivered by living and mobile organisms such as pollination and natural pest control, whose potentials are determined by multi-scale variables and processes.

A comprehensive assessment of every ES is, however, often not feasible. This thesis shows how the use of different modelling methods and the tiered approach can assist in the assessment of multiple ES. Proxy indicators and models should be used whenever empirical data and knowledge of ecological processes are limited. Indicators and models are, however, only simplified representations of complex processes. ES mapping and assessment outputs should therefore be interpreted considering the assumptions behind the models and knowing the associated uncertainties.

Keywords: Ecosystem service providers, species richness, ecosystem condition, pollination, natural pest control, arthropods, tiered approach, multifunctional landscapes, land use planning.

Zusammenfassung

Landwirtschaftliche Ökosysteme (ÖS) sind anthropogen stark veränderte ÖS, die hauptsächlich darauf ausgelegt sind, die Bereitstellung von Ökosystemleistungen (ÖSL) wie Nahrung, Material und Brennstoff zu maximieren - oft auf Kosten anderer ÖSL. Insbesondere die konventionelle Landwirtschaft und die Vereinfachung der Agrarlandschaft sind wesentlich mitverantwortlich für den Klimawandel, die Verschlechterung von ÖS und den Verlust der biologischen Vielfalt. Gleichzeitig hängt die Fähigkeit eines ÖS Nahrung und andere Rohstoffe zur Verfügung zu stellen von anderen, hauptsächlich regulierenden, ÖSL ab. Langfristig hängen die Lebensfähigkeit landwirtschaftlicher ÖS und die Bereitstellung von ÖSL von nachhaltigeren landwirtschaftlichen Praktiken und der Erhaltung von Ökosystemen in gutem Zustand und der Biodiversität ab. Räumlich explizite Bewertungen von ÖSL sind ein Schlüssel zur Unterstützung eines nachhaltigen Landnutzungsmanagements: Sie informieren, wie und wo Ökosysteme beeinflussen werden können, über potenzielle Kompromisse zwischen der Bereitstellung verschiedener ÖSL und helfen bei der Entwicklung gezielter Maßnahmen zur Erhaltung von ÖSL. Insbesondere räumliche Informationen zu ÖSL können wirtschaftliche Entscheidungen unterstützen: Höhere Bestäubungs- und natürliche Schädlingsbekämpfungspotentiale von ÖSL können beispielsweise die Ernteerträge steigern und Ressourcen sparen.

Die zentrale Frage dieser Arbeit ist es zu bewerten wie verschiedene ÖSL-Bewertungsmethoden die Vorhersagen des ÖSL-Versorgungspotentials auf lokaler Ebene beeinflussen. Dafür wurden mehrere ÖSL-Kartierungs- und Bewertungsmethoden unter Verwendung einfacher (Stufe 1) bis hin zu komplexeren (Stufen 2 und 3) Ansätzen entwickelt und auf ein Fallstudiengebiet in Norddeutschland angewendet. Darüber hinaus sollen Landnutzungsplaner und Entscheidungsträger über die Fähigkeit der Landschaft informiert werden mehrere ÖS bereitzustellen. Zunächst wurde der ÖSL-Matrix-Ansatz (Stufe 1) verwendet, um die Bedeutung der räumlichen Auflösung und der Berücksichtigung des Ökosystemzustands (Stufe 2) zu bewerten. Die beiden nachfolgenden Studien entwickelten und implementierten komplexere Methoden (Stufe 3) auf der Grundlage von Artenverteilungsmodellen („species distribution models“ - SDMs). SDMs wurden verwendet, um die Beziehungen zwischen ÖSL-Anbietern (hier Wildbienen und natürlichen Feinden) und mit abiotischen und biotischen Faktoren auf verschiedenen Skalen zu modellieren.

Die Ergebnisse dieser Arbeit zeigen, dass die Gestaltung multifunktionaler Landschaften eine umfassende Bewertung erfordert. Für die meisten regulatorischen und kulturellen ÖSLs sind einfache Proxys nicht für eine lokale quantitative Bewertung von ÖSL geeignet, da sie die räumliche Heterogenität von ÖSL-Kapazitäten und -Funktionen, die sich aus unterschiedlichen Ökosystemeigenschaften und -bedingungen ergeben, nicht ausreichend abdecken können. Dies gilt insbesondere für ÖSL, die von lebenden und mobilen Organismen wie Bestäubung und Schädlingsbekämpfung geliefert werden, deren Potenziale durch mehrskalige Variablen und Prozesse bestimmt werden. Eine umfassende Bewertung aller ÖSL ist jedoch oft nicht praktikabel. Diese Arbeit zeigt, wie die Verwendung verschiedener Modellierungsmethoden und der gestufte Ansatz bei der Bewertung mehrerer ÖSL helfen können. Proxy-Indikatoren und -Modelle sollten verwendet werden, wenn empirische Daten und Kenntnisse über ökologische Prozesse begrenzt sind.

Schlüsselwörter: multifunktionale Landschaften, Landnutzungsplanung, abgestufter Ansatz, Ökosystemzustand, Arthropoden, Artenreichtum, Bestäubung, natürliche Schädlingsbekämpfung.

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List of abbreviations

AES	Agri-environmental schemes
AIC	Akaike information criterion
AICc	Akaike information criterion corrected
ANN	Artificial neural networks
AUC/ROC	Area under the curve of the receiver operating characteristics
BRT	Boosted regression trees
CABI	Centre for Agriculture and Bioscience International
CAP	Common Agricultural Policy
CBD	Convention on Biological Diversity
CICES	Common international classification of ecosystem services
CORINE	Coordination of information on the environment
CSA	Case study area
EPF	Ecological Production Function
ES	Ecosystem services
ESTIMAP	Ecosystem Services Mapping tool

EU	European Union
FDA	Flexible discriminant analysis
GAM	Generalized additive models
GBIF	Global Biodiversity Information Facility
GLM	Generalized linear models
HMSC	Hierarchical Modelling of Species Communities
IMAGINE	Integrative Management of Green Infrastructures Multifunctionality, Ecosystem integrity and Ecosystem Services
InVEST	Integrated Valuation of Ecosystem Services and Tradeoffs
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN	International Union for the Conservation of Nature
jSDM	Joint Species Distribution Model
LDA	Linear discriminant analysis
LULC	Land use/land cover
MA	Millennium Ecosystem Assessment
MAES	Mapping and Assessment of Ecosystem and their Services
MAXENT	Maximum entropy
PCA	Principal component analysis
RF	Random Forest
RLI	Red List Index
SDM	Species Distribution Model
SNH	Semi-natural habitats
SOC	Soil Organic Carbon
TEEB	Economics of Ecosystems and Biodiversity
TSS	True skill statistics

Chapter 1

Introduction

1 Introduction

1.1 Motivations and objectives

Ecosystems are deteriorating worldwide and more rapidly than ever, with dramatic impacts on people and all other species (Díaz et al., 2020). These are key messages from the latest plenary session of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), based on the systematic review of scientific, government and local knowledge on the relationships between human activities and nature over the last five decades (IPBES, 2019). Human existence depends on healthy and resilient ecosystems. Ecosystems are, however, degraded by human activities and their consequences, such as land use change, pollution, resource overexploitation, biodiversity loss and climate change, which can jeopardise their capacity to deliver life-essential ecosystem services (ES). ES can be defined as “the contributions of ecosystem structure and function – in combination with other inputs – to human well-being” (Burkhard et al., 2012a). These contributions underpin several dimensions of people’s health and quality of life, including the provision of human basics needs such as food, clean air and water. The ES concept has gained importance in environmental management and policy, particularly in the European Union (EU) as it highlights the interactions between nature (conservation and use) and human well-being (Maes et al., 2012a). One of the triggers was the EU Biodiversity Strategy to 2020’s call on Member States to map and assess the state of ecosystems and their services, a necessary step to maintain and enhance ecosystems’ conservation status and their services (Maes et al., 2018).

Agricultural landscapes represent nearly half of the total terrestrial surface of Earth (IPBES, 2019). Over the last 50 years, food security objectives coupled with technological progress and incentive policies have led to the adoption of intensive agricultural management in many regions of the world (IPBES, 2019). Agricultural intensification is characterised by landscape simplification across scales, through large-scale monocultures, simplification of rotation schemes, less diversity in non-crop habitats and systems relying on high levels of synthetic fertilisers and pesticides. The intensification of agriculture, while supporting high yields, has enormous negative impacts on natural resources and biodiversity. It is furthermore a major factor contributing to land use change, pollution, resource overexploitation and climate change (Potts et al., 2016; Garibaldi et al., 2017; IPBES, 2019). Agriculture has become one of the primary causes of biodiversity loss globally (IPBES, 2019) and accounts for almost one quarter of the global anthropogenic greenhouse gas emissions (Arneth et al., 2019).

Global warming, resource overexploitation and pollution make agriculture increasingly vulnerable to extreme weather, disease and pest outbreaks (Arneth et al., 2019). Global warming has already begun to alter growing seasons and reduce crop yields through warmer temperatures, increasing extreme climatic events and changing precipitation patterns. Biodiversity loss and the resulting decline in functional diversity can threaten ES delivery and ultimately the sustainability of crop production as well (Aizen et al., 2009; Bommarco et al., 2013; Gagic et al., 2015). There is evidence that essential ES such as crop pollination (Kremen et al., 2002; Potts et al., 2010), natural pest control (Bianchi et al., 2006; Thies et al., 2011) and soil-related ES (Wall et al., 2015) can be jeopardised in highly intensified agricultural landscapes. Moreover, agricultural intensification is no longer enhancing the yields of many major crops (Ray et al., 2012; Gaba et al., 2016; Lechenet et al., 2017), partly because the benefits of intensification are limited by the decreasing availability of critical ES (Deguines et al., 2014; Catarino et al., 2019; Montoya et al., 2019). In the long term, ensuring crop production can therefore only be achieved by a sustainable management of landscapes, preserving biodiversity and various ES (Foley et al., 2005; Tilman et al., 2011; UN, 2017) and by adapting to and mitigating climate change impacts (FAO et al., 2018).

There are increasing social pressures to move towards a more sustainable agricultural management, with agricultural landscapes that deliver a broad range of ES instead of focusing solely on the maximisation of provisioning services (Rockström et al., 2017; IPBES, 2019; Kleijn et al., 2019). Improving the sustainability of agroecosystems has a high priority on (global) authorities' agenda (Landis, 2017). Hence, promoting sustainable agriculture is one of the Sustainable Development Goals of the United Nations (UN, 2017). Similarly, increasing agroecosystems' sustainability is one major goal of the European Commission, through the second pillar of the Common Agricultural Policy (CAP) (European Commission, 2013). Various existing farming approaches can help to reach this objective, including ecological intensification (Bommarco et al., 2013; Kleijn et al., 2019; Vanbergen et al., 2020). Ecological intensification is defined as an alternative land use management based on the integration of ES conservation and management into agricultural production systems to minimize the negative impacts of external inputs and sustain agricultural production (Bommarco et al., 2013). Ecological intensification practices include the establishment of semi-natural habitats (SNH) such as hedgerows and flower strips, intercropping, pesticide use reduction or increasing the proportion of fallow lands (Potts et al., 2016). These practices have been shown to benefit a variety of ES Providers (ESP) (Tschumi et al., 2015; Holland et al., 2017) and to help to tackle ES losses in agricultural landscapes (Holland et al., 2017). There are, however, still numerous barriers to the implementation of mitigation measures, including financial and institutional barriers, the absence of incentives or awareness and a limited demonstration of effectiveness (Vanbergen et al., 2020). Particularly, there is no consensus on how ecological measures contribute to (or affect) crop production and where these measures should be implemented to maximise their impacts on different ES at the landscape scale. As land is a limited resource, assuring crop production whilst restoring or maintaining multiple ES requires spatially optimising land use and management. This implies understanding local to landscape contexts and the spatial distribution of ES potentials.

The spatial-explicit quantification of ES and ES mapping approaches are powerful tools to assess and communicate on the interdependency between human well-being, human activities and the environment as well as how ecosystems are impacted by human activities at various scales and to guide policy decisions (Maes et al., 2012a; Burkhard et al., 2012b; Schröter et al., 2015; Burkhard and Maes, 2017). In agricultural systems, ES mapping and assessment can be used to assist the transformation of agriculture systems towards more sustainable management, i.e., that conciliates multiple objectives on a specific territory and in particular, food security, rural development, climate change mitigation and biodiversity conservation. Specifically, it can inform on potential trade-offs and synergies between the delivery of different ES, such as between crop production and regulating services (e.g., pollination and natural pest control) (Egoh et al., 2008; Raudsepp-Hearne et al., 2010). Finally, ES mapping and assessment outputs can be used to design targeted and effective conservation measures for biodiversity and ES conservation.

Driven by the needs of policy and decision-makers to assess ES at different scales, ES mapping, assessment and decision-support methods have expanded fast over the past decades (Egoh et al., 2012; Martínez-Harms and Balvanera, 2012; Maes et al., 2016). The selection of the appropriate methods and providing useful information for a specific research question can therefore be complex. The mapping and assessment purpose, the scale of the study area but also technical capacity and knowledge, data availability and quality affect the decision on which methods should be employed for each ES assessment. Different methods can be suitable for different mapping and assessment purposes, and all methods are not applicable to all cases. Grêt-Regamey et al. (2015) proposed the "tiered approach" to help to select ES mapping and assessment methods adequate to specific research or policy questions. The different tiers are distinguished according to the purpose and the needed level of detail of the ES analysis. This allows the ES analysis to provide relevant information to decision-makers and to avoid the use of too complex or too simple methods. A general issue when studying ecosystems is the lack of appropriate data at an appropriate scale. ES assessments are therefore often partly driven by data availability and/or rely on the use of available models and indicators. For this reason, information on the limitations of the selected mapping and assessment approach, such as feasibility, reliability, accuracy and uncertainty, is essential. Besides, the multiplicity of stakeholders involved in different planning processes can require the use of ES assessment methods of different complexity levels (Dunford et al., 2017).

The central objective of this thesis is to assess how different ES assessment methods influence the predictions of ES potential at the local scale. The aim was to develop and refine methodological approaches for modelling and mapping the delivery of ES in agricultural landscapes, building on the tiered approach framework, to support sustainable land management in agricultural landscapes. Specifically, this thesis aims to answer the following research questions:

1) Does a high spatial resolution and the integration of ecosystem condition information affect the ES assessment and can patterns between different ES and ES categories be detected? How can the employed methods affect the resulting maps?
2) How do biotic and abiotic factors affect pollinator and natural enemy species distributions and their associated ES potentials? What are the implications for an ES assessment in the case study area?
3) Do we observe spatial asynchrony between ES potential and demand for pollination and natural pest control in the selected case study area?
4) What conclusions can be drawn for practical applications in landscape management to optimise ES delivery and particularly the conservation measures for wild bee and natural enemy species?

The developed models were applied in an agriculture-dominated case study area (CSA) in northern Germany to 1) explore the suitability of information derived from indicators and models to inform decision-making on land use planning and 2) derive recommendations for decision-making on land use planning, particularly to support the design of effective conservation measures for wild bee and natural enemy species.

1.2 Structure of the thesis

This thesis is a cumulative dissertation consisting of three original and peer-reviewed articles in international journals (Chapters 3, 4 and 5). In the first Chapter, the background information from which the topic of this thesis has emerged is outlined, including a description of the CSA and the definition of the central concepts. Chapter 2 describes the different methods used throughout this thesis. In Chapter 3, ES potential and the landscape multifunctionality of the CSA were assessed, with the following central question: how do spatial resolution and the inclusion of information on ecosystem condition influence the ES assessment at the local scale? Chapters 4 and 5 focus on quantifying, modelling and mapping pollination and natural pest control service potentials using species distribution model (SDM) approaches and the Ecological Production Function (EPF) framework developed by Kremen et al. (2007). ES potential is extrapolated from species distribution based on the EPF framework: certain ES are directly provided by organisms or species communities, whose occurrence, abundance and capacity to provide ES are impacted by multiple environmental factors and the landscape context (Kremen et al., 2007). These two last ES models aimed to better understand ecological processes underlying the delivery of specific ES and how bioclimatic variables, land cover and landscape complexity impact the distribution patterns of ESPs and thereby the delivery of associated ES. This work also aimed at providing recommendations for decision-makers and stakeholders on how to optimise the delivery of multiple ES at the landscape scale in the selected CSA. The last chapter summarizes the main findings of the three research papers, followed by a discussion on the implication of the results for landscape management and the needed further research on this topic.

The doctoral thesis was conducted within the BiodivERsA research project IMAGINE: “Integrative Management of Green Infrastructures Multifunctionality, Ecosystem integrity and Ecosystem Services: From assessment to regulation in socioecological systems”. The scope of this project was to quantify the multiple functions, ES and other benefits provided by green infrastructures in different contexts from rural to urban landscapes[1]. This research project involved six universities and research centres from five different European countries and the close collaboration with local stakeholders from five different CSAs. The outcomes aimed at developing an integrated framework for the assessment and management of green infrastructure multifunctionality in different contexts (e.g., Mortelmans et al. (2019) and Blust et al. (2021)) and at providing stakeholders with decision-making tools that integrate multiple green infrastructure design and management scenarios for a more sustainable landscape management (e.g., Suškevičs (2019), Billaud et al. (2020) and Turkelboom et al. (2021)).

1.3 Conceptual and methodological framework

1.3.1 Case study area: Bornhöved Lake District

The different developed models for this thesis were applied in a CSA located in the region of the Bornhöved Lake District in the federal state of Schleswig-Holstein in northern Germany (Figure 1). The extent of the CSA is approximately 140 km². The central part of this study area was the focus of a long-term ecosystem research project (Müller et al., 2006; Fränzle et al., 2008) and several previous research on ES assessment: for instance, the first theoretical use of the ES matrix approach (Burkhard et al., 2009; 2014), an assessment of the importance of scale when mapping provisioning ES (Kandziora et al., 2013b), a study on how to assess and map nutrient regulation ES potential (Bicking et al., 2018; Bicking et al., 2019) and an assessment of a broad range of ES using the matrix approach in the federal state of Schleswig-Holstein (Müller et al., 2020).

Agroecosystems dominate the landscape (almost 75% of the area) that is located in a catchment area of several glacially formed and consecutively connected lakes (Figure 1). Agricultural production is dominated by the cultivation of annual crops such as barley, wheat and rapeseed. The CSA shows a suite of SNH with a high proportion of hedges and wall hedges, that are characteristic of the province, shaping a highly diverse and fragmented landscape (see Figure 1 and Fränzle et al., 2008). It contains

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[1] https://imagine.inrae.fr

only small settlements, following a north-south alignment. Besides agricultural production, the study site is also a local recreation area for the inhabitants of the city of Kiel (250,000 inhabitants), located 35 kilometres away.

Locally, the main challenge is to optimise agri-environmental schemes (AES) to preserve the landscape, biodiversity and ES (Roche, 2021). Broader concerns about the drastic decline in insects due to agricultural intensification have recently emerged in Germany (Hallmann et al., 2017; Deutscher Bundestag, 2017; Seibold et al., 2019). This raised awareness of the need for a better integration of biodiversity and ES conservation in decision-making processes such as land-use planning and land management in agricultural areas. A local ES assessment has the potential to help to improve land-use planning and the design of AES. Particularly, it can support decision-makers to address the potential conflicts resulting from the implementation of ecological measures within the region, for a better understanding and acceptance among the different stakeholders.

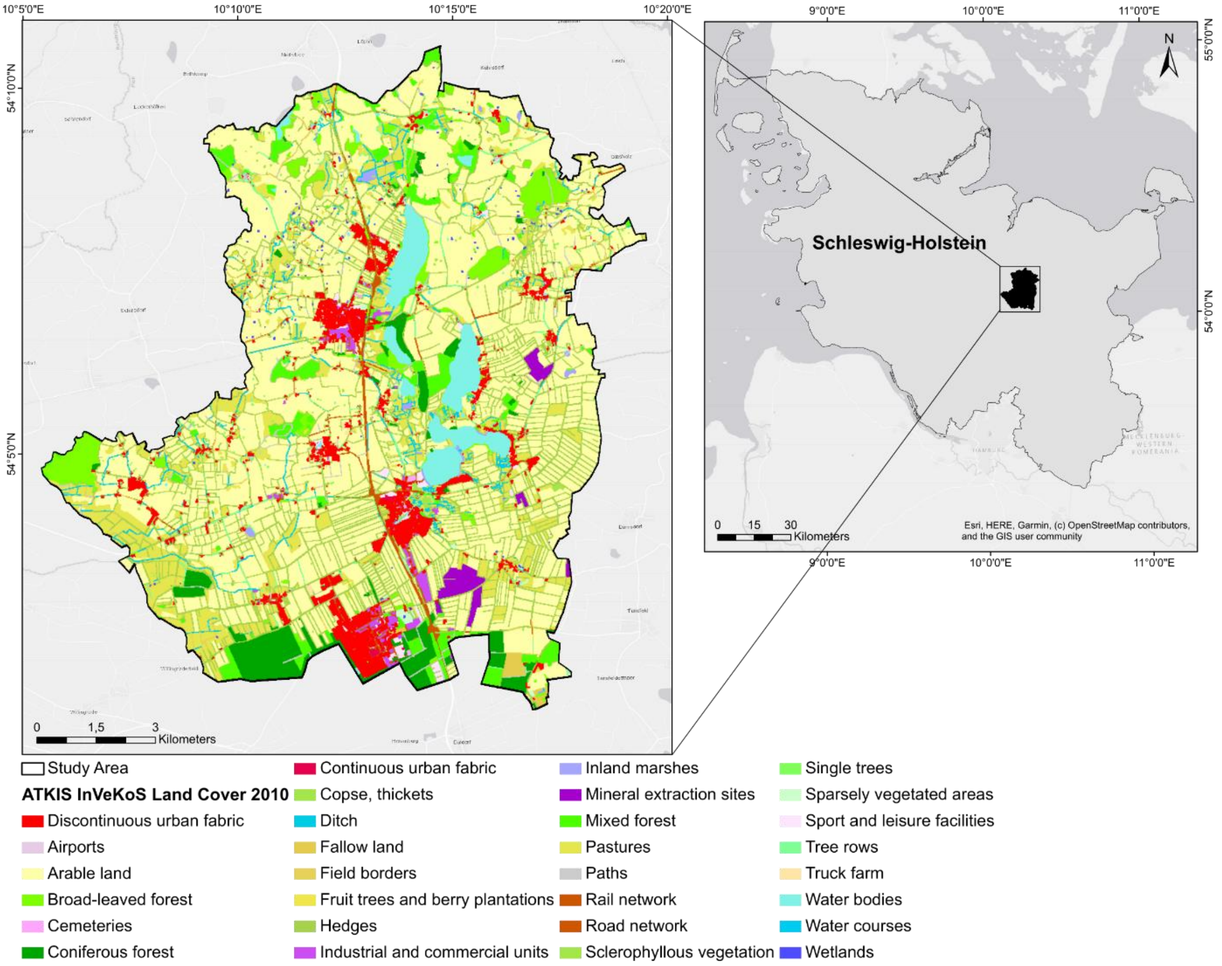


Figure 1: Location of the case study area in northern Germany and distribution of land use/land cover classes within the area (based on the Integrated Administration and Control System (InVeKoS) and the Authoritative Topographic-Cartographic Information System (ATKIS) data).

1.3.2 Definitions and concepts

1.3.2.1 Ecosystems and their services

ES are defined as the direct and indirect benefits that people obtain from ecosystems (Costanza et al., 1997; TEEB, 2010; Millennium Ecosystem Assessment, 2005). More recently, ES have been defined as the contributions of ecosystems, *in combination with other inputs*, to human well-being (Burkhard et al. 2012a). This definition highlights that ES form only through interaction with human capital, social capital and their built environment (Costanza et al., 2014; Costanza et al., 2017). Ecosystems are defined as "dynamic complex of plant, animal and microorganism communities and their non-living environment interacting as a functional unit" (UN, 1992). Consistent ES description and classification are necessary preambles of any ES assessment (Burkhard and Maes, 2017). Several ES classification systems coexist (Potschin and Haines-Young, 2016). To fit with previous ES assessments in the studied region, the ES classification presented by Müller et al. (2020) was used throughout this thesis. In this classification, ES are categorised in "provisioning", "regulation and maintenance" and "cultural" ES (similar to the Common International Classification of Ecosystem Services (CICES) typology (Millennium Ecosystem Assessment, 2005; Haines-Young and Potschin, 2012)). Provisioning services are the products and goods directly produced by ecosystems, such as cultivated crops, timber or wild food. Regulating services refer to how ecosystems can mediate natural processes, such as pollination, natural pest control, nutrient and air quality regulation. Cultural services are the intangible benefits of ecosystems that contribute to human well-being, including cognitive and spiritual enrichment, inspiration and recreational enjoyment.

ES delivery can generally be distinguished between potential, supply, demand and flow (Villamagna et al., 2013; Burkhard and Maes, 2017). Throughout this thesis, the focus is on the supply side of ES, i.e., how ecosystems contribute to the provision of ES and particularly on ES potentials. ES potentials are defined as the amount of ES that can be provided sustainably, in a particular area (Burkhard and Maes, 2017) or the hypothetical maximum yield of selected ES (Burkhard et al., 2014). In Chapters 4 and 5, ES demand was also considered, defined as the potential human need for specific ES in a particular area (Burkhard and Maes, 2017). The demand for pollination ES is generated by the farmers' decision to plant pollination-dependent crops (Lautenbach et al., 2011). Similarly, the demand for natural pest control ES depends on the presence of cultivated crops potentially affected by pests, as pests are defined as species that compete with humans for common resources. ES flow is the amount of mobilized ES in a specific area and time; the notion was however not used in this thesis. Regulation services such as pollination and natural pest control are not final ES or consumed goods (Burkhard et al., 2014). They underpin the production of many crops that, in turn, directly contribute to human well-being. Throughout this thesis, pollination potentials and pollination ES potentials were therefore distinguished: pollination can occur wherever pollinators are and it becomes an ES where it potentially contributes to crop production (the same distinction was made for natural pest control).

This thesis builds on the Mapping and Assessment of Ecosystems and their Services (MAES) conceptual framework (Figure 2, Maes et al., 2016). This conceptual framework describes how biodiversity, ecosystem processes, functions and services benefit human well-being and illustrates the possible implications of ecosystem degradation for human well-being. The capacity of an ecosystem to provide ES depends on its properties and condition (or state), which underpin ecological functions, processes, services and final benefits that people retrieve from ecosystems. The MAES framework also highlights how societal and governance decisions on land use and management can affect ES delivery. The concept of ES is consequently socio-ecological, which implies research in the fields of ecology, economy and social sciences. The thesis focuses on the assessment of the capacity of ecosystems to deliver services (i.e., on the ecological side of the ES concept). The social aspects of ES demand are not addressed in detail. The presented thesis is part of a project with a larger scope (IMAGINE, presented in the Introduction), which addressed social and political implications of the conservation and ES and biodiversity, using, among others, stakeholder perceptions and policy coherence assessments (Roche, 2021). This thesis is therefore part of an interdisciplinary research project, aiming at providing a comprehensive ES assessment in the selected CSAs (Roche, 2021).

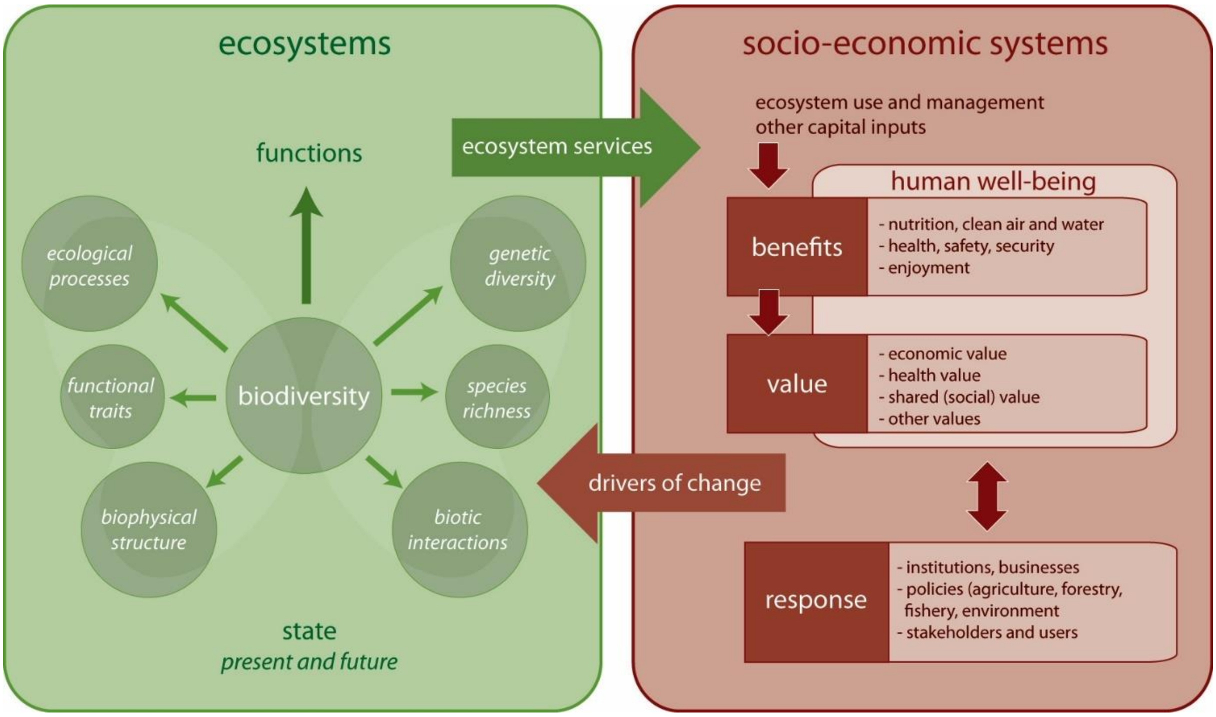


Figure 2: MAES conceptual framework illustrating the interrelations between biodiversity, ecological processes, functions and services and the socio-economic systems (Maes et al. 2016).

1.3.2.2 Ecosystem condition

The capacity of an ecosystem to sustain ES is determined by its physical, chemical and biological characteristics, which together determine its condition (also called ecosystem quality, state or health) (Millennium Ecosystem Assessment, 2005; Maes et al., 2018). Information on the condition of ecosystems is therefore a prerequisite for a comprehensive ES assessment (Maes et al., 2016; Syrbe et al., 2017). Assessing ecosystem condition is still hampered by a lack of data and the limited knowledge of how different pressures quantitatively affect the physical, chemical, and biological characteristics and processes of an ecosystem (Maes et al., 2016). It is usually approached using indicators, mainly describing habitats, species and environmental quality of the ecosystem. To improve ES and ecosystem condition assessments and foster homogenisation throughout European countries, the MAES initiative provided guidance on how to integrate ecosystem condition in ES assessments, and lists sets of potential ecosystem condition indicators (Maes et al., 2018). The mapping of ecosystem condition at European or national scales has made significant progress following MAES's works, but developments for multiple services and at a finer spatial resolution are still limited (Rendon et al., 2019). One issue when using these indicators is that they are hardly adapted to an assessment at a fine spatial resolution because the necessary information is not provided with sufficient quantitative spatially explicit information (European Environmental Agency, 2015). Another challenge is the general lack of knowledge on how ecosystem condition affects the supply of different ES. In Chapter 3, how the list of indicators provided by the MAES can be adapted to assess ecosystem condition at the local scale was illustrated.

1.3.2.3 Biodiversity and ecosystem services

Biodiversity underpins ecological processes and functions and thereby plays a key role in the supply of many ES (Hooper et al., 2005; Cardinale et al., 2012; Mace et al., 2012; Haines-Young and Potschin, 2010; Balvanera et al., 2014; Maes et al., 2016). It is however often still unclear how specific aspects and elements of biodiversity underlie the provision of different ES (Hooper et al., 2005; Bello et al., 2010; Balvanera et al., 2014; Harrison et al., 2014). ES are generally generated from numerous biodiversity elements, processes and spatio-temporal interactions occurring in complex systems (Harrison et al., 2014). Complex interrelations have already been described between biodiversity elements, ecosystem functions and ES for specific ES. For instance, the production of food is supported by soil formation, nutrient cycling, water filtration and infiltration capacity, pollination and natural pest control, which in turn rely on different biodiversity attributes (Zhang et al., 2007). Similarly, Isbell et al. (2011) showed that a high level of plant diversity was essential to promote ecosystem functioning and increased grassland productivity. Some ES such as water purification and atmospheric regulation are facilitated at the species community level and by whole ecosystems, whereas other ES such as timber production tend to rely on fewer species (Harrison et al., 2014). Pollination ES is supported by pollinator diversity (Brittain et al., 2013; Senapathi et al., 2021), abundance and functional diversity (Hoehn et al., 2008; Woodcock et al., 2019) and diverse bee communities (Blitzer et al., 2016). It is however still argued that mainly few and abundant species might be doing most of the job in crop fields (Kleijn et al., 2015). Natural pest control ES has been shown to benefit from a high species diversity (Dainese et al., 2017; Dainese et al., 2019), however not in every landscape (Tscharntke et al., 2012b; Martin et al., 2013; Jonsson et al., 2017). Because of the complex nature of ecosystems and ES, and of the lack of understanding of how ES are sustained by different biodiversity elements, ecosystem components, processes and functions, there is no consensus yet on how to define the (quantitative) relationships between biodiversity attributes and the delivery of many ES (Harrison et al., 2014). Numerous approaches to assess and map ES are therefore based on the use of simplified approaches based on proxy indicators and models (Eigenbrod et al., 2010; Harrison et al., 2014). Models are also valuable approaches to explore the role of biodiversity in ES delivery (Kremen, 2005).

1.3.2.4 Ecosystem Service Providers

In some cases, the supply of ES can be linked to the presence, abundance, richness and/or functional diversity of key species that act as Ecosystem Service Providers (ESPs, Kremen, 2005; 2007; Luck et al., 2009). ESPs can be taxa, communities or functional groups that sustain the ES of interest. This approach has been used to assess different ES, including wood production, carbon sequestration, regulation of water quality and flow, pollination, natural pest control and landscape aesthetics (Luck et al., 2009; Cardinale et al., 2012; Harrison et al., 2014; Dainese et al., 2019). Chapters 4 and 5 focus on pollination and natural pest control provided by arthropods (i.e., the ESPs). These ES were selected as they are essential in agricultural landscapes and because there is extended knowledge of the corresponding ESPs.

Pollination ES are defined as the fertilisation process done by living organisms that maintains or increases the abundance and/or diversity of plant species that people use or enjoy (Haines-Young and Potschin, 2018). A large majority of plants and approximately 75% of cultivated crops are, to some extent, dependent on animal pollination, mainly provided by birds, bats and insects (Ollerton et al., 2011; Klein et al., 2007). By contributing to many crops' productivity and quality, pollinators highly contribute to healthy diets (IPBES, 2016). The total global annual market value of animal pollination has been estimated to be between 235 and 577 billion US dollars (Lautenbach et al., 2012). Beyond food provisioning, pollinators contribute to the provision of medicines, fibres and have inspirational and recreational values (Potts et al., 2016). Bees are important pollinators because of the diversity and complementarity of their functional traits (e.g., hairiness and visitation behaviour) (Potts et al., 2016; Ollerton, 2017). Many plant and bee species developed a highly specialized and mutual relationship, making the survival of both plants and bees dependent on each other presence and abundance. Honeybees are often the most abundant pollinator species in crop systems, but wild bee species are usually the more important crop pollinators, and for some plants, wild bees can be more efficient than honeybees (Garibaldi et al., 2013; Potts et al., 2016; Page et al., 2021). Most crop pollination is probably provided by a relatively small number of species (Kleijn et al., 2015). Pollinator diversity can however increase crop yield and quality through species synergy and complementarity (Brittain et al., 2013; Woodcock et al., 2019). Moreover, pollinator diversity can lead to more stable yields under different environmental conditions (Garibaldi et al., 2011; Brittain et al., 2013; Winfree et al., 2018). Wild bee individual species, richness and communities are therefore essential ESPs in agricultural landscapes, both for the production of crops and wild food as well as the delivery of cultural ES (IPBES, 2016). In Chapter 4, ESPs are wild bee species that pollinate rapeseed flowers (one of the main pollinator-dependent crops in the CSA).

Pest control ES are defined as the reduction by biological interactions of the incidence of pests, i.e., the species that reduce the output of food or material by consumption or reduction of biomass (Haines-Young and Potschin, 2018). Natural pest control or pest control by natural enemies (i.e., predators, pathogens or parasitoids of organisms that humans consider as pests) plays an essential role in reducing pests and therefore in maintaining or increasing crop yields (DeBach, 1964). Even when pesticides are used, natural pest control is a major factor in pest reduction (Pimentel et al., 2005). Natural pest control ES were evaluated at more than $400 billion per year globally (Costanza et al., 1997). Besides, the intensive use of pesticides poses severe problems for environmental and human health. In some cases, it can even increase pest outbreak risks because of the inadvertent destruction of natural enemies and the capacity of pests to develop resistance to pesticides (Oerke, 2006). Moreover, the increasing use of pesticides over the last decades did not result in a reduction of crop losses due to pests (Oerke, 2006). There are therefore strong ecological and economic advantages to replacing the use of pesticides by enhancing the ability of natural enemies to reduce and control pest populations (Bommarco et al., 2013). Many arthropods are involved in natural pest control (Thies et al., 2011), as parasites, pathogens or predators. Most parasites and pathogens are highly specialized in a restricted number of host species. Predators can be generalists and feed on pests as well as other natural enemy species. Natural enemy species show complex interactions, including mutualism (Thies et al., 2011), predation and competition (Wilby et al., 2005; Straub and Snyder, 2006). Managing natural pest control ES is complex as increasing natural enemy diversity might increase intra-guild predation or competition in some configurations, especially in simplified landscapes (Tscharntke et al., 2012b; Martin et al., 2013). In complex systems, however, species complementarity tends to be more frequent than negative interactions and a high species richness usually increases the overall natural pest control service potential (Thies et al., 2011; Letourneau et al., 2009; Snyder, 2019; Dainese et al., 2019). Because natural enemies can interact with each other, modelling the associated ES potential requires not only assessing species richness and abundance but also accounting for negative and positive species interactions between natural enemies. In Chapter 5 of this thesis, the ESPs are composed of natural enemies of aphids in crop fields (mainly spiders, carabids and rove beetles), considering positive and negative species interactions.

1.3.3 Ecosystem services provider decline

Biodiversity is currently declining globally at alarming rates, with evidence for a wide range of taxonomic groups (Ceballos et al., 2015; IPBES, 2019; Ceballos et al., 2020). A growing number of studies are specifically providing evidence of the decline of arthropod abundance and diversity (Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; van Klink et al., 2020; Wagner, 2020; Hallmann et al., 2021; Wagner et al., 2021). Butterflies, wild bees and dung beetles are probably globally the terrestrial species the most affected (Sánchez-Bayo and Wyckhuys, 2019). In Europe, according to the International Union for the Conservation of Nature (IUCN) European Red Lists of threatened species, almost one in ten bee and butterfly species, one in five saproxylic beetle species and a quarter of all grasshopper species are at risk of extinction in Europe (Nieto and Alexander, 2010; van Swaay et al., 2010; Nieto et al., 2014; Hochkirch et al., 2016).

The main drivers of this massive reduction of arthropod abundance and diversity are habitat change, pollution (which includes the widespread use of insecticides) and climate change (IPBES, 2019; Wagner et al., 2021) as well as their combined effects (see Figure 3). Habitat change is principally driven by land use changes such as urbanisation, agricultural expansion and intensification (Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021). Especially, the disappearance, reduction and fragmentation of suitable habitats such as forests and other SNH like grasslands, hedgerows, and small set-aside areas negatively impact many arthropod species, populations and communities (Habel et al., 2019). Landscape homogenisation reduces species diversity, as arthropod species usually have specific needs for foraging, shelters, nesting and/or overwintering, and rely on the presence of multiple habitats, even if some species are more ubiquitous than others (Westrich, 2018).

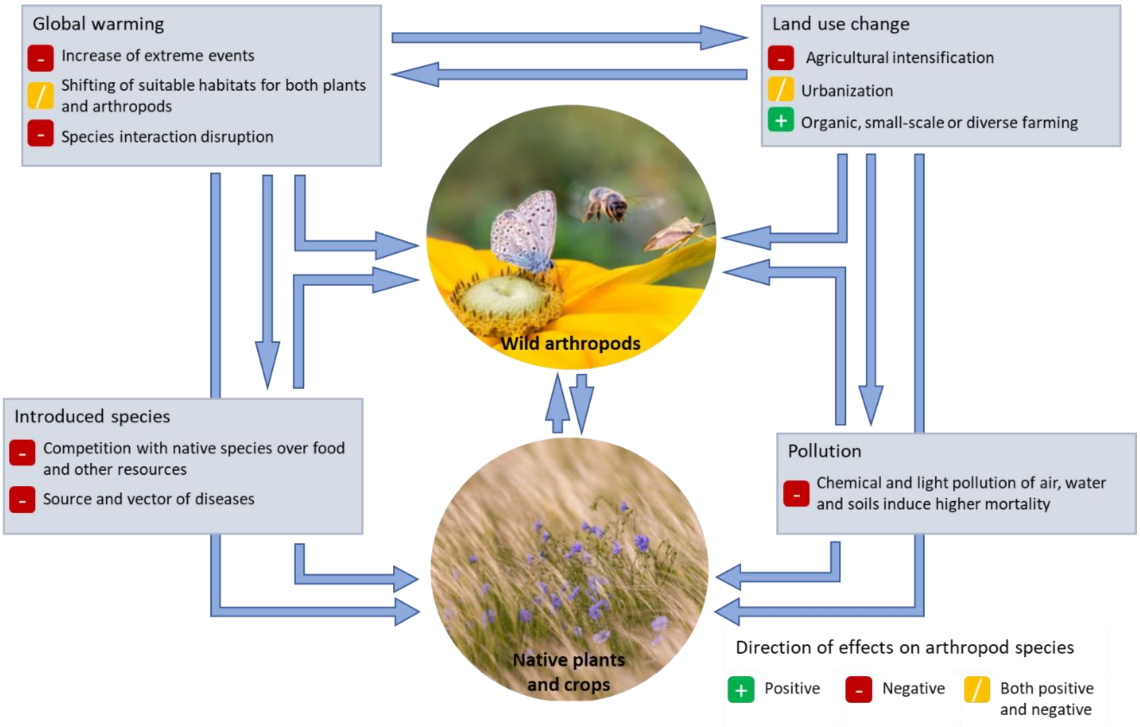


Figure 3: Impacts and combined effects of the many pressures faced by arthropod species (adapted from IPBES (2016) and Wagner et al. (2021)).

Complex agroecosystems can provide suitable habitats for numerous arthropod species (Rusch et al., 2010; Kennedy et al., 2013; Senapathi et al., 2015; Potts et al., 2016; Wagner, 2020). Intensive agriculture and landscape simplification, however, have a substantial negative effect on arthropod diversity (Sánchez-Bayo and Wyckhuys, 2019; Raven and Wagner, 2021; Wagner et al., 2021). The impact of urbanisation on arthropods is species-specific: Urban areas can for instance benefit wild bees (Baldock et al., 2015; Hall et al., 2017) depending on the degree of urbanisation (Fenoglio et al., 2020). However, this might not be the case for all arthropod species (Martinson and Raupp, 2013). Several factors can explain a relatively high insect diversity in urban areas: Urban gardens and parks can provide highly diverse habitats and therefore suitable environment, providing foraging and nesting resources for many species (Goddard et al., 2010; Baldock et al., 2015; Peng et al., 2020). Urban areas also tend to create warmer microclimates and therefore suitable conditions for the development of ectothermic species such as arthropods (Meineke et al., 2013). Finally, the lower use of pesticides can explain why some species can be better off in urban environments (Martins et al., 2017).

Climate change has multifaceted effects on species: it can induce a shift in species’ geographic ranges, alteration in migration patterns and phenology, changes in community structure, compromise species interactions and induce population collapses, depending on species’ plasticity and its dispersal capacity (Potts et al., 2016; Sánchez-Bayo and Wyckhuys, 2019). By shifting the suitable habitat ranges for wild plants, crops, pollinators, pests and natural enemies, climate change can also lead to desynchronisation in time and space of essential species interactions and thereby trigger the emergence of new pests (Biesmeijer et al., 2006; Renner and Zohner, 2018; Damien and Tougeron, 2019). Climate change also causes increasing the frequency of extreme weather events, such as drought and flooding, which may lead to higher mortality rates and eventually population extinctions (Maxwell et al., 2019). Effective conservation of arthropods and the ES they deliver therefore implies understanding how multiple factors, from climatic to land use variables, shape the distribution of ESP species.

1.3.4 Ecological niche of ecosystem services providers

Mapping pollination and natural pest control relies on spatial information on the distribution of pollinators and natural enemies. While a high variety of species can provide these ES, this thesis focused on arthropods as pollination and natural pest control ESPs. Predicting species occurrence is still one of the greatest challenges in ecology and requires understanding how multiple biotic and abiotic factors shape species communities across scales. How landscape complexity, defined as landscape composition and configuration, influences arthropod species and the provision of ES has been widely explored (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Holland et al., 2017; Veres et al., 2013; Martin et al., 2019; Kleijn et al., 2019). Landscape complexity refers to the coverage and diversity of natural and semi-natural or non-crop habitats (Chaplin-Kramer et al., 2011). There is growing evidence that landscape complexity is essential to support pollinator and natural enemy species in agricultural landscapes (Chaplin-Kramer et al., 2011; Martin et al., 2016; Landis, 2017; Martin et al., 2019; Haan et al., 2020). Particularly, the amount of natural and semi-natural habitats and a high density of edges between crop fields and non-crop areas both largely contribute to arthropod abundance and richness in agricultural landscapes (Landis, 2017; Birkhofer et al., 2018; Martin et al., 2019; Haan et al., 2020). Conversely, how different bioclimatic factors influence the presence of arthropods and their associated ES remains understudied (Lobo, 2016). In addition, how the different drivers may interact with each other and increase the overall impact on arthropod species is still unresolved (Hallmann et al., 2017).

Modelling the ecological niches of arthropod species can be tedious because each arthropod species has specific bioclimatic, habitat needs and dispersal capacities, which determine their occurrence and distribution in the landscape (Hill et al., 2015; Lobo, 2016; Carrié et al., 2017). Moreover, each organism experiences its environment at different scales, depending on its dispersal capacity and foraging behaviour (Miguet et al., 2016). In addition, biotic interactions can also shape species' spatial distributions and are determinants to consider when assessing natural pest control service potentials as many natural enemy species are known to interact with each other (via predation, competition or mutualism) (Martin et al., 2013; Jonsson et al., 2017; Snyder, 2019). Multi-scales, multi-variables and multi-species assessment and modelling should therefore improve knowledge about the spatial distribution of ESPs and the delivery of the associated ES, thereby increasing the reliability of the models' predictions. Moreover, assessing how different bioclimatic and land use factors influence species occurrence and diversity is essential to be able to predict the potential impacts of global change (i.e., climate change and land use change) on ESPs and how it can affect the delivery of the associated ES (Settele et al., 2016; Deutsch et al., 2018). In this thesis, new ES modelling methods based on previous knowledge about ESPs' ecology were developed. By combining SDMs at the regional scale and species-specific habitat filtering at the local to landscape scale, the developed methods allow to simultaneously consider the main drivers affecting species occurrence.

1.3.5 State of the art of mapping ecosystem services

There is a high availability of ES mapping and assessment techniques, including maps that build on primary data or proxy indicators, process-based and correlative models and integrated modelling tools (Egoh et al., 2012; Crossman et al., 2013; Bagstad et al., 2013; Lautenbach et al., 2019). ES assessment methods based on primary data are generally considered more accurate than those relying on proxies or models (Crossman et al. 2013). However, the lack of primary data and the resource-intensity of field surveys often make the use of primary data unpracticable (Eigenbrod et al., 2010). Besides, not all ES are directly measurable or quantifiable. Their assessment, therefore, relies on modelling or extrapolation using proxy indicators (Maes et al., 2015). Land use/land cover (LULC) is a commonly used indicator to estimate ES supply (Egoh et al., 2012; Lautenbach et al., 2019), either based on simple look-up table methods (i.e., ES matrix), which attribute ES values for each land use category considered or embedded in more complex models using land use intensity, biophysical and socio-ecological variables (Jacobs et al., 2015). LULC has been shown to be a key determinant of the range of ES that a landscape can potentially provide (Campagne and Roche, 2017). However, in addition to land use, ES also depend on ecosystem processes, functions and therefore biophysical characteristics, which are not sufficiently accounted for when using solely LULC proxies (Eigenbrod et al., 2010; Stoll et al., 2015; Lavorel et al., 2017). Therefore, approaches only based on LULC as proxies for ES are usually associated with high uncertainties (Eigenbrod et al., 2010; Stoll et al., 2015; van der Biest et al., 2015).

Approaches combining ES matrices with variables describing biotic and abiotic factors can increase the precision and reliability of the ES assessment outputs (Burkhard et al., 2012b; Jacobs et al., 2015; Lavorel et al., 2017). Correlative and process-based models usually address the role of ESPs (i.e., individual species, species richness, diversity or functional traits) for the delivery of specific ES. Correlative models refer to quantifying ES approaches, based on statistical relationships with biophysical variables and the delivery of specific ES. Process-based models are built on causal relationships between driving factors, ecosystem properties, processes and ES. Process-based models have mostly been used to map provisioning services (e.g., food, fibre and fuel), climate regulation and erosion control (Lavorel et al., 2017). Correlative and process-based models can be particularly useful to accurately assess ES for which the ESPs are clearly identified (Lavorel et al., 2017). For instance, niche-based models have been used to assess cultural ES derived from the presence of key species (e.g., with spiritual or aesthetic values) and the provisioning of wild food (Schulp et al., 2014b).

There are several existing integrated modelling approaches to map pollination ES. The Integrated Tool to Value Ecosystem Services and their Trade-offs (InVEST, Kareiva et al., 2011) is probably the most popular tool to model ES and particularly pollination. InVEST is an open-access suite of models that was developed under the Natural Capital Project. The Ecosystem Services Mapping tool (ESTIMAP, Zulian et al., 2014) has been initially designed to support policies at the European scale and contains a series of ES models, from outdoor recreation to crop pollination. Both tools use an expert-based assessment to estimate the capacity of different land cover categories to support different pollinators and thereby sustain pollination. One critical issue when relying on expert judgment is that the results can be biased depending on the experts selected and their knowledge of the whole system under assessment (Martin et al., 2012; Jacobs et al., 2015).

Natural pest control services have been mainly modelled using correlative models and using mechanistic models (see Alexandridis et al., 2021 for a review on natural pest control models). Existing models generally suffer from a lack of generality or from a lack of realism, which limit their applicability (Alexandridis et al., 2021). For instance, models based on local field studies (e.g., Jonsson et al., 2014) aim at best fitting the local context, making the results not transferable to other contexts (i.e., lack of generality). Besides, local field studies often focus on one or few aspects of the landscape (typically proportion of crop cover, non-crop cover or SNH), at one single scale (typically between 500 m radius and 1 km radius around sampling plots (e.g., Rusch et al., 2016)), whilst other components (including landscape composition and configuration, i.e., landscape complexity) at multiple scales (from few meters to few kilometres) have been shown to be important drivers of species richness and diversity (Martin et al., 2019; Sirami et al., 2019; Haan et al., 2020). In addition, correlative approaches generally neglect the importance of climatic variables and biotic interactions in shaping species communities (e.g., Rega et al., 2018). Mechanistic models aim at a highly realistic description of pest-natural enemy interactions, generally described using numerous ecological processes such as reproduction, mortality, and dispersal capacity of pests and their predators (Alexandridis et al., 2021). These models, therefore, require a high amount of data and a detailed understanding of the underlying processes and considered species, restricting their use for many species communities (Holland et al., 2020; Alexandridis et al., 2021), particularly because natural enemies show a great diversity of traits.

Finally, few ES modelling approaches are based on the use of ecological niche modelling (e.g., Civantos et al. (2012), Polce et al. (2013), Schulp et al. (2014b) and Nogué et al. (2016)). This approach can help to determine the habitat suitability of species based on bioclimatic variables, often neglected in other modelling approaches. However, existing ES models based on the ecological niche approach are typically developed at a coarse spatial scale (national or European scale) and do not consider important potential habitats at a finer scale such as hedgerows and flower strips, restricting their use to determine species and ES distribution at the landscape to local scales.

Combining the advantages of different approaches can improve our ability to predict ESP diversity and their associated ES: species distribution predictions through SDMs and correlative approaches to assess the importance of different landscape variables at different scales.

1.3.6 Using ES mapping and assessment outputs for decision-making processes

ES mapping and assessment methods are used to inform a variety of decisions in different contexts, including, among others, awareness-raising, communication, biodiversity conservation planning as well as ES accounting. The ES concept is increasingly integrated into environmental instruments, policies and practices (Grêt-Regamey et al., 2017). For instance, globally, the International Platform on Biodiversity and Ecosystem Services (IPBES) and the Convention on Biological Diversity (CBD) work towards raising awareness on biodiversity values and how to integrate these values in decision-making processes (UN, 1992; IPBES, 2019). Similarly, the Economics of Ecosystems and Biodiversity (TEEB) provided insights into the economic importance of ecosystems and their services and how to create market-based instruments to derive economic incentives for nature conservation, aiming at introducing the concept of ES in policy making (TEEB, 2010). In Europe, the EU Biodiversity Strategy to 2020 aimed under Target 2 to maintain and enhance ecosystems and their services by establishing green infrastructure and restoring at least 15 % of degraded ecosystems (European Commission, 2011). Besides, under Action 5 of the Strategy’s Target 2, ecosystems and their services shall be mapped and assessed. This initiated the MAES working group with one key task to develop an indicator framework for mapping and assessing ES (Maes et al., 2016). The general focus of MAES were the national ES assessments for each EU Member State and a European ecosystem assessment. Global and national ES assessments are essential for raising awareness and measuring progress toward national environmental conservation targets. ES mapping and assessment at the landscape to local scale are however often more appropriate for a wide range of land use planning, management and decision-making tasks.

In the EU, agricultural land use, management and practices are largely influenced by the CAP (Lefebvre et al., 2012). Originally targeting to increase agricultural production, the CAP has evolved and now includes environmental objectives, of which AES represent the most prominent available instruments (Hodge et al., 2015). AES measures provide incentives to compensate for the costs and income losses resulting from the adoption of nature-friendly practices. The role of AES in effectively halting biodiversity loss and enhancing environmental condition is still questioned, mainly due to unclear objectives and partly inadequate design (Batáry et al., 2015). ES mapping and assessment at the landscape and the local scales can support the design of context-specific and targeted AES measures. Thereby, it can help to increase their effectiveness in enhancing ES and biodiversity conservation.

1.3.7 Importance of spatial scale

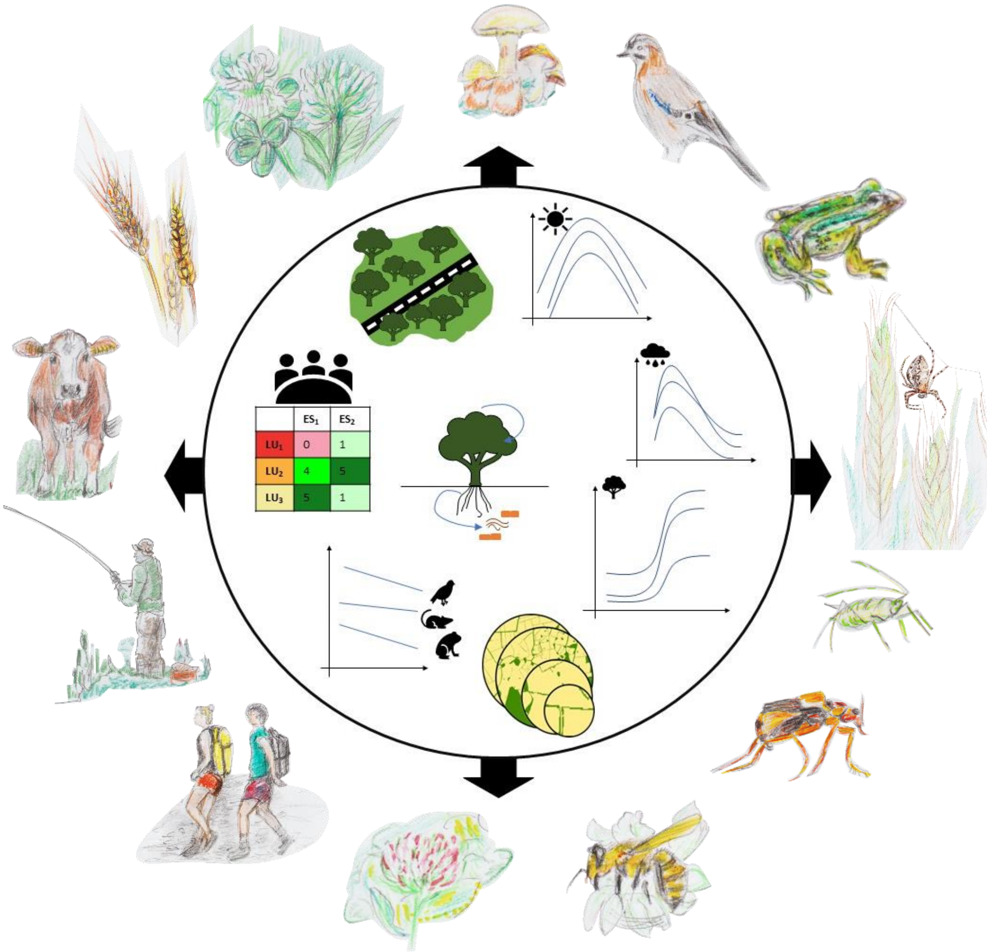
Despite the development of a broad array of ES mapping methodologies and assessment frameworks consecutive to increasing interests of policy and decision-makers (e.g., MA 2005, TEEB 2010, MAES and IPBES), there are still some important aspects of the ES concept that need to be improved, such as how to determine the appropriate spatial scale to assess ES and how this choice can affect the accuracy, precision and therefore reliability of the ES assessment (Raudsepp-Hearne and Peterson, 2016). Scale refers to the spatial or temporal dimension of an object or process and is characterised by extent and resolution. Both extent (dimension of the considered geographic area, coverage or temporal period) and resolution (unit of measurement or grain size) of ES mapping have an impact on the assessment’s results. For instance, carbon sequestration and climate regulation operate at highly different temporal and spatial scales. Carbon sequestration mechanisms are better explained at fine temporal and spatial scales (i.e., trees, one hectare of grassland, yearly) (Harmon, 2001), while climate regulation needs a global assessment, using longer temporal and broader spatial scales (West et al., 2011).

This thesis focused on the spatial dimension of scale. The spatial extent of ES assessments is generally determined by the purpose of the analysis. However, only few ecological processes are associated to a specific geographical extent; most of them occur across extents and are shaped by interactions between different ecosystems at various spatial (and temporal) scales (Bennett et al., 2009; Raudsepp-Hearne et al., 2010; Raudsepp-Hearne and Peterson, 2016). Similarly, the appropriate ES assessment resolution (or grain size) is generally ES-specific and depends on the underlying biophysical processes (Potschin and Haines-Young, 2011). Using different spatial extents and grain sizes can therefore lead to different conclusions for biodiversity trends (Rahbek, 2005; Steinbauer et al., 2012) and ES potentials (Grêt-Regamey et al., 2014). Provisioning ES can often be defined at a rather fine resolution: for instance, timber production can be assessed precisely and determined for single trees or forests (Grêt-Regamey et al., 2014). Similarly, crop production can be assessed for single-crop plants or fields (Kandziora et al., 2013b). Statistical data on provisioning ES capacity are nevertheless usually aggregated to coarser resolutions, typically corresponding to administrative borders, which usually do not correspond to ecological processes. Crop yield statistics are for instance often only available at the district resolution for the selected CSA (Kandziora et al., 2013b) and are therefore not usable for a finer spatial assessment. Regulation ES such as flood regulation capacity and cultural ES such as recreational ES are typically provided by processes that are better assessed at coarser spatial resolutions (Grêt-Regamey et al., 2014).

This study aimed at modelling ES in the CSA to test several ES mapping and assessment methods at a scale relevant to decision-making processes. The delimitation of the geographical extent was therefore determined by (district) administrative borders (see Figure 1). In practice, the resolution of the assessment is often determined by available data. The LULC resolution is of great importance as landscape patterns tend to disappear with increasing grain size. At coarser resolution, spatial information is aggregated and the landscape representation becomes more homogeneous, which can lead to a significant reduction of the variance in the ES assessment (Grêt-Regamey et al., 2014). Aggregated data or processes occurring at finer resolution also tend to increase data uncertainty and decrease the precision of the assessment. One of the research questions of Chapter 3 is to determine how spatial resolution influences the outputs when mapping ES at the local scale for different ES (analysing map structural similarity, i.e., correlation, variation and local mean (Jones et al., 2016)). Scale is also highly relevant for species distribution modelling: Macroecological studies generally have global scope and coarse resolution, whereas conservation planning requires detailed ecological understanding adapted to the local context. Besides, species distribution is determined by different processes at various scales (Pearson and Dawson, 2003; Pearson et al., 2004) and the appropriate assessment scale should be determined by the species characteristics and how each species interacts with the spatial arrangement of environmental predictors. For Chapters 4 and 5, a multiscale and hierarchical assessment was used to determine ESP occurrence and the associated ES potentials.

Chapter 2

Methods



2 Methods

The challenge of modelling and mapping ES lies in the variety of ES and the complexity of the different processes involved in the delivery of ES. This thesis follows the tiered approach to assess and map the potential supply of different ES in an agricultural landscape.

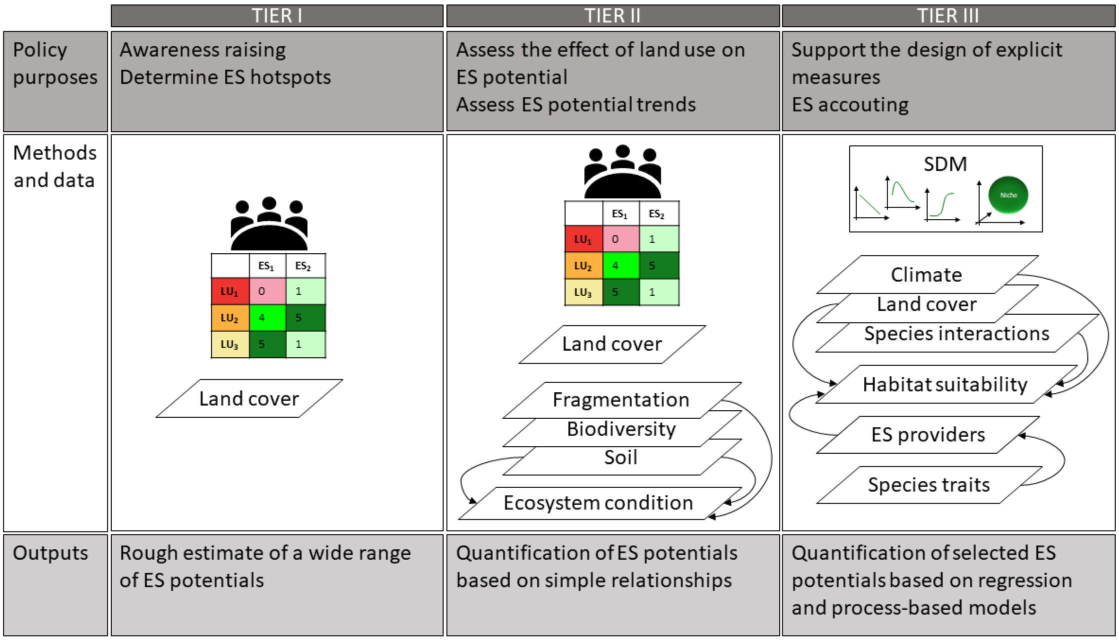
2.1 The tiered approach

The multitude of ES mapping and assessment methods can make the selection of an appropriate method tedious. The tiered approach presented by Grêt-Regamey et al. (2015) provides a conceptual framework on how to select an appropriate ES assessment method and how to combine different levels of complexity for an integrated approach. The method used should primarily be selected based on the purpose of the ES assessment, knowing the strengths and shortcomings of the selected method(s) and knowing that there is a general trade-off between feasibility and accuracy. Following this approach, depending on the research question, a tier 1 approach (such as simple assessments based on land use proxy) can be used to provide a rough overview of a phenomenon or for awareness-raising. In case process-understanding is needed, such as, for instance, to support local planning decisions, a tier 3 (e.g., correlative, process-based or socio-ecological system models) approach should be envisaged.

The simultaneous assessment of a broad range of ES is needed to understand the interrelations between services, potential trade-offs and synergies and how services are impacted by land use and land management but also climate change (Bennett et al., 2009). Particularly, the multi-functionality of ecosystems and landscapes can only be assessed when accounting for potential synergies and trade-offs between different ES. Because of the high complexity of ecosystems and processes involved in ES delivery, ES assessment generally implies the simplification of the studied systems. The specific context, the scale of application and the purpose of the ES assessment should determine the degree of simplification of the whole system. There is often a compromise between a holistic assessment of multiple services and the reliable assessment of each ES. For an assessment of a broad range of ES, tiers 2 and 3 are hardly conceivable. This is particularly the case for an ES assessment adapted to local context and characteristics, for which correlative, process-based and socio-ecological system models set in another region of the world cannot easily be applied without adjustments. In practice, mapping ecosystems and their services depends to a very large extent on the availability of spatially explicit data, expertise and time constraints.

The tiered approach can also be used to overcome the limitations of data availability, to build an integrated mapping and assessment using multiple approaches (Burkhard et al., 2018): for instance, combining a simple assessment based on LULC data as a basis and expert-based knowledge about ES and/or more complex and detailed information on ecosystem processes and functions whenever the ecological processes are better understood. Particularly, the complexity of agricultural landscapes and their interlinked social-ecological components call for integrated and flexible assessment approaches, addressing the various dynamics of ecosystems and ES at different scales. The use of a multi-tiered approach offers more flexibility than single assessment methods and is more adapted to reach multi-stakeholders, which then increases the possibility to integrate ES considerations in land use and management decision-making processes (Dunford et al., 2017). Moreover, using a multi-tiered approach has the potential to increase the feasibility of the assessment, the accuracy and the understandability of the results.

The different ES assessment methods applied in this thesis follow this tiered approach (Figure 4). At tier 1, ES mapping was performed using the Coordination of information on the environment (CORINE) Land Cover dataset and the matrix approach, i.e., an expert-based ES assessment method. At tier 2, information on ecosystem condition and a LULC database with a higher spatial resolution was integrated into the assessment. The third tier corresponds to more complex modelling methods, which were developed to assess pollination and natural pest control ES potentials in the CSA. The application of a tiered approach also reflects the varying level of knowledge about different ES and gives the opportunity to integrate a wide range of data with different qualities and the use of different mapping methods with various levels of complexity, increasing the strength of the overall ES assessment.

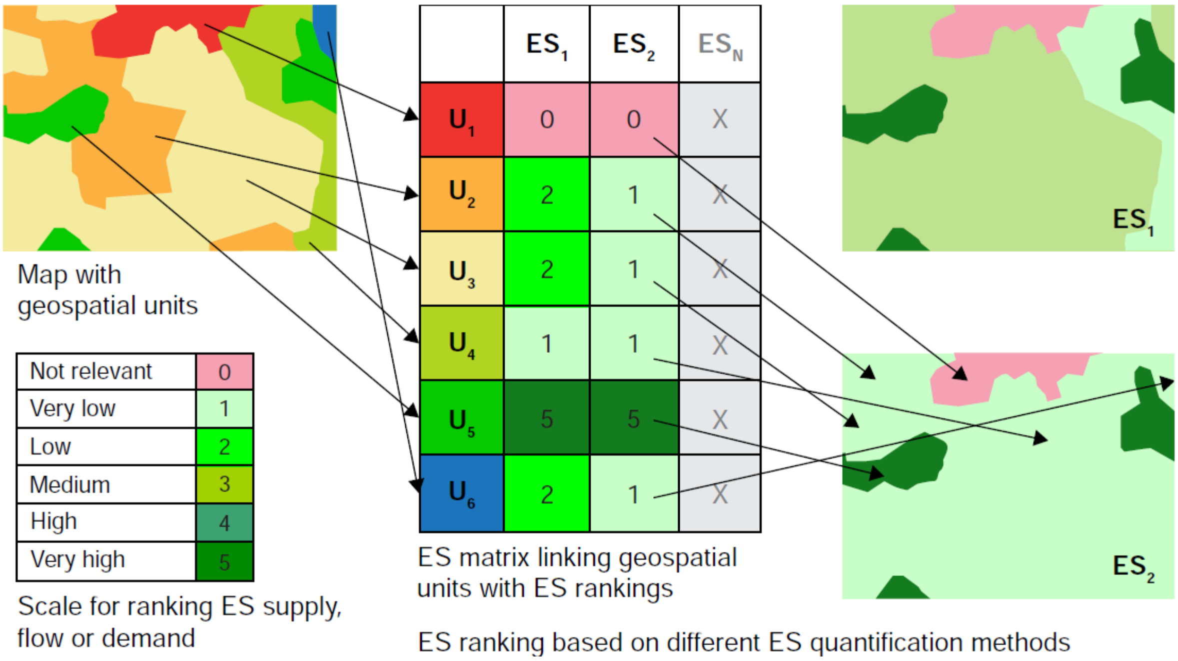


	TIER I	TIER II	TIER III
Policy purposes	Awareness raising Determine ES hotspots	Assess the effect of land use on ES potential Assess ES potential trends	Support the design of explicit measures ES accouting
Methods and data	Land cover	Land cover Fragmentation Biodiversity Soil Ecosystem condition	SDM Climate Land cover Species interactions Habitat suitability ES providers Species traits
Outputs	Rough estimate of a wide range of ES potentials	Quantification of ES potentials based on simple relationships	Quantification of selected ES potentials based on regression and process-based models

Figure 4: Illustration of the tiered approach for assessing and mapping ES, and the different methods presented in this thesis. The mapping outputs of the three tier levels can be used to address distinct decision-making issues. At tier 1, ES potentials were estimated using the ES matrix and land cover data. At tier 2, the assessment was completed by ecosystem condition indicators. At tier 3, more complex models were developed to assess pollination and natural pest control ES potentials in the case study area.

2.1.1 Tier 1

At tier 1, ES potentials were assessed using the expert-based ES matrix approach developed by Burkhard et al. (2009, 2014). The ES matrix approach is a flexible ES assessment method that links LULC classes, ecosystem types or other appropriate geospatial units to ES values (potential, supply, flow or demand) (Burkhard et al., 2009; 2014). The approach consists of a look-up table with the ES as columns (or rows) and the geospatial units (generally LULC classes) as rows (or columns) (see Figure 5). In a tier 1 setting, a pool of appropriate experts is then asked to value or score the ability of each geospatial unit to provide each ES, on a scale of 0 (no relevant potential) to 5 (high potential). This expert-based method has been widely used, with various spatial and temporal scales as well as mapping purposes (Campagne et al., 2020). Expert-scoring tools have the advantage to provide a comparably fast and efficient way to evaluate ES (potential, supply, flow or demand) and are particularly useful in data-scarce environments (Jacobs et al., 2015). The main critics are: they have a restricted capacity to cover ES spatial variability, because of the lack of mechanistic links between LULC and the delivery of ES and a potential high variability in the results depending on the pool of selected experts (Hou et al., 2013; Jacobs et al., 2015). To overcome these shortcomings, the LULC- and expert-based ES matrix approach can be enhanced by more detailed geospatial data and the use of suitable indicators and methods for ES quantification.



	ES_1	ES_2	ES_N
U_1	0	0	X
U_2	2	1	X
U_3	2	1	X
U_4	1	1	X
U_5	5	5	X
U_6	2	1	X

Not relevant	0
Very low	1
Low	2
Medium	3
High	4
Very high	5

Figure 5: Principle of the ES matrix approach, illustrated in a fictive study area (from Burkhard and Maes (2017)). Each land cover type or geospatial unit (top-left corner) is given a value corresponding to its capacity to deliver specific ES according to a panel of experts (table in the middle). The resulting ES matrix can be then used to map the different ES capacities of the study areas (maps on the right side).

2.1.2 Tier 2

At tier 2, the ES matrix approach was combined with ecosystem condition indicators, based on the assumption that the capacity of an ecosystem to deliver ES is determined by its condition (i.e., its physical, chemical and biological quality). The condition of an ecosystem is determined by its biotic and abiotic characteristics (Maes et al., 2018). Identifying appropriate variables that define and capture the essential characteristics of an ecosystem is still challenging, with no ready-to-use data (Hein et al., 2020; Czúcz et al., 2021). The condition of an ecosystem is therefore generally measured using indicators (Rendon et al., 2019). For this thesis, an ecosystem condition index was developed based on the indicator list provided by the MAES working group. Key features for good indicators are: they are quantifiable, spatially-explicit and sensitive to changes regarding ecosystem health and biodiversity policy targets (Maes et al., 2018). The major issue was to find quantifiable, with the required resolution and non-redundant data to build quantified indicators as recommended by the 5th MAES report. Among the multiple indicators listed in the 5th MAES report, three indicators were selected to this end: Landscape Fragmentation Index, the Red List Index (RLI) for ecosystems and Soil Organic Carbon (SOC).

The Landscape Fragmentation Index measures the extent to which the ecosystems that compose the landscape have been transformed into smaller, isolated and unconnected ecosystems due to the construction of transport networks, built-up areas and natural barriers. The RLI measures the status and trends in the overall extinction risk of species living in each ecosystem presents in the CSA and is a measure of the status of the different ecosystems in terms of biodiversity. The SOC is an indicator of the soil quality and of the below-ground microorganism activity. The indicators were combined into an ecosystem condition index and aggregated with the ES matrix outputs to map the ES potential of the CSA.

2.1.3 Tier 3

At tier 3, niche-based models were developed to predict the presence of ESPs and thereby the potential delivery of the related ES. The two model frameworks were inspired by the Ecological Potential Function (EPF) presented by Kremen et al. (2007) to model ES from mobile species (originally pollination ES from wild bees) and further developed by Jonsson et al. (2014) to model natural enemies and natural pest control ES. The EPF is a tool for framing current knowledge on how different ecological variables and processes are involved in the ES production (Bruins et al., 2017). It helps to express ecological processes through quantitative, qualitative expressions or models explaining the relationships between the geographical context, landscape characteristics, land use and management, biotic interactions, ESPs and the provision of ES.

The presence of one specific ESP or species at a specific location is primarily determined by the physiological characteristics of this species and if this location has suitable bioclimatic conditions, mainly determined by temperature and precipitation at specific times of the year or the presence of a particular resource (Pearson and Dawson, 2003; Guisan and Thuiller, 2005; Soberón, 2007). At the local scale and within its bioclimatic niche, the ecological niche of a species is determined by specific biotic resources and biotic interactions. For instance, the presence of wild bees depends on the proximity of specific habitats, providing foraging and nesting resources (Lonsdorf et al., 2009; Kennedy et al., 2013; Westrich, 2018). The amount and spatial configuration of natural and semi-natural habitats (i.e., landscape complexity) are determinant to sustain natural enemy communities (Martin et al., 2019; Haan et al., 2020). The spatial configuration of the different landscape elements is determinant as ESPs often have limited mobility. Wild bees can fly between foraging sites and nesting sites, with typical and maximal flying distances correlated with their body size (Greenleaf et al., 2007). This flying distance determines the capacity of a bee to pollinate crop fields, as crop fields are typically not suitable nesting sites. Many wild bee species are specialists and pollination-dependent crops are not pollinated by every species. The resulting wild bee species pool determines the pollination ES potential of a specific area.

Similarly, natural pest control ES potential is often determined by the capacity of natural enemies to colonise crop fields. The occurrence of natural enemies in crop fields frequently depends on the proximity of overwintering sites or shelters. Besides, the resulting ES potential depends on the feeding habits of each species. Some natural enemies are specialists and will only feed on the targeted pests, whereas other natural enemies are generalists and will feed on pests as well as on other natural enemies. Intraguild predation can potentially disrupt natural pest control potential (Martin et al., 2013; Jonsson et al., 2017). Behavioural interactions and apparent competition between natural enemy species can also negatively impact the final natural pest control potential in the fields (Straub et al., 2008; Letourneau et al., 2009). Natural enemies can also show positive interactions linked to niche partitioning or redundancy. Therefore, the relationships among natural enemy species should also be accounted for when modelling natural pest control. The resulting community determines the natural pest control ES potential of a specific area.

2.2 Ecological niche modelling

The niche-based models were built using species distribution models (SDMs). SDMs are statistical methods that derive species distribution patterns from observations of species occurrences and environmental variables. They are typically used to determine the main environmental drivers of a species, to assess the relationships between species and their environment, aiming at understanding and making species distribution pattern predictions (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). SDMs are also known as, among others, bioclimatic models or envelopes, habitat suitability modelling and ecological niche models. They have many application fields, e.g., to support the management of threatened or invasive species and to predict the impacts of climate or land use changes on the geographical range of a particular species (Guisan and Thuiller, 2005). SDMs are particularly adapted to assess the habitat suitability of an area for a specific species and can assist the design of biodiversity conservation measures (Kadoya et al., 2009; Sousa-Silva et al., 2014; Uden et al., 2015). SDMs have already been used to assess ES, particularly for wild food provision (Schulp et al., 2014b), pollination (Polce et al., 2013; Nogué et al., 2016) and natural pest control (Civantos et al., 2012).

SDMs derive from the niche concept of Hutchinson (1957), which is defined as the multidimensional environmental space with suitable conditions for a defined species, i.e., which allows population growth. The theoretical assumptions behind SDMs are the following: 1) there is an equilibrium or pseudo-equilibrium between species and their environment, 2) the main environmental predictors are being considered at the relevant resolution, and 3) species observations used to fit the models are suitable and contain no severe bias (Elith and Leathwick, 2009). Under these assumptions, SDMs can be used to predict species distribution in areas that are not sampled or under different scenarios of future environmental conditions.

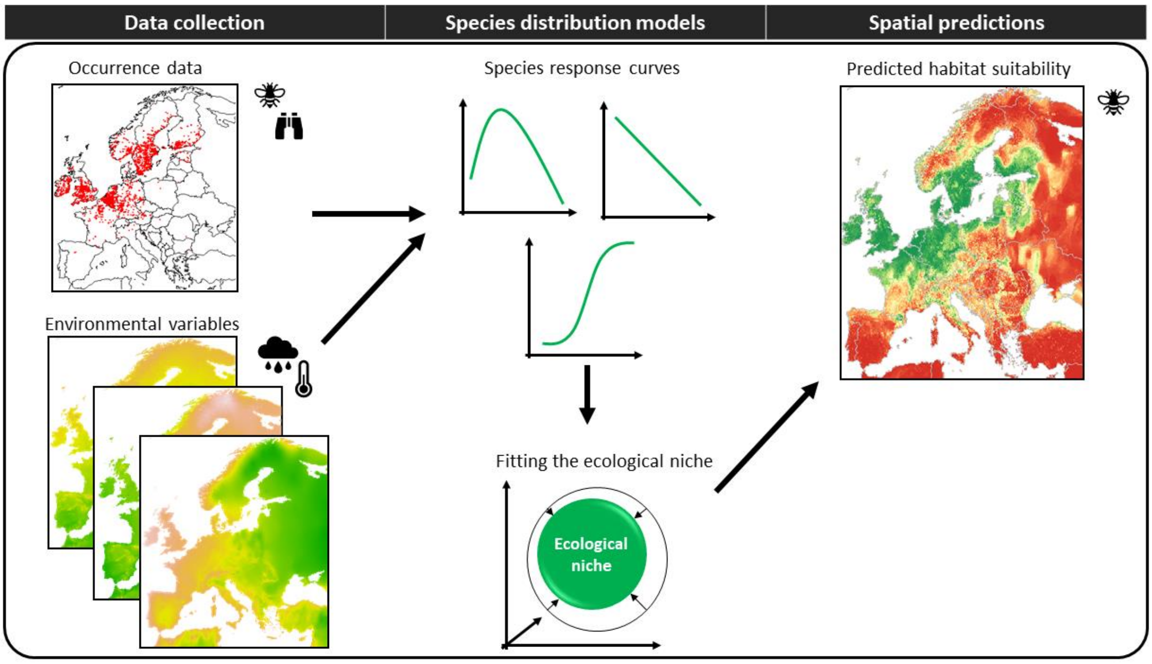


Figure 6: Principle of species distribution modelling, illustrated on a study area representing Europe (adapted from Guisan et al. (2017)).

SDMs minimally require species occurrence data, a set of environmental predictors representing the environmental space of the focal species and one or several modelling methods (Figure 6). One major challenge is to assemble a suitable species occurrence dataset. These data can be presence-only, presence-absence or abundance data. They can be provided by recording data in the field using a sampling approach specifically designed for the purpose of the study or extracting data from biodiversity databases such as GBIF (Global Biodiversity Information Facility[2]), CABI (Centre for Agriculture and Bioscience International[3]), IUCN's red List (International Union for the Conservation of Nature[4]) and Map of Life[5]. Study-specific field sampling usually provides high-quality data and leads therefore to a better model accuracy (Amano et al., 2016). Field sampling is, however, time and energy intensive and only feasible for a limited number of species, time and geographic extents. Besides, models trained at small geographical scales are usually unable to capture the complete niche of species as the chances of missing important predictors are high, which can lead to inaccurate predictions (Titeux et al., 2017). Models trained at local scales are generally not adapted to assess the impact of climate change on species distributions and are not easily transferable to other regions with different bioclimatic contexts.

Data from large biodiversity databases consist of accumulated collected data for different field surveys, historical museum collections or citizen science. Biodiversity databases have clear advantages over in-field recorded data: they provide an unrivalled amount of data, covering a long period and a large spatial extent. However, as these data come from different sources, they potentially contain numerous issues and biases: mainly uncertainty in data quality (for instance, species misidentification or geographical mislocation) and a lack of sampling design and therefore potentially a biased (incomplete and uneven) spatial coverage of the species (Zizka et al., 2020). These issues can be partly addressed by carefully cleaning the extracted data and resampling the data to reduce spatial biases inherent to large biodiversity datasets (Zizka et al., 2020). There is, however, an inherent trade-off between keeping a high amount of (or even sufficient) species occurrence data and dealing with spatial biases. Moreover, spatial biases of occurrence data can be due to the uneven distribution of the species, for example, a species with a restricted niche. As spatial biases and species distribution can be confounded, dealing with not evenly distributed data is an issue with no perfect solution yet.

Species data are usually in the form of presence-only records as absence of species is not easily recordable. This issue is exacerbated for mobile and/or small species, for which recording true absence is often unfeasible, even with dedicated field sampling (Mackenzie and Royle, 2005). As SDMs require presence-absence data, one way to deal with presence-only data is to inform the model with background data or pseudo-absences (i.e., inferred absence data based on the information available about the locations where the target species is present). Several methods have been presented by Barbet-Massin et al. (2012) and Phillips et al. (2009). In Chapters 4 and 5, the target background method was used, which consists of restricting background areas to sampled areas where the targeted species was not found.

The selection of environmental predictors is a determinant step in the modelling process. Environmental predictors need to be as proximal as possible, i.e., physiologically and ecologically

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[2] http://www.gbif.org

[3] https://www.cabi.org

[4] https://www.iucn.org

[5] https://mol.org

meaningful variables for the modelled species and thereby the main drivers of the species' range (Austin, 2007). One issue is that many environmental variables are correlated with each other and therefore a correlation between species patterns and one factor does not necessarily imply a causal relationship (Dormann et al., 2013). For instance, most species show clear elevation patterns, whereas the direct physiological effect of elevation on species distribution is debatable (Körner, 2007). Instead, some proximal variables and particularly temperature and precipitation are strongly (locally) correlated with elevation, generally explaining the elevation patterns. As correlation between predictors can be an issue for most statistical techniques (also called multicollinearity issues), a necessary preliminary step is to assess and reduce multicollinearity between predictors (Dormann et al., 2013). Moreover, most statistical methods require a minimal number of observations for each variable considered (Pearce and Ferrier, 2000; Stockwell and Peterson, 2002). A high number of environmental variables can become an issue if only a low number of observations is available. Another hurdle is that predictors with sufficient quality and accuracy are not always available at the desired scale or not in a spatially explicit form. The spatial resolution of predictors is critical as using a too coarse resolution can lead to spurious correlations and undetected spatial patterns (Guisan and Thuiller, 2005). There are several approaches to reduce the number of variables considered, among them, assessing the correlation between the variables using Pearson or Spearman correlations, using the principal component analysis (PCA) or the Akaike information criterion (AIC or AICc, the Akaike's information criterion corrected for small sample-size) (Dormann et al., 2013). PCA is a popular approach for dimension reduction, i.e., to select a low-dimensional set of variables from a larger set. Basically, PCA are used to determine the directions of the data along which the observations vary the most and to select the variables (or combinations of variables) that explain most of this variation (Jolliffe and Cadima, 2016). The AIC is a stepwise variable selection procedure (Akaike, 1973; Harrell et al., 1984). AIC has two components: the log-likelihood, which measures how the model fits the observed response and bias correction factor, which increases with the number of parameters included in the model. Thus, AIC helps to identify the most parsimonious model from among the candidate set of predictors (Johnson and Omland, 2004). In Chapter 4, PCA and Pearson correlation were used to reduce the dimension of the set of explaining variables. In Chapter 5, variable importance was assessed using AIC and Spearman correlation.

The relationship between species occurrence and environmental predictors is inferred using statistical modelling techniques. SDMs' modelling techniques vary from (simple) regression-based approaches to machine learning techniques (Elith and Franklin, 2013): among them, generalized linear models (GLM, Nelder and Wedderburn (1972)), generalized additive models (GAM, Hastie and Tibshirani (1986)), artificial neural networks (ANN, Ripley (1996)), linear and flexible discriminant analysis (LDA, FDA, Hastie et al. (2009)), boosted regression trees (BRT, Friedman (2001) and Elith et al. (2008)), Random Forest (RF, Breiman (2001)) and maximum entropy (MAXENT, Phillips et al. (2006)). The choice of modelling algorithm can affect the model's predictive performance (see Elith et al. (2006) for a comparison). As no single method has consistently better performances than others (Elith et al., 2006; Pearson et al., 2006), current standards advise developing ensemble models, i.e., to combine the outputs from different modelling techniques (IPBES, 2016; Araújo et al., 2019; Zurell et al., 2020a). Here, ensemble models were built based on three different algorithms: GLM, FDA and RF in Chapter 4 and GLM, RF and BRT in Chapter 5.

GLMs are extensions of regression models and allow the response variable to follow other distributions than the normal distribution (contrary to linear regressions). In GLMs, the predictors are linked to the mean of the response variable through a link function, used to transform the response to linearity. If the response is not a linear function of predictors, the predictors can be transformed (typically into polynomial regressions). Commonly used distributions are: normal, Poisson, binomial (typically used for presence-absence data), gamma and negative binomial. GLMs tend to retrieve models with lower performance compared to more sophisticated ones but have the advantage of being relatively simple to describe, understand and interpret (Elith and Graham 2009). FDA is a classification model equivalent to multi-response, non-linear regression models, using optimal scorings and multiple adaptive regression splines to generate the discriminant surface between classes (Hastie et al., 1994). This algorithm does not make any assumption about the predictors, can deal with non-linear combinations of predictors and works particularly well with a high number of predictors. RF is a widely used bagging approach, which combines randomized decision trees and aggregates predictions by averaging them (Breiman, 2001). BRT is a boosting procedure that iteratively fits simple trees to the training data and then fits each new tree to the residuals of the trees previously developed. RF and BRT are so-called machine learning methods.

Regression-based methods are less flexible than other statistical approaches and tend to underfit observed complex occurrence-environment relationships (Merow et al., 2014). As a result, they generally have a high bias. Overly complex models, on the contrary, tend to overfit the data and have higher variance (Merow et al., 2014) and can inadvertently ascribe patterns to noise observed in the data. This phenomenon is commonly known as the variance-bias trade-off: simple models tend to have low variance and high bias, whereas complex models tend to have high variance and low bias. Machine-learning methods usually outperform regression-based methods in variable selection and predictive performance, because they allow to automatically detect and fit interactions between predictors (Elith et al., 2006). RF and BRT also have the advantage to have inherent procedures reducing the variance of the model predictions, mainly committee averaging (Breiman, 2001) and stochastic gradient boosting (Elith et al., 2008). Model complexity should nevertheless be constrained through model fitting, data resampling and algorithm selection (see Merow et al. (2014) for guidelines on how to design SDMs with appropriate levels of complexity). Here, model complexity was constrained by carefully selecting variables before modelling, minimizing multicollinearity, checking if data sampling was sufficient, using cross-validation assessments and combining simple with more complex algorithms to produce the final models.

2.3 Measuring model fit

Model fit (or performance assessment) can be assessed in terms of explanatory power, i.e., how well the model explains the patterns observed in the data that were used to fit the model, or predictive performance (or generality), i.e., how well the model predicts data not used to fit the model. SDMs' predictive performance is evaluated by comparing model predictions (the probability of the presence of a species) to observations (presence-absence data) using independent data (i.e., different data than the dataset used to train the model) (Guisan and Thuiller, 2005; Guisan et al., 2017; Araújo et al., 2019; Zurell et al., 2020b). This is usually done through data partitioning, e.g., k-fold cross-validation, where the whole dataset is randomly divided into k groups and using one group for validation and the remaining k-1 groups as training set or, less frequently, using another dataset (from another sampling event for instance). Assessing the strengths and weaknesses of a particular model generally implies the use of different metrics. Model performance can be evaluated in terms of accuracy, discrimination, calibration and precision (Figure 7, Norberg et al. (2019)). Accuracy measures the degree of proximity between the predicted and the true value (Figure 7a). Depending on the data and algorithm used, accuracy can be measured using the root mean squared error (RMSE), the coefficient of determination (R^2) or the percentage of deviance explained. Model performance can also be evaluated according to its discrimination capacity, i.e., its capacity to discriminate presences from absences (or occupied from unoccupied sites) (Figure 7b).

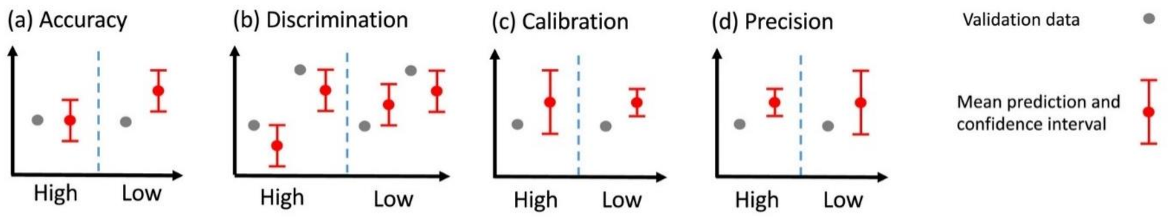

Figure 7: Accuracy, discrimination, calibration and precision are four aspects of model performance. In each panel, the grey dot shows the true value and the red dot with error bar shows the mean model prediction and its confidence interval (from Norberg et al. (2019)).

Several metrics have been developed to measure discrimination, the most used being the area under the curve of the receiver operating characteristics (AUC/ROC, Fiedling and Bell, 1997) and the true skill statistics (TSS, Allouche et al. (2006)). AUC/ROC and TSS are both threshold-dependent metrics: comparing continuous predictions to presence-absence data requires converting the continuous prediction to a binary scale. This is done by choosing a threshold value above which the predictions are considered as presence. Then the sensitivity (proportion of true positives correctly identified) and the specificity (proportion of true negatives correctly identified) of the models are calculated. The AUC/ROC metrics are measured using a curve representing all values of sensitivity against the corresponding 1 – specificity value and then calculating the area under this curve (or surface). AUC/ROC values vary between 0 (no discrimination power) to 1 (perfect discrimination). The TSS is calculated using the following formula: TSS = sensitivity + specificity - 1 and relies on the selection of an appropriate threshold (Liu et al., 2005; Liu et al., 2013). The TSS ranges from – 1 to + 1, where + 1 indicates a perfect agreement and 0 or less a performance no better than random (Allouche et al., 2006). These methods, and particularly AUC/ROC, should not be used as standalone evaluation metrics when applied to presence-pseudo-absences (Phillips and Elith, 2010). However, they are still powerful metrics to compare models built with similar data and design (Zurell et al., 2020a). Calibration measures the distance between the test dataset and the predictions, i.e., the statistical consistency between distributional predictions and the true values. Measures of calibration include calibration plots, which compare the proportion of observed presence/absence to predicted probability classes, such as the presence-only calibration plot (Phillips and Elith, 2010) and the Boyce index (Boyce et al., 2002) (Figure 7c). Precision measures the width of the predictive distribution and can be evaluated through confidence intervals and standard errors (Figure 7d). Finally, model predictions can be checked for plausibility by looking at the shape of the response of the fitted species-environment relationships and by comparing the predicted distribution to existing maps.

Not all performance metrics can be used for all data types nor modelling frameworks. For instance, the use of presence-data, presence-absence data, continuous data or count data will imply different model fit assessments (Guisan et al., 2017). In Chapters 4 and 5, AUC/ROC, TSS and the Boyce index were used to compare the results of different modelling algorithms and to assess the overall model performance. The predictive performance of the final models developed in Chapters 4 and 5 was also evaluated using in-field collected data, using accuracy measures (R^2 or explained deviance). Plausibility was also assessed by looking at the shape of the response of the fitted species-environment relationships and looking at existing distribution maps when available.

2.4 Hierarchical species distribution modelling

Species distribution is determined by many factors and processes operating at different scales. The relative importance of multiple factors to explain observed species distributions depends on the scale of the assessment and many patterns will only emerge at a specific scale (Soberón, 2007). At the global scale, the species' fundamental niche is delimited by its physiological characteristics, abiotic constraints and dispersal limitations. Resource availability and biotic interactions shape the species distribution at the local scale. These drivers together influence and determine the species' realized niche (i.e., the observed spatial distribution of the species). Figure 8 illustrates the hierarchical approach for modelling species occurrence used in Chapters 4 and 5. On one hand, models that are only trained at coarser spatial resolution and global or regional scales usually overpredict species distributions as they do not account for local ecological processes. On the other hand, models only trained at smaller spatial resolution are unable to accurately determine the whole ecological niche of a species. One approach to account for different ecological processes occurring at different scales is to apply a hierarchical modelling approach (Pearson et al., 2004; Mateo et al., 2019a; 2019b). This approach has been demonstrated to be more reliable than single-scale SDMs and has the advantage to provide applicable and ecological meaningful predictions to guide (local) conservation measures (Milbau et al., 2009; Hattab et al., 2014; Petitpierre et al., 2016; Fournier et al., 2017; Mateo et al., 2019a; 2019b; Bellamy et al., 2020).

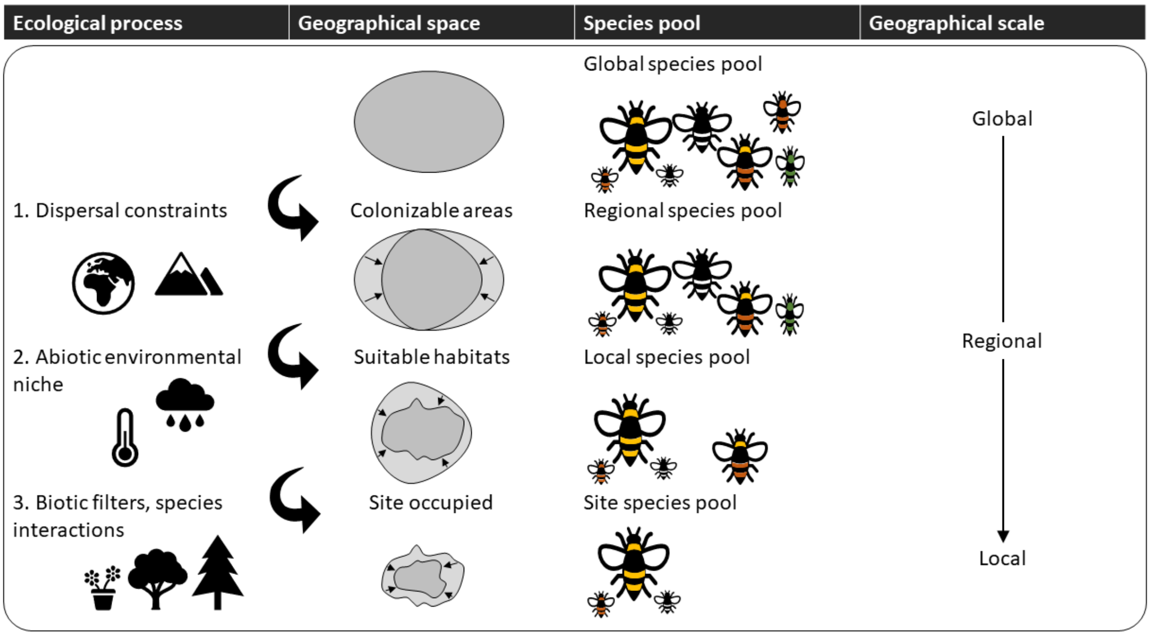

Figure 8: Hierarchical view of the three main influences determining species occurrence at a given site (adapted from Guisan et al. 2017).

Many techniques, from simple to more complicated, have been used to build hierarchical SDMs. Also, simple methods have been shown to perform well (Fournier et al., 2017; Mateo et al., 2019b; Mateo et al., 2019a; Bellamy et al., 2020). Building on Mateo et al. (2019b), the hierarchical models of Chapters 4 and 5 were built using a rather simple method: by combining models from different scales and multiplying the prediction values of the models produced at different scales.

2.5 Influence of landscape complexity on ecosystem services potential

Arthropods represent an extremely diverse group and tend to have complex life cycles, composed of several stages (generally eggs, larvae, pupae and adults). They have different strategies for surviving winter, including overwintering, migrating and hibernating. They also have different feeding and foraging habits (generalists or specialists, ground-dwelling or foliage-dwelling) and different mobility capacities. Arthropods generally depend on the presence of SNH, which provide overwintering habitats, nesting sites, shelters and alternative resources (Roschewitz et al., 2005; Thies et al., 2005; Holland et al., 2016; Westrich, 2018; Tamburini et al., 2020). Their mobility is generally determined by their size, which in turn determines at which scale they experience their environment and the extent to which they can deliver ES. Heterogeneous landscapes should facilitate exchanges between SNH and crops and therefore benefit most of the species (Hendrickx et al., 2007; Holzschuh et al., 2010; Fahrig et al., 2011; Tscharntke et al., 2012b; Blitzer et al., 2012; Haddad et al., 2017; Martin et al., 2019; Haan et al., 2020).

In Chapters 4 and 5, two different approaches are used to assess and account for the impact of landscape complexity on the ESP communities. For wild bees, following Londsdorf's model (2009), a habitat filter was applied and each bee species was directly linked to its specific habitat(s). For natural enemy species, the meta-analysis from Martin et al. (2019) was used to assess and predict the effect of landscape complexity on the presence of each species, as this showed to be the main driver of species occurrence at the landscape scale (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Holland et al., 2017; Veres et al., 2013; Martin et al., 2019; Kleijn et al., 2019; Haan et al., 2020).

2.6 The role of biotic interactions for ecosystem services potential

Species rarely occur alone, instead, they are generally organized in communities and biotic interactions can play an important role in species distribution (van der Putten et al., 2010; Wisz et al., 2013). For instance, competition may restrict niches in otherwise environmentally suitable areas (Götzenberger et al., 2012) or the presence of other species or taxa can be an essential resource for the modelled species (Planillo et al., 2021). Biotic interactions can also be a determinant factor for the distribution of mutualistic species (Gutiérrez et al., 2005; Heikkinen et al., 2007). Complex biotic interactions have already been described in natural enemy communities, such as inter- and intraguild predations (Martin et al., 2013; Jonsson et al., 2017; Snyder, 2019), as well as mutualistic or facilitating relationships (Schmidt et al., 2003).

Joint species distribution models (jSDMs) have been developed to account for biotic interactions in SDMs and to disentangle environmental and biotic influence on species occurrence (Pollock et al., 2014; Warton et al., 2015; Hui, 2016; Ovaskainen et al., 2017; Wilkinson et al., 2021). jSDMs are Bayesian statistical models and can be considered as extensions of GLMs. jSDMs use latent variables (or residual correlations) between species occurrences after accounting for their response to environmental conditions to assess biotic interactions (Wilkinson et al., 2019). Residual correlations of species occurrence capture patterns in the co-occurrence of species that cannot be attributed to the considered environmental predictors. Such co-occurrence can be indicative of biotic interactions such as competition or facilitation (Pollock et al., 2014; Warton et al., 2015). In Chapter 5, how the presence of specific natural enemy species can affect the overall natural pest control potential of an area was assessed using the jSDM approach developed by Ovaskainen et al. (2017), called HMSC (for Hierarchical Modelling of Species Communities). This method was selected because it shows good performance and a shorter running time compared to other models (see Wilkinson et al. (2019) for a comparison of the different jSDM approaches) and because it allows modelling nested sampling design. HMSC is a hierarchical multivariate generalized linear mixed model fitted with Bayesian inference (for conceptual and mathematical details see Ovaskainen et al. (2017)). jSDMs were used in Chapter 5 to determine which arthropod species are effective predators of aphids and which/if interspecific interactions potentially can decrease the capacity of natural enemy communities to provide pest control services. As wild bee communities are probably not primarily determined by biotic interactions (Westrich, 2018), the community was determined simply using stacked SDMs in Chapter 4.

Chapter 3

Refining the tiered approach for mapping and assessing ecosystem services at the local scale: A case study in a rural landscape in Northern Germany

Perennes, M., Campagne, C. S., Müller, F., Roche, P. and Burkhard, B.
Land (2020), 9, 348

In this Chapter, ES potential and the landscape multifunctionality of the case study area were assessed, with the following central question: how do spatial resolution and the inclusion of information on ecosystem condition influence the ES assessment at the local scale?

land

Article

Refining the Tiered Approach for Mapping and Assessing Ecosystem Services at the Local Scale: A Case Study in a Rural Landscape in Northern Germany

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Received: 17 August 2020; Accepted: 22 September 2020; Published: 24 September 2020

Abstract: Spatially explicit assessments of ecosystem services (ES) potentials are a key component in supporting a sustainable land use management. The ES matrix method is a commonly used approach as it allows for a comparably fast, comprehensible and accessible ES assessment. As it is often based on land use/land cover data (LULC) with no spatial variability, a main critique is that the results fail to assess spatial variability at landscape levels, which limits the reliability of the outputs for spatial planning applications. By using the case study area of Bornhöved in northern Germany, we analyzed three assessment methods that combine expert judgments, LULC data with different resolutions and ecosystem condition indicators, in order to find the required resolution and data for ES assessment and mapping at a local scale. To quantify map discrepancies, we used the structural similarity index (SSIM) and analyzed the differences in local mean, variance and covariance between the maps. We found that using different spatial resolutions led to a relatively small difference in the outcomes, in which regulation and maintenance services are more affected than the other services categories. For most regulation, maintenance and cultural ES, our results indicate that assessments based only on LULC proxies are not suitable for a local quantitative assessment of ES, as they cannot sufficiently cover the spatial heterogeneity of ES capacities that arise from different ecosystem conditions.

Keywords: ES matrix assessment; ecosystem condition indicators; statistical map comparison

1. Introduction

Ecosystem services (ES) are defined as the benefits that ecosystems provide in support of human well-being [1]. ES assessment and mapping have become popular approaches for sustainable planning and management of natural resources, for instance in EU policies [2,3]. ES approaches can also help to preserve and enhance landscape multifunctionality [4,5]. Different methodologies have been developed for assessing and mapping ES (for a review see [5]), that can be classified in three different tiers [6]. The appropriate ES assessment methods or tier depend on the purpose of the assessment (e.g., research or policy questions). The first tier includes simple methods that establishes binary links between LULC, and ES scores obtained from previous studies or based expert knowledge approaches: experts are asked to rank LULC classes according to the potential of these classes to supply an ES. The second tier includes the methodologies that rely on information about relationships between indicators and ES, mainly obtained from literature. Methodologies of the third tier extrapolate ES estimates of primary data and quantitative regression model approaches. Depending on the research question, a Tier 1 approach can be used to provide a rough overview of a phenomenon or for awareness raising. However, a Tier 3 is needed to support local planning decisions. For an assessment of multiple ES, the Tiers 2 and 3 are hardly applicable, as higher Tier approaches are usually more data-intensive. This is particularly the case for an ES assessment adapted to local characteristics, for which regressions and socio-ecological system models set in another region of the world cannot be applied without adjustments.

One commonly used method for ES potential assessment is the ES matrix approach by Burkhard et al. [7–9] (Tier 1 to 2), in which ES "potential" was defined as the capacity of an ecosystem to deliver ES based on ecological properties and functions, independent of an actual demand for these services [10]. With the ES matrix approach, the ES potential of a landscape can be estimated based on various ES quantification approaches [11]. Expert scorings of ES potentials—in combination with geospatial units such as LULC types—are one of the most commonly used approaches in ES matrix applications [12,13]. Thus, LULC types are used as basic units for the capacity of a given area to supply ES, under the assumption that there are explicit causal relationships between LULC types and the delivery of ES. The ES matrix approach is a tool for decision support in sustainable resource management as it is highly adaptable to various socio-ecological system settings, easily accessible and enables an efficient and relatively fast comprehensible assessment [14]. This method allows the spatial modelling and mapping of multiple ES at different scales and reflects the multifunctionality of landscapes, i.e., the capacity of different ecosystem types within a landscape to provide a broad range of ES.

ES matrix models are often used along with CORINE land cover data (CLC) [12,15], as this dataset is freely accessible, is regularly updated by the European Environmental Agency and covers all EU member states. A landscape analysis based on LULC may be adequate for some ES and ecosystems, e.g., heavily human-managed ecosystems dedicated to the production of one or a few services [16]. This is particularly the case for biomass production in forests or food production in croplands, as these ecosystems mainly rely on human inputs and less on natural processes (via e.g., the selection of plant and animal species, the use of fertilisers and pesticides, irrigation water input, energy and labor use). However, the CORINE dataset is quite coarse (usually 25 ha minimum mapping unit (MMU)) and may not be suitable for local-scale assessments, as semi-natural elements, small habitats but also transport networks are not well identified in this dataset. Moreover, the assessment of non-target ES or non-marketed ES such as many regulation services is generally more challenging than the valuation of provisioning ES [10]: the supply of most of the regulation ES depends on several ecosystem structures and processes, which often occur over larger spatial and temporal scales. There is also a considerable lack of knowledge on the mechanisms of the processes underlying the supply of these services [17–19]. Moreover, regulation and maintenance ES supply usually varies considerably within one land cover type [14,20–22] and depends on additional ecosystem conditions such as vegetation cover and biodiversity, soil types and texture or water availability [23,24]. Cultural ES potentials usually also depend on a complex mix of biophysical and anthropogenic landscape characteristics such as topography, presence of species and accessibility. Thus, regulation and maintenance and cultural ES tend to rely on additional ecological and management features and may not be appropriately assessed solely based on LULC proxies.

This summarizes two of the main critiques in regard to LULC-based approaches. First, CLC data are too coarse for an accurate ES assessment supporting local decision-making processes [22,25,26]. Second, ES assessments cannot be done simply based on LULC data as the assessment tends to be not accurate enough to catch spatial variability within individual land cover classes and between landscapes

[13,14,22]. Accuracy is defined as how well a model estimates the true distribution of a phenomenon [16]. The accuracy of a model partly depends on its capacity to capture ES heterogeneity, i.e., the "degree of spatial variation within the spatial distribution of an ES", so on how ES potential relies on ecosystem conditions [16]. The application of a suitable method for modelling heterogeneous ES potentially increases the accuracy of the outputs, but it usually requires more effort and increases information costs. Furthermore, different research questions or mapping issues require different resolutions.

This paper explores how different levels of spatial resolution and ES matrix assessment complexity impact the outcomes of a local-scale analysis by applying three different levels of assessment. Using the ES matrix approach, we first examine how spatial resolution influences the assessment by comparing predicted ES potentials based on the open-access CLC dataset with the ATKIS (authoritative topographic and cartographic information system)/InVeKoS (Integrated Administration and Control System) datasets, which have a finer spatial resolution and include small habitats and landscape elements. We then select and calculate ecosystem condition indicators based on the fifth mapping and assessment of ecosystems and their services (MES) report (http://biodiversity.europa.eu/mes) to develop an ecosystem condition index. This assessment level combines the resulting index with the ES potential matrix to analyze how data on ecosystem condition influence the outputs of ES assessments. We applied these three assessment methods in a case study area in northern Germany.
The following three research questions are addressed in this study:

- How does a higher spatial resolution with more information on small landscape elements affectthe results of an ES-matrix assessment on a local scale?
- Does the integration of ecosystem condition information add value to the ES assessment and canpatterns between different ES and ES categories be detected?
- What conclusions can be drawn for practical applications in landscape management?

2. Material and Methods

2.1. Case Study Area (CSA)

The CSA is located in the region of the Bornhöved Lake District in the province of Schleswig–Holstein in northern Germany (Figure 1). It was the focus of a former integrative ecological study project and is a long-term ecological research (LTER) site. The present study area is bigger than the former LTER site and includes the administrative borders of the constitutive municipalities, resulting in a CSA of 147 km2. Agroecosystems dominate the landscape in a catchment area of five glacially formed and consecutively connected lakes. The CSA is composed of relatively small and diverse ecosystems, as well as a high proportion of hedgerows, shaping a highly diverse and fragmented landscape (see Figure 1 and [27]). The former LTER site was used in several ES assessments focusing on one single ES [28] or a group of ES [7–9,26].

2.2. Ecosystem Services Assessments

To guide through the following section, we introduce the workflow of the different levels of assessment developed in this study. Figure 2 illustrates this workflow and how the different datasets are integrated in the different levels of assessment. We prepared two geospatial maps using three different datasets: the CLC datasets for the first assessment level, the ATKIS and InVeKoS datasets were combined for the second and third assessments. We used the LULC classes from the three datasets to build a unique ES matrix based on a common typology and solicited local experts. For the first and second level assessment, we applied the resulting matrix to the different geospatial datasets to map ES potential in the CSA. For the third level assessment, we added ecosystem condition indicators to the analysis: ES potentials were calculated based on the environmental condition scores of each ecosystem and the ES scores from the matrix. Finally, we statistically compared the different levels of assessment and the differences in the resulting ES potential maps.

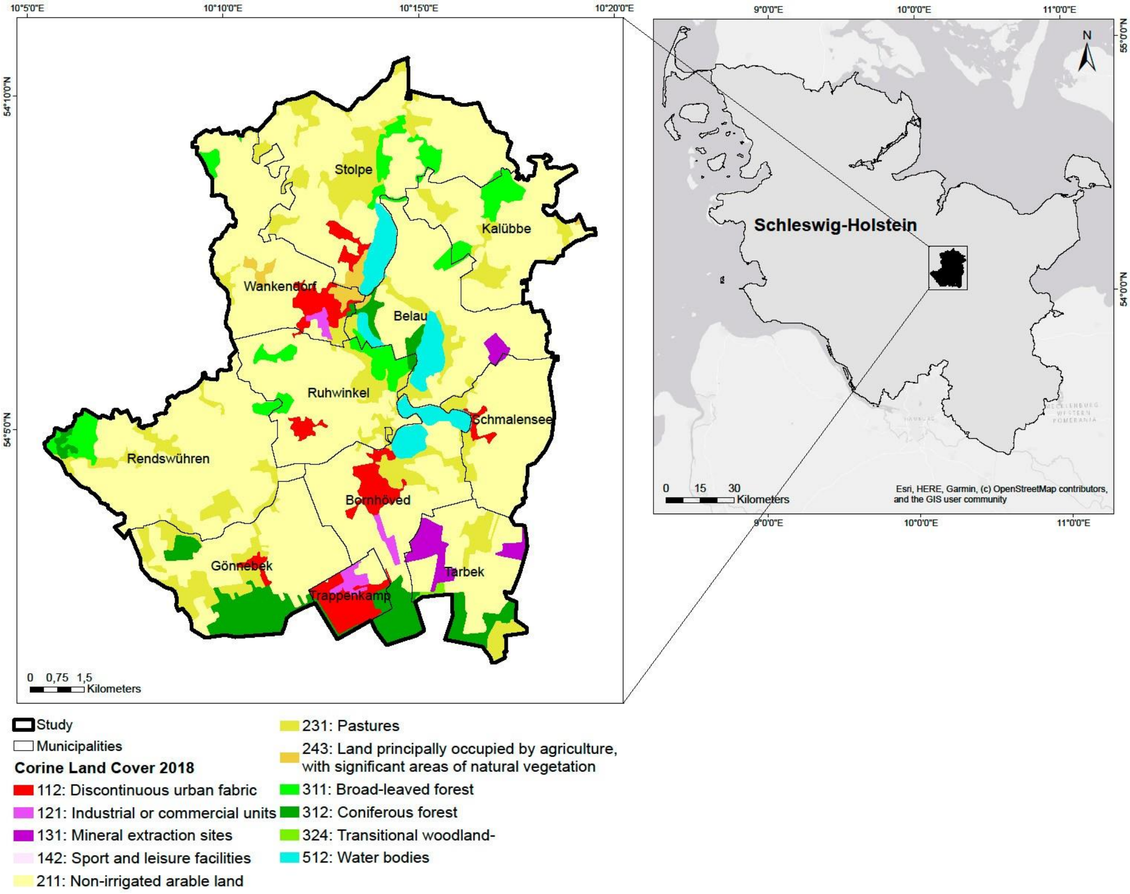

Figure 1. Location of the study area in northern Germany (on the right) and distribution of administrativedistricts and Corine land-cover classes (CLC2018) (on the left).

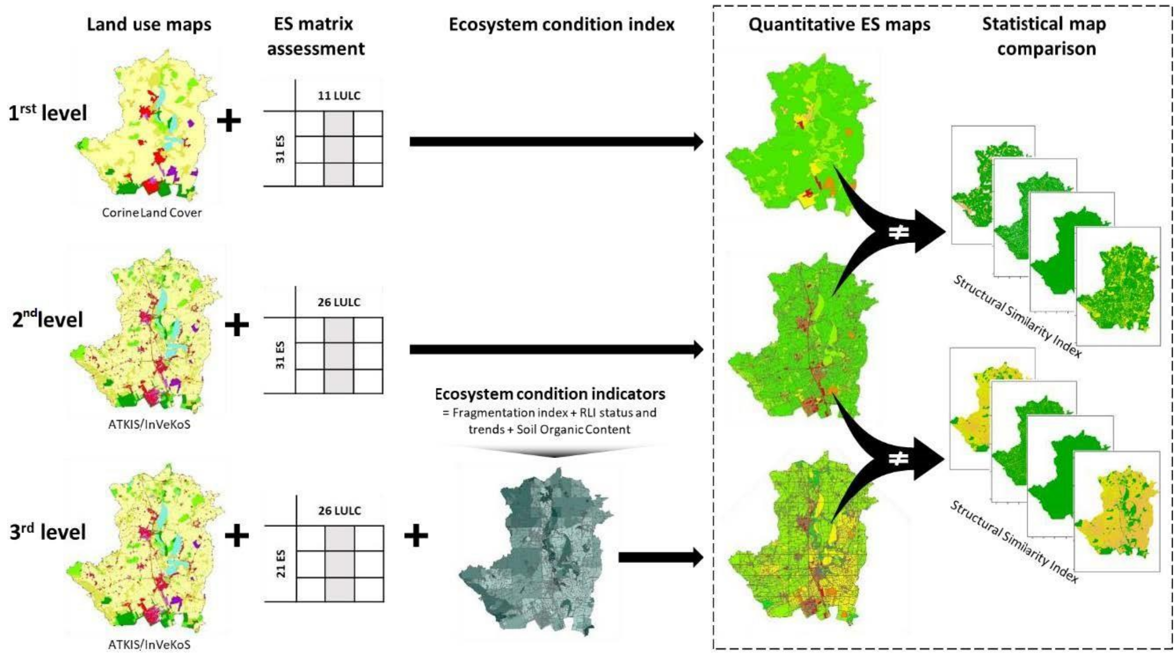

Figure 2. Working flow chart.

2.2.1. Geospatial Datasets

The LULC typology used for the first level assessment is derived from the CLC 2018 dataset (https://land.copernicus.eu/pan-european/corine-land-cover/clc2018).

The geospatial dataset used in the second level assessment is composed of ATKIS (version 2012) and improved by using InVeKoS data (version 2010). ATKIS is a national standardised topographic information system provided by the German Federal Surveying Authorities. InVeKoS is a control system established by the European Commission to control payments of income support from the European Common Agricultural Policy to farmers. Both datasets feature an object-based comprehensive description of the Earth's surface. Topographical and LULC features are modeled as points, polylines or polygons. The spatial resolution of these two datasets depends on the feature classes and has a MMU between 0.1 and 1 hectare [29] compared to the 25 hectares of CLC.

The two datasets differ in represented LULC classes: "transitional woodland-shrub" and "land principally occupied by agriculture, with significant areas of natural vegetation" from the CLC dataset are not part of the ATKIS/InVeKoS classification systems. The CLC class "transitional woodland/shrub" corresponds to "areas representing natural development of forest formations, consisting of young plants of broad–leaved and coniferous species, with herbaceous vegetation and dispersed solitary adult trees. Transitional process can be for instance natural succession on abandoned agricultural land, regeneration of forest after damages of various origin (e.g., storm, avalanche), stages of forest degeneration caused by natural or anthropogenic stress factors (e.g., drought, pollution), reforestation after clearcutting, afforestation on formerly non-forested natural or semi-natural areas, etc." (https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html/index-clc-324.html). The CLC class "land principally occupied by agriculture, with significant areas of natural vegetation" is defined as "areas principally occupied by agriculture, interspersed with significant natural or semi-natural areas (including forests, shrubs, wetlands, water bodies, mineral outcrops) in a mosaic pattern." (https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html/index-clc-243.html).

Table 1 and Figure 3 show all LULC classes and their respective proportions for each LULC dataset are shown in Table 1. The main differences between CLC and ATKIS/InVeKoS are found in the higher number of LULC classes and also in total surface covered by "arable land", by landscape elements (LULC subclass which regroups the classes "hedgerows", "tree rows", "copse, thickets", "single trees", "field borders") as well as by artificial surfaces.

Table 1. Differences in land use/land cover data (LULC) classes shares in the study area in 2018 (CLC) and 2010 (ATKIS/InVeKos) for the two LULC datasets.

CLC Level 2	CLC Level 3 Classes	Corresponding ATKIS/InVeKoS Classes	% Total ATKIS/InVeKoS	% Total CLC Level 3
Arable land	Non–irrigated arable land	Arable land	59.81%	67.25%
		Fallow land	0.36%	
		Truck farm	0.48%	
Permanent crops	Fruit trees and berry plantations	Fruit trees and berry plantations	0.02%	
Pastures	Pastures	Pastures	11.76%	13.12%
Heterogeneous agricultural areas	Land principally occupied by agriculture, with significant areas of natural vegetation	–		0.84%
	–	Hedgerows	2.36%	
	–	Tree rows	0.21%	
	–	Copse, thickets	0.15%	
	–	Single trees	0.08%	
	–	Field borders	0.11%	

Table 1. *Cont.*

CLC Level 2	CLC Level 3 Classes	Corresponding ATKIS/InVeKoS Classes	% Total ATKIS/InVeKoS	% Total CLC Level 3
Forests	Broad–leaved forest	Broad–leaved forest	3.34%	4.22%
	Coniferous forest	Coniferous forest	3.85%	4.95%
	Mixed forest	Mixed forest	3.48%	
Scrub and/or herbaceous vegetation associations	Transitional woodland–shrub	–		0.10%
	Sclerophyllous vegetation	Sclerophyllous vegetation	0.33%	
Open spaces with little or no vegetation	Sparsely vegetated areas	Sparsely vegetated areas	0.17%	
Urban fabric	Continuous housing area	Continuous housing area	3.15%	
	Discontinuous urban fabric	Discontinuous housing area	1.65%	4.32%
Industrial, commercial and transport units	Industrial or commercial units	Industrial and commercial units	0.99%	0.72%
	Airports	Airports	< 0.01%	
	Road and rail network	Rail network	0.09%	
		Road network	2.32%	
Mine, dump and construction sites	Mineral extraction sites	Mineral extraction sites	0.89%	1.41%
	–	Paths	0.52%	
Artificial, non-agricultural vegetated areas	Sport and leisure facilities	Sport and leisure facilities	0.61%	< 0.01%
Inland waters	Water courses	Water courses	0.08%	
	Water bodies	Water bodies	3.70%	3.07%
	–	Ditch	0.35%	
Inland wetlands	Inland marshes	Wetlands	0.08%	

2.2.2. ES Matrix Approach

The ES matrix approach by Burkhard et al. [7–9] is based on a look-up table where the capacity of each geospatial unit (e.g., LULC types) to supply ES is quantified. In this study, we assessed the ES potential of the different LULC classes. We did not consider the actual use or flow of ES, nor the demand for ES (see Syrbe et al. [30] for definitions of ES potential, stock, use and demand). ES potentials are scored on a scale from zero (no relevant potential) to five (very high relevant potential). The methodology is also described in Burkhard and Maes [31] and in Campagne and Roche [13]. We adhered to the following steps: (1) identification of the relevant ES and ecosystems to be assessed, (2) selection of an expert panel, (3) collection of expert scorings and (4) compilation of the final matrix values.

The list of ES in the matrix is based on the common international classification of ecosystem services (CICES V5.1) [32] and covers all three main CICES sections, i.e., regulation and maintenance ES, provisioning ES and cultural ES. Each ES is briefly explained in the matrix in the supplement materials (Table 1). The list of ecosystems corresponds to the CLC, ATKIS and InVeKoS LULC classes in the CSA (see Table 1 "Corresponding ATKIS/InVeKoS classes"). The experts had a wide range of ES and ecosystems expertise, had researched the study area and were familiar with ES concepts.

Müller et al. [33] developed an ES assessment matrix for CLC land cover classes within the German Federal State of Schleswig–Holstein, to which more than 55 experts contributed. We used this matrix for the first ES assessment, as all the selected ES and LULC were scored in this matrix. For the second assessment, we completed the matrix with all the missing LULC, i.e., the LULC classes within the ATKIS/InVeKoS datasets that were not represented in CLC classes. These classes were assessed through a new evaluation process, in which several preliminary discussion rounds were organized with four experts, in order to identify in the missing values of the matrix. Other experts were then contacted by email and asked to modify the potential scores in the preliminary matrix in case of differing opinions (only for the LULC classes missing in the matrix from Müller et al. [33]). Materials that were provided to experts included a map of the CSA as well as a matrix. In total, 10 local experts in environmental management, soil, ecology, agriculture and climate sciences contributed to the new assessment. The final matrix included 31 LULC classes and 34 ES and can be found in the supplement materials (Table 1).

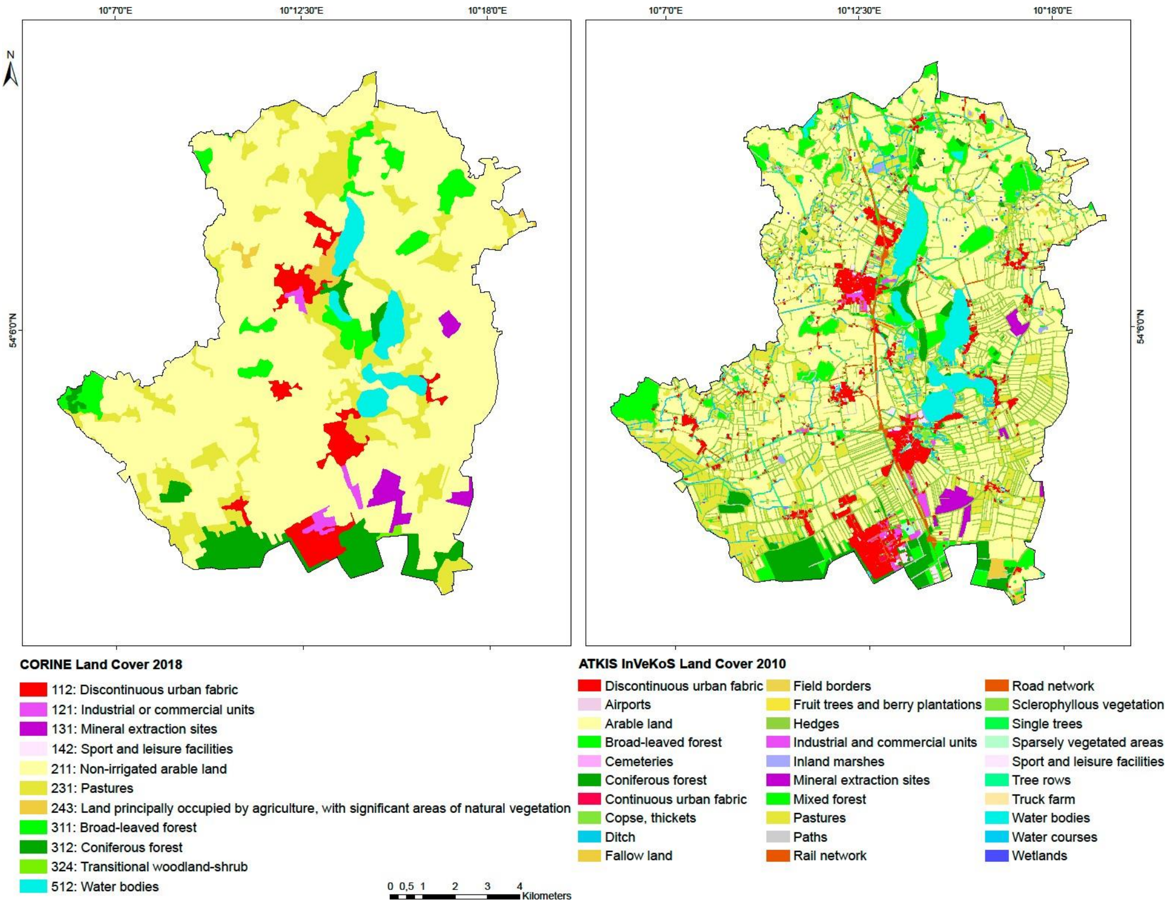

Figure 3. Distribution of CORINE land cover data (CLC) (Level 1, 2018) and ATKIS/InVeKoS (Level 2,2010) land cover classes in the study area Bornhöved. Agriculture represents 81.2% (CLC) or 72.4% (ATKIS/InVeKoS) of the total area, from which 67.2% (CLC) or 60.6% (ATKIS/InVeKoS) is dedicated to arable land. Forests covers only 9.2% (CLC) or 10.7% (ATKIS/InVeKoS) of the case study area. 6.4 (CLC) to 3.8% (ATKIS/InVeKoS) of the area is covered by artificial surfaces. In the CLC datasets, 0.1% of the area is covered by transitional woodland-shrub which has no equivalent in the other dataset. Landscape elements represent 2.9% of the total area in the ATKIS/InVeKoS datasets.

2.2.3. Ecosystem Condition Indicators

Selecting Suitable Indicators

The MAES working group of the European Commission (http://biodiversity.europa.eu/maes) aims at providing support to the EU member states in regard to ES mapping and assessment [34]. The fifth MAES report presents a list of key indicators for mapping and assessing ecosystem condition of the main ecosystem types at the European level [35]. From this report, we selected ecosystem condition key indicators for which we could find local data or easily develop an equivalent that was spatially explicit and sensitive to local land use change. Whereas MAES provides one list of indicators per ecosystem type, the indicators selected for this study are not ecosystem type-dependent and are relevant for artificial areas, agroecosystems, forests as well as other natural and semi-natural ecosystems. Three indicators were selected: the landscape fragmentation index, a Red List Index for ecosystems and the soil and organic carbon (SOC) (Table 2).

Table 2. Overview of the data used as ecosystem condition indicators.

	Indicators	References	Spatial Resolution
Ecosystem attributes	Landscape fragmentation index	EEA landscape fragmentation per km (mesh)	1 km^2
	Red List Index for ecosystems	Schleswig–Holstein Red Lists and ATKIS/InVeKoS LULC classes	Variable (from +/- 3 m to less than 1 ha as ATKIS and InVeKoS resolution)
Structural soil attributes	Soil organic carbon (SOC)	Federal Institute for Geosciences and Natural Resources (BGR)	0.25 km^2

Landscape Fragmentation Index

Landscape fragmentation results from the transformation of large natural and semi-natural ecosystems into smaller and isolated, fragmented ecosystems [36]. This process can for instance be caused by the construction of transport networks and built-up areas, which have greatly expanded over the last 50 years. Accessibility is a prerequisite for the exploitation and supply of a wide range of ES. Up to a given density, there is a positive relationship between road density and the potential use of provisional and cultural services, as it generally depends on access to the ES supply areas. However, a high fragmentation has a negative impact on agricultural and timber production, as small land parcels tend to have lower yields [36]. Transportation networks also have negative impacts on cultural ES, above all for recreational use and landscape aesthetics. Fragmentation seriously affects regulation ES by, among other, species movement impediment and habitat reduction [37], water cycle disruption [38] and erosion phenomenon exacerbation [38]. A detailed list of the effects of fragmentation on ecosystem conditions and services can be found in the report of the European Environment Agency (EEA) [36].

The EEA applied the method of effective mesh density to measure the degree of landscape fragmentation in the EU member states [36]. This landscape metric unit is based on the probability that two points chosen randomly in an area are connected and not separated by any natural or man-made barriers. The effective mesh size represents the degree of fragmentation of a landscape: the smaller the value, the more fragmented the landscape. The datasets used to calculate the mesh are CLC (2006) for artificial areas such as urban and industrial units but also waterbodies, TeleAtlas Multinet for the roads and railroads, WorldClim and Nordregio for topographic and climatic barriers [36]. The resulting map presents landscape fragmentation at 1 km2 resolution.

Local Red List Index

The Red List Index (RLI) is one prominent indicator in the Convention for Biological Diversity (CBD) indicator sets for biodiversity conservation [39], but has until now not been used for ES assessments. RLI is a key condition indicator in the fifth MAES report that indicates “conservation status and trends of species of community interest” and “conservation status and trends of habitats of community interest” [35] and that aims at supporting the evaluation of the efficiency of conservation policies. The RLI measures status and trends in the overall extinction risk of species by using weight scores based on the Red List status of each assessed species, which range from 0 (least concern) to 5 (extinct/extinct in the wild). To date, global RLIs have been calculated for birds, mammals, amphibians, corals and cycads [40]. They serve as indicators to evaluate progress towards meeting the CBD “2010 biodiversity target” and help to develop a better understanding of which taxa, regions or ecosystems are declining or improving globally. Global RLIs and Red List assessments are hardly sensitive to local land-use management and decisions, so we instead used local extinction risk assessments lists provided by the State Agency for Nature and Environment of Schleswig–Holstein [41–43]). Moreover, as we needed a spatially explicit indicator, we calculated local RLIs for each ecosystem and not for each species group, following the method by Juslén et al. [44]. Each species was associated to one or more ecosystems based on their habitats described in national or Schleswig–Holstein Red List assessments. A total of 214 species of birds, 44 mammals and 18 amphibians and reptiles were included in the assessment.

The RLI values were calculated following the method developed by Butchart et al. [40]. We multiplied the number of taxa in each ecosystem by the category weight (0 for least concern, 1 for near threatened, 2 for vulnerable, 3 for endangered, 4 for critically endangered and 5 for extinct/extinct in the wild). These products are summed up and then divided by the number of taxa multiplied by the maximum weight 5, the "maximum possible denominator", which corresponds to the "worst case scenario". To obtain the RLI value, this sum is subtracted from 1. The resulting index varies between zero and one: the lower the value, the closer the set of taxa living in the ecosystem is heading towards extinction. The Red List status of the pool of species living in an ecosystem is used as a proxy for this ecosystem condition. To make this indicator sensitive to land management change, we included the RLI value trends as well as the values from the last Red List assessment. The "RLI status" corresponds to the values from the last Red List assessment. The "RLI trend" corresponds to the difference between the last and the first Red List assessment values (i.e., RLI status—RLI 1990 (or 1995)) for each ecosystem.

Soil Organic Carbon (SOC)

Soil is a key component of terrestrial ecosystems and plays an essential role in ecosystem functioning [45]. Despite its importance, relatively little emphasis has been placed on soil in studies that map ES, mainly because our understanding on how soils support ES delivery is incomplete [46,47]. Soil quality and its capacity to provide a wide range of ES depend on key properties such as soil type and texture, soil organic carbon content, pH, soil porosity and structure [48–50]. Soil organic carbon (SOC) is mainly determined by the balance between net primary production and the rate of decomposition of organic material, which both depend on land use, climate and microorganism action. A literature review showed that SOC can be (directly or indirectly) linked to a broad range of ES, in all three ES CICES categories [48]. As no map was readily available at the desired local scale, we developed a SOC map based on the data and method from the Federal Institute for Geosciences and Natural Resources' (BGR) soil information system (FISBo), which provides soil information at land and national scale [51,52]. The method from the BGR allows us to determine the SOC from soil characteristics, climatic data and land cover types.

2.3. *ES Potential Maps*

2.3.1. First and Second Level

Ecosystem mapping was carried out for the CSA using CLC (first assessment level) and ATKIS/InVeKoS (second assessment level) datasets. All spatial analyses were executed using ArcGis 10.6.1. ES potential maps were obtained by joining each LULC map with the ES potential matrix. Exemplary ES potential maps (crop production, pollination and recreation and tourism) are presented in the results, the other maps can be found in the Supplementary Materials.

2.3.2. Third Level

For the third level assessment, we assume that good ecosystem condition is prerequisite for a high supply of ES [35] and therefore first combined the three selected indicators into one ecosystem condition map (Figure S1). However, most provisioning ES, such as agricultural production (crop, livestock, biomass for energy, fodder and fiber production) but also timber production, often arise much more from human interventions than from ecological properties and functions of the ecological system [53] (but see Balvanera et al. [54] and Harrison et al. [55]). Some ecosystem properties have a direct positive impact on agricultural production, but it can be generally substituted by human actions.

For example, a high SOC maximises crop and pasture biomass. A low SOC can be however compensated by adding off-farm organic residues. As we cannot assume that the potential of agricultural and timber production services increases with ecosystem conditions, we did not include them into the third assessment level.

A second assumption, in the absence of further evidence [19], was that each indicator equally contributes to the ecosystem condition of each ecosystem type except aquatic ecosystems for which the SOC is not relevant, following the Equation (1):

$$EC = \frac{1}{4}(FI + RLI_{trend} + RLI_{status} + SOC \tag{1}$$

where EC is the aggregated indicator value for the ecosystem condition, FI the fragmentation index, RLI$_{\text{status}}$ the RLI for Schleswig–Holstein for 2014 and RLI$_{\text{trend}}$ the improvement or degradation of the RLI over the years, SOC the soil organic content. All indicators are scaled down to the interval [0,1], to give all the indicators an equivalent weight. The EC values are also scaled into the range [0,1]. EC values from zero (the ecosystem is in a very bad condition) and one (the ecosystem is in a very good condition).

As the SOC is not relevant for aquatic ecosystems, we did not include this indicator in the EC of water bodies nor water courses. For these ecosystems, Equation (2) is defined as follows:

$$EC = \frac{1}{3}(FI + RLI_{trend} + RLI_{status} + SOC \tag{2}$$

The ecosystem capacity to deliver ecosystem services is determined by the ecosystem condition, following Equation (3):

$$ES_{potential} = EC \times ES \tag{3}$$

where ES$_{\text{potential}}$ is the calculated ecosystem services potential resulting from the ecosystem condition (EC) and the ES potential scores (ES) from the matrix.

2.4. *Influence of Typology and Resolution*

The CLC and ATKIS/InVeKoS datasets use different typologies to describe some of the LULC classes. The differences in the ES maps resulting from the different LULC datasets are therefore not only due to different resolutions but also to a difference in typologies. To differentiate these two effects, we compared the two maps using the Union tool from ArcGIS. The resulting map is a map containing each input feature from the two LULC datasets, associated with its attributes. The resulting attribute table shows how the two datasets overlap and this allowed to determine which CLC LULC classes corresponds to each ATKIS/InVeKoS class. Using this attribute table, we then calculated the percentage of each CLC class, which was classified (or not) to the corresponding ATKIS/InVeKoS class (see Table 1). To assess the effect of spatial resolution, we assessed the percentage of LULC classes that were misclassified according to the size of each feature.

2.5. *Statistical Maps Comparison*

We first compared the maps resulting from the first and second assessments to evaluate the improvement in mapping precision. We then compared the maps resulting from the second and third assessments to estimate the mapping accuracy discrepancy. We used the structural similarity index (SSIM index) from Jones et al. [56] for visual interpretation and statistical analysis. This index provides three distinctive measures of spatial heterogeneity in map structures: similarity in means (SIM), similarity in variance (SIV) and similarity in pattern (SIP) of spatial covariance. SIM is the ratio of twice the product of the local means to their summed squares. It ranges from 0 to 1, in which 0 characterizes two maps for which means are dissimilar (in this case, different modelled ES local abundances), 1 if means are similar (similar modelled ES local abundances). The SIV is the ratio of twice the product of the local standard deviations to their summed variances. SIV ranges from 0 to 1, in which 0 is indicated if variances are dissimilar (ES are not similarly distributed), 1 if variances are similar (ES are similarly distributed). The SIP is the ratio of the local covariance to the product of the local standard deviation. It ranges between −1 and 1, in which −1 indicates a negative spatial correlation, 1 a positive spatial correlation and 0 indicates that the distributions are independent. The SSIM index compares output values of maps at pixel level and accounts for the values of neighboring pixels through a window of 3 × 3 pixels. The method allows for a spatially explicit difference analysis between two maps, including spatially explicit differences in means, variances and covariances, taking spatial dependencies between neighboring cells into account. All statistical analyses were conducted using the software R [57] and based on the script provided by Jones et al. [56].

3. Results

3.1. First Level Assessment

For the first level assessment, the ES potential supply was evaluated and mapped using the ES assessment matrix and CLC data. Figure 4 shows the spatial distribution of three ES potentials in the CSA: crop production, pollination and recreation and tourism services. A relative scale ranging from zero (no relevant capacity) to five (very high relevant capacity) was used. As the study area is mainly composed of "arable land" (see Table 1 for a description of land use classes share within the CSA), the maps show an overall high crop production potential, a low pollination potential and a moderate recreation and tourism potential for the area. High and very high pollination potentials are patchily distributed and correspond to "broad-leaved forest", "coniferous forest", "Pastures" and "land principally occupied by agriculture, with significant areas of natural vegetation". High and very high recreation and tourism potentials correspond to "broad-leaved forest", "coniferous forest" and "water bodies".

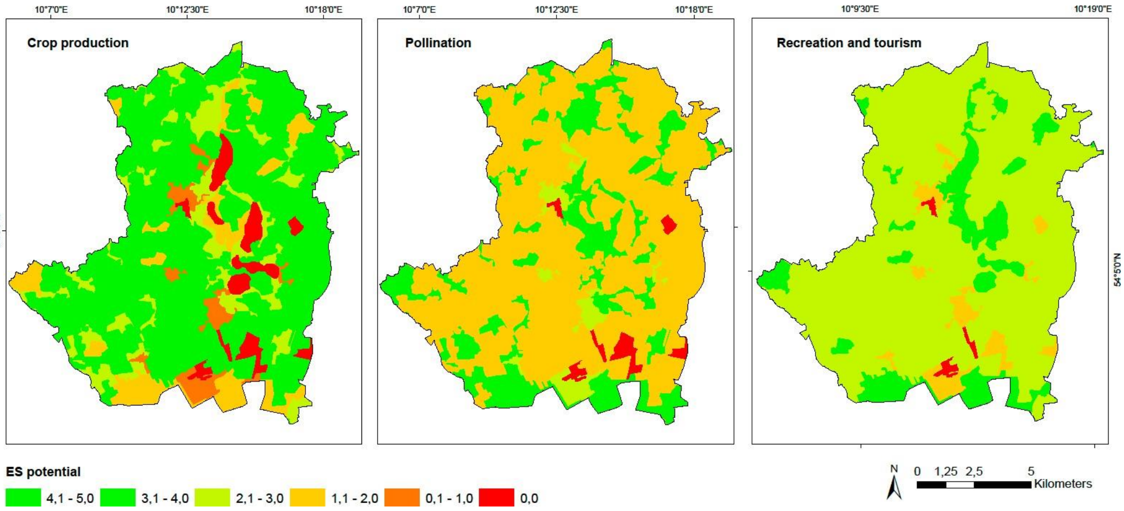

Figure 4. Examples of three ecosystem services (ES) potential maps (crop production, pollination and recreation and tourism) using CLC land cover data and the ES potential matrix. 0.0: no potential, 0.1–1.0: very low potential, 1.1–2.0: low potential, 2.1–3.0: moderate potential, 3.1–4.0: high potential,4.1–5.0: very high potential.

3.2. Second Level Assessment

Figure 5 shows the spatial distribution of three ES in the CSA: crop production, pollination and recreation and tourism services. These maps are based on the ATKIS/InVeKoS datasets and show a more fragmented ES potential than the maps from the first level assessment, due to the inclusionof small habitats and landscape elements. Yet the resulting maps show the same global patterns (Figure 5):

fewer areas sustain crop production, but have an overall high crop production potential,a low pollination potential and a moderate recreation and tourism potential.

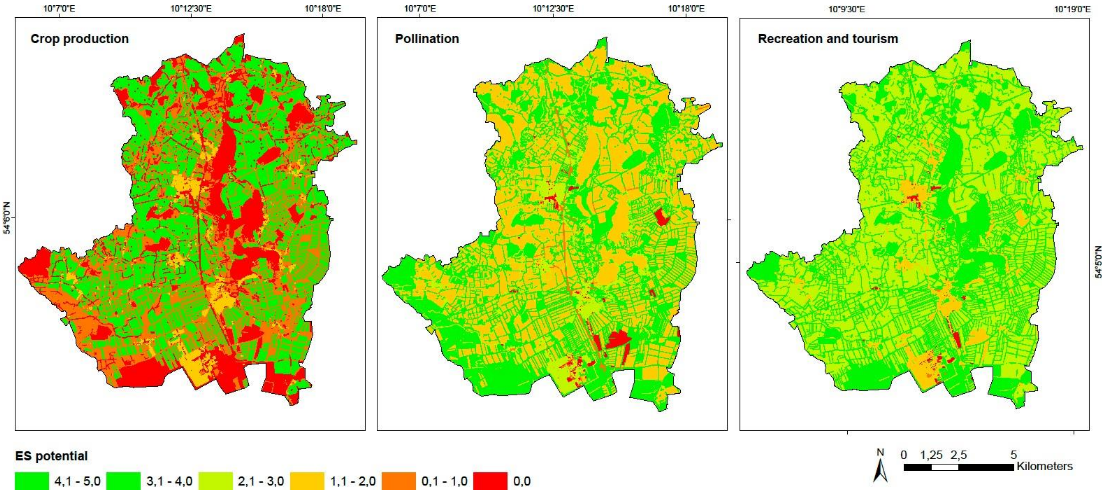

Figure 5. Examples of three ES potential maps (crop production, pollination and recreation and tourism) using ATKIS and InVeKoS land cover data and the ES potential matrix. 0.0: no potential, 0.1–1.0: very low potential, 1.1–2.0: low potential, 2.1–3.0: moderate potential, 3.1–4.0: high potential, 4.1–5.0: very high potential.

3.3. Third Level Assessment

The final ES potential maps (Figure 6) were obtained by combining the ecosystem condition index map (Figure S1 in the Supplementary Materials) and the ES potential maps from the second level of assessment. Only those ES which have a positive relationship with EC were included in this assessment (see Section 2.2.3), so for instance crop production was excluded. As none of the ecosystems in the CSA is in a very good condition (EC values are between 0.052 and 0.514, whereas the maximum achievable value is 1), the overall potentials of the CSA to supply ES are greatly reduced.

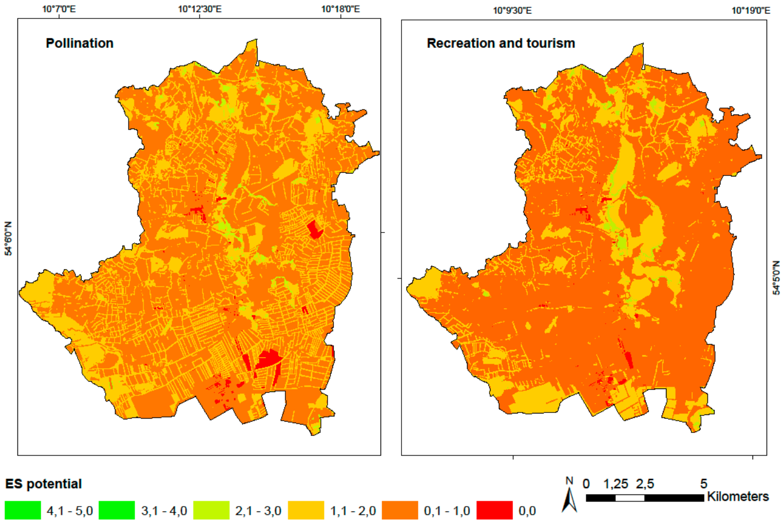

Figure 6. Examples of two ES potential maps (pollination and recreation and tourism) using ATKIS and InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators. 0.0: no potential; 0.1–1.0: very low potential; 1.1–2.0: low potential; 2.1–3.0: moderate potential; 3.1–4.0: high potential;4.1–5.0: very high potential.

3.4. CORINE Land Cover and ATKIS/InVeKoS Typology Differences

Overall, there is a relatively high correspondence between the two datasets: around 70% of the CSA area is classified in the same LULC class in the two datasets. The main difference between CLC and ATKIS/InVeKoS datasets comes from the different resolutions for the LULC classes in both datasets, as LULC classes, which are mainly composed of large elements in the ATKIS/InVeKoS dataset, have a high matching level with CLC LULC classes: this is the case for "water bodies" (99%), "non-irrigated arable land" (81%), "industrial or commercial units" (64%) and "coniferous forest" (63%) classes. The LULC classes "discontinuous urban fabric", "mineral extraction sites", "pastures" and "broad-leaved forest" have however a matching level around 50% with a perfect correspondence for elements bigger than the CLC MMU.

There is a clear typology mismatch between the two datasets for the LULC classes that can be found only in the CLC dataset: The CLC LULC class "land principally occupied by agriculture, with significant areas of natural vegetation" mainly corresponds to arable land (27%) or pastures (42%) in the ATKIS/InVeKoS LULC classification, whereas "transitional woodland/shrub" is mainly classified as arable land (52%) or mixed forest (37%). Unlike the CLC classification, the ATKIS/InVeKoS dataset does not differentiate conventional arable land or pastures from agricultural land with natural areas. The ATKIS/InVeKoS classification considers "transitional woodland/shrub" areas as arable land or mixed forest, but does not consider afforestation/deforestation processes unlike the CLC classification(see Section 2.2.1 for a definition of CLC classes).

ES scores were recalculated for each CLC LULC class according to the percentage of each composing ATKIS/InVeKoS LULC class and their ES matrix scores (for instance, if the CLC LULC Class 1 was composed of 10% ATKIS/InVeKoS Class 1 (ES score 2) and 90% of the ATKIS/InVeKoS Class 2 (ES score 0), then the CLC LULC Class 1 has a ES score of 0.2 in the recalculated matrix). The ES scores from the original and the recalculated matrix were then compared. The LULC class "land principally occupied by agriculture, with significant areas of natural vegetation" showed a low variance between the ES scores from the initial matrix and the recalculated matrix (0.6 point) but showed a high variance for the CLC class "transitional woodlands, sclerophyllous vegetation" (1.6 point). This explains some variations in ES mapping, however only for a relatively small fraction of the CSA (the LULC classes "land principally occupied by agriculture, with significant areas of natural vegetation" and "transitional woodlands, sclerophyllous vegetation" represent less than 1% of the area).

For those LULC classes that were not included in the CLC dataset, the landscape elements correspond in the CLC map to the "non-irrigated arable land" (77%) and "pastures" (17%). This indicates that landscape elements are not considered in the CLC map, as they do not match the "land principally occupied by agriculture, with significant areas of natural vegetation" CLC LULC class. We can therefore assume that this LULC class is not integrated in the CLC map because the MMU is too coarse.

3.5. Statistical Comparison of First and Second Level Assessment

The resulting maps have similar ES potentials local abundance, variance and are highly correlated with a high to very high similarity in mean values (73.85 to 99.80% of the CSA has a SIM > 0.5), a high similarity in their variances (83.24 to 99.19% of the CSA has a SIV > 0.5) and a high positive spatial correlation (99.61 to 100% of the CSA has a SIP > 0) (Table S2 in the Supplementary Materials). Different patterns can be observed for the different ES and ES categories: the higher discrepancies between ES maps are for nutrient regulation, crop (Figure 7) and fiber productions, water purification and global climate regulation services, whereas minerals and fish provisioning have the lowest discrepancy. The differences between crop and fiber supply maps are mainly due to higher dissimilarity in local abundance, whereas the nutrient regulation maps differ in local abundance and variance. Cultural services tend to have a higher SIM than other services maps. Most of the regulation and maintenance services such as pollination, nutrient regulation and global climate regulation, but also cultural services and wild food production maps have a relatively lower SIV, whereas provisioning services are characterised by a high SIV (see Figure 7 for exemplary spatial agreement maps showingcrop production services).

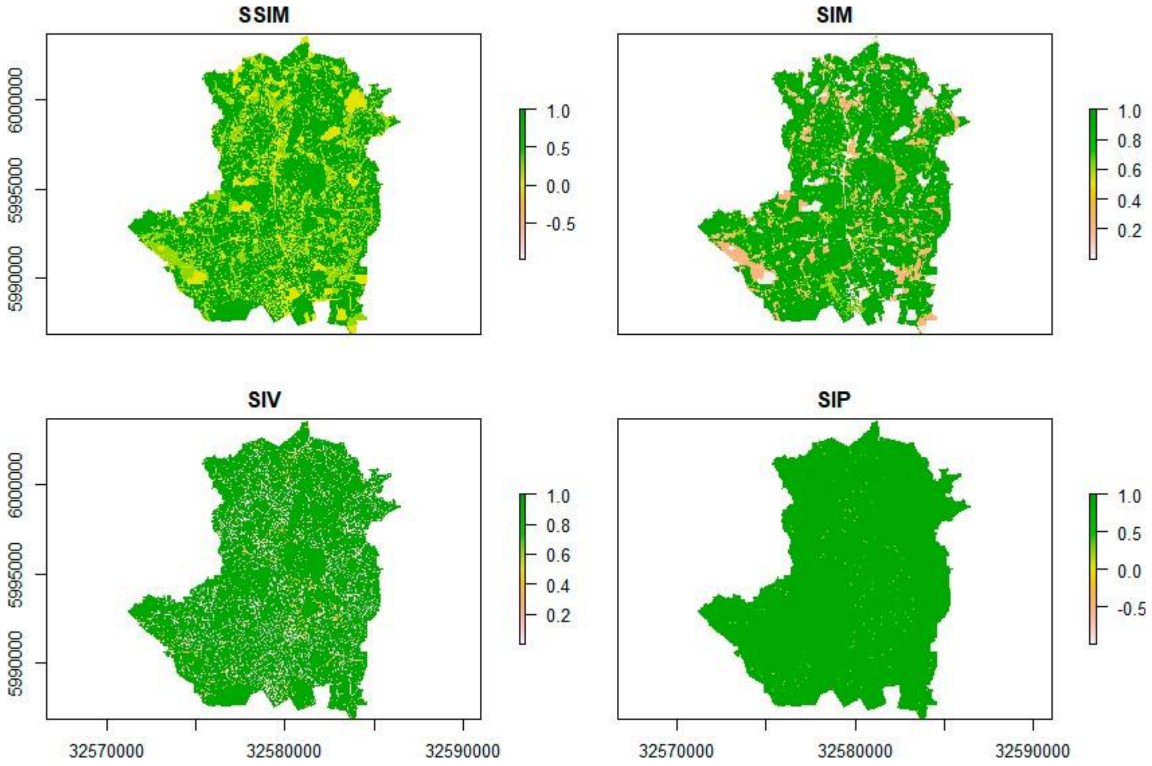

Figure 7. Map comparison between the crop production service potential with CLC and ATKIS/InVeKoS datasets. SSIM—structural similarity Index; SIM—similarity in means; SIV—similarity in variance; SIP—similarity in pattern of spatial covariance.

3.6. Statistical Comparison Second and Third Level Assessment

For most of the ES maps, the two mapping methods show highly different local ES potentials, however the variances and covariances have a low to a very high similarity in means (21.71 to 99.11% of the CSA has a SIM > 0.5), but very high similarity in variance (89.09 to 99.82% of the CSA has a SIV > 0.5) and an almost perfect spatial correlation (99.96 to 100% of the CSA has a SIP > 0) for all the ES (Table S3 in the Supplementary Materials). The correlation between the maps is to be expected as the map of the third level assessment is calculated based on the other map. We observe different patterns for each ES category: cultural services have the lowest SSIM values, followed by regulation services (except nutrient regulation) and provisioning services, which have the highest SSIMs. Overall, regulation and maintenance services tend to have a lower SIV than other ES categories (except for groundwater recharge and air quality regulation).

The spatial agreement between the maps depends on the number of ecosystems that deliver each ES, their sizes, the state of the ecosystem and the proportion of the area that potentially deliver each ES. ES that rely on few and in good condition LULC classes tend to have a higher SIM: fish provisioning has the higher SIM values and is sustained by few LULC classes (water bodies and water courses), which represent a small fraction of the CSA and tend to have a better ecological condition than other LULC classes. Nutrient regulation is supplied by a broader range of LULC types and has a high SIM (Figure 8). This may be due to the fact that this ES is mainly sustained by ecosystems that do not represent a high share of the total CSA (landscape elements and forests).

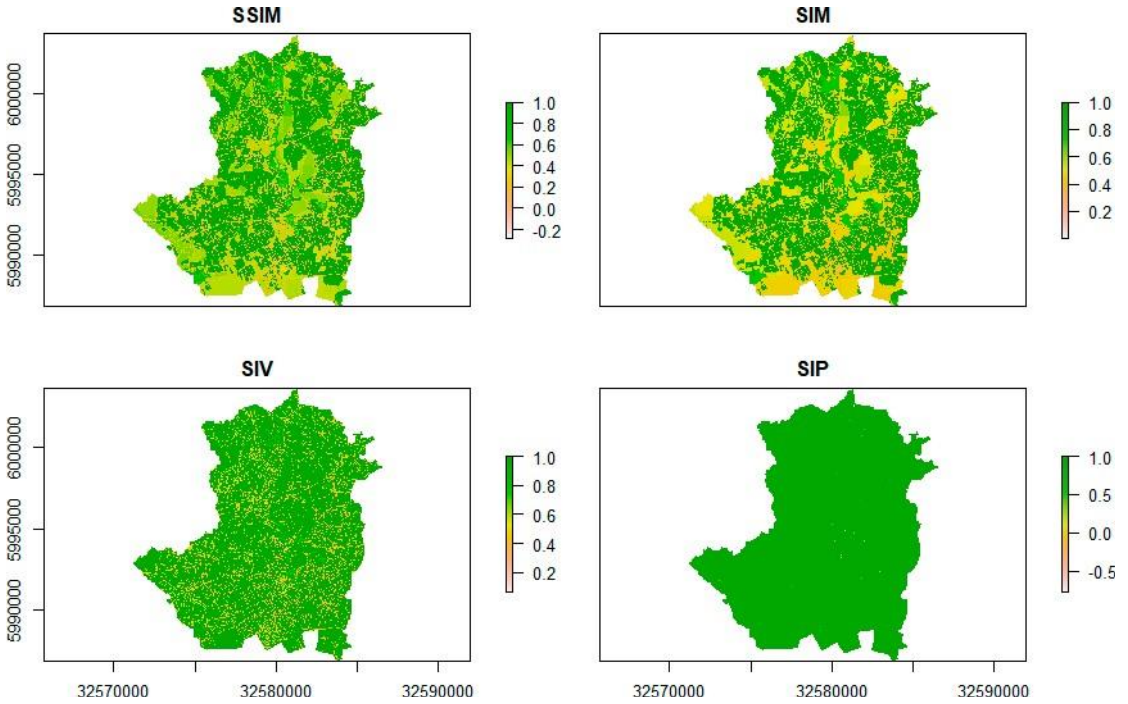

Figure 8. Map comparison between the nutrient regulation service potential with only LULC data and LULC combines with EC indicators. SSIM—structural similarity index; SIM—similarity in means; SIV—similarity in variance; SIP—similarity in pattern of spatial covariance.

4. Discussion

4.1. Discrepancies in ES Maps Based on Different Spatial Resolutions

The results of the statistical map comparisons show that using coarse spatial resolution leads to a relatively small, but still nonnegligible differences. Most of the provisioning services and regulation and maintenance services maps are more affected by the spatial resolution than the cultural services maps. The differences in SSIM can be explained by the overestimation or underestimation of different ecosystems in the CLC dataset and by the capacity of these ecosystems to provide multiple or single ES. Arable lands mainly deliver one provisioning ES: crop production. Arable lands are overestimated in the CLC dataset, and increasing the spatial resolution reduces the total arable land area. Hence, the capacity of the CSA to produce crops diminishes in the second assessment. Landscape elements (such as hedgerows and field borders) can provide a wide range of ES, particularly maintenance and regulation services. Landscape elements only appear in high resolution LULC data; therefore, maintenance and regulation services are not appropriately mapped when using CLC as input data. As landscape elements are relatively small, the two mapping approaches using different LULC datasets still have a high similarity in variance. Cultural services are generated by more diverse LULC classes and are therefore relatively less affected by the spatial resolution.

For an ES assessment at the scale of the CSA, using CLC or more detailed LULC data would provide outputs with a low degree of structural differences, particularly for cultural services. There is however no unique appropriate resolution and our conclusions may be valid only for a similar scale of assessment. Kandziora et al. [26] showed for instance that the ATKIS/InVeKoS dataset was required for a reliable ES assessment of provisioning services at the plot scale. Similarly, Rioux et al. [58] showed that a spatial resolution of 5 m or finer is required to adequately map the ES provided by small greenspaces in urban areas. This would be especially true for highly fragmented landscapes, with a high share of linear elements and small habitats, which cannot be captured by coarse spatial resolution data such as CLC [59]. On the other hand, a high level of accuracy can be misleading when working at a larger scale and the results may not be serviceable for or understood by decision makers.

4.2. Discrepancies in ES Maps Based on Different Data Complexity

The results of the statistical map comparisons show that including ecosystem condition indicators in ES assessments has a high influence on the resulting maps for most of the ES, mainly because of the dissimilarities in mean values, however with a low variance discrepancy and a high spatial correlation. This suggests that LULC proxies, even with a high spatial resolution, do not sufficiently capture spatial heterogeneity in ES potential: for most of the considered ES potentials, local abundance would change considerably when accounting for ecosystem condition. These results concur with the studies by Eigenbrod et al. [25] and van der Biest et al. [22] who question the appropriateness of using LULC data as ES delivery proxies for different assessment scales and for different mapping purposes (but see Roche and Campagne [13] for contrasting results). LULC proxies are not appropriate for a local quantitative assessment i.e., to assess how much ES can be delivered at a specific location, under the assumption that it substantially depends on ecosystem condition. However, the high similarity in variances implies that the maps have similar spatial ES clusters and therefore that mapping ES hot spots and cold spots with the two different LULC datasets would obtain similar results.

4.3. Validation

We compared statistical maps to measure the degree of spatial conformity between comparable models with different spatial resolutions and data complexities. This does not constitute a measure of the overall accuracy of the assessment. Assessing model accuracy generally implies a validation using independent data such as primary data, which is generally feasible only for some provisioning services such as agricultural or timber productions [60], but see Sinclair et al. [61] and Chabert and Sarthou [62]. However, models adapted to a local context, with a higher spatial resolution or taking site-specific characteristics into account, generally provide a more precise assessment of ES processes, and their outputs are more reliable [63]. Moreover, if we assume that the capacity of an ecosystem todeliver ES depends on its condition, the results including EC indicators should be closer to the true distribution of ES potential.

4.4. Sources of Uncertainties of the Method

ES assessment at the landscape scale is subject to intrinsic uncertainties, which originate from the complexities of landscape and ecosystem processes. First, land cover classifications can imply uncertainties, mainly because of scale mismatches between landscape structure and the spatial data [21]. Even though the accuracy of spatial data has significantly increase with the development of remote sensing technologies, LULC classifications still contains landscape simplifications (as every map), generalizations or even misclassifications [64]. The use of higher spatial resolution data can help to reduce data uncertainties, so in this sense, the use of ATKIS/InVeKoS datasets is more reliable than the CLC dataset.

Second, uncertainties are inherent to the ES assessment field and our still insufficient knowledge on the relationships between ecosystems and ES supply [17–19]. For many ES, it is difficult to allocate ES delivery to specific LULC classes, above all for regulation and cultural services, as they are often provided by a combination of LULC with specific characteristics. Even if the importance of a good ecosystem condition for the delivery of ES is widely recognized [24,55,65], the effects of ecosystem condition parameters on ecosystem functioning and the basic mechanisms are still poorly understood [4,66]. van Oudenhoven et al. [67], Kandziora et al. [68], Balvanera et al. [18] and Harrisonet al. [55] provide overviews of relationships between different EC/ES indicators and (some) ES, but they do not reach a consensus. Moreover, according to Braat and Brink [69] and Cardinale et al. [70], there may not be a linear relationship between biodiversity, EC and ES. As there is no clear and quantifiable information, it was not possible to adjust the importance of each indicator for each ES.

Lastly, the method entails uncertainties inherent to expert-based methods. Resulting ES assessments are strongly dependent on the level of knowledge of experts which can be subjective in scoring procedures [21]. For instance, less well-known ecosystems and non-directly used services may be underestimated by experts [14,71]. The number and selection of experts are critical and can reduce the level of uncertainty of the model [13,21]. The small size of the CSA considerably reduced the number of potentially relevant experts, as the task necessitates local knowledge on ecosystems and related ES.

4.5. Suggestions for Improvement

4.5.1. Data Availability

The feasibility of the different levels of assessment generally depends on the data availability for the study area. Among the data used in this study, only CLC and landscape fragmentation data are directly available and usable for all EU member states. Land cover datasets with a high resolution (covering for landscape elements) may or may not be available for other countries or regions. In Germany, this information can however not be accessed freely, due to data protection (InVeKoS) or commercial (ATKIS) reasons. For most of the ecosystem condition indicators recommended by the MES report, the needed data were not available for our CSA. Another issue is the scale for which the different indicators have been developed: most of them are not adapted to the local scale and their spatial resolutions do not allow for a local differentiation, and therefore spatially explicit assessment. Even if the availability of remote-sensing data has increased (e.g., Sentinel-2 based data products), data accessibility and availability is still a major issue for ES assessment. A typical example is data on ecosystem pressures such as the use of pesticides, fertilisers and biomass uptake that would greatly improve the index. The data should be made available and used in models to increase the accuracy of results.

4.5.2. Selecting Adapted Ecosystem Condition Indicators

The three ecosystem condition indicators used for this study were chosen because they were recommended in the fifth MAES report (see Maes et al. [35]). These indicators were developed to support national ecosystem assessments and were selected due to their spatial explicitness and sensitivity to change. Indicators that are suitable at the national scale may not necessarily be suitable for a sub-national or a local assessment: the spatial resolution may not be adaptable, and the indicators may be not sensitive to local land management and/or ecosystem condition changes. From the MAES list of recommended key indicators, we selected only relevant and complementary indicators, as a relatively large number of the indicators proposed in the report can be considered redundant and/or not adaptable to the local scale. The three ecosystem condition indicators selected for this study are still not completely independent and to some extent contain redundant information. For example, as biodiversity is usually positively affected by SOC values and negatively by landscape fragmentation, RLIs probably already include some information on the first two indicators. Despite their redundancy, the chosen indicators provide different information on ecosystem condition and their combination provides a relatively good estimation of the condition of different ecosystems. Another issue is that the different indicators are strongly linked to LULC: the different RLIs were calculated per ecosystem type and the SOC and fragmentation values are also largely a consequence of local land use. The outcomes of the second and third level assessments could have been more contradictory if the ecosystem condition indicators would have been measured differently, e.g., based on field data or if we had selected other ecosystem condition indicators.

5. Conclusions

Our study addresses some important issues in regard to ES assessments at a local level, where the quality of data is often critical. To our knowledge, this is one of the first studies to assess and map ES at the local scale based on ecosystem condition indicators recommended by the fifth MAES report.

In contrast to most of the previously published work, a broad range of ES was considered, and we compared the effects of different assessment methods on individual ES and on ES categories.

One of the main challenges for local ES assessments and mapping is finding and applying indicators, related quantification methods and data for comprehensible, reliable and feasible assessments. A reliable analysis should be as detailed as necessary and possible but is however often hampered by the lack of appropriate data for the quantification of each service. The context in which the assessment is implemented should guide the selection of the ES assessment methods and data. Yet a critical aspect for mapping accuracy is the capacity of the used model to capture spatial heterogeneity of ES potentials at the desired level. This paper compared three assessment methods that combine expert judgments, LULC data and ecosystem condition indicators in order to find the required resolution and data for an assessment in a local-scale case study.

Our results suggest that a high spatial resolution including landscape elements (such as hedgerows and field borders) does not drastically change the output of the spatial assessment at the local scale. However, by introducing LULC classes spatial variability, the use of EC indicators in the mapping can lead to different ES potential spatial patterns. This mainly depends on the number and characteristics of the chosen LULC classes, but also the landscape patterns of the studied area: map discrepancies tend to increase with the variety and size of LULC that are linked to ES in the matrix and the proportion of small elements in the studied area.

The results of this study show that expert-based methods combined with local data on ecosystem condition can be a feasible and efficient method for a local assessment of the capacity of a landscape to provide a wide range of ES. Nevertheless, the ES assessment method needs to be improved by exploring the different relationships between ES and the different EC indicators, but also by adding other essential ecosystem condition indicators and socioecological factors. Knowledge of the causal relationships between ES and ecosystem conditions needs to be better documented in different ecosystem types. This should also increase the accuracy of ES models.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-445X/9/10/348/s1, Table S1: ES assessment matrix with expert scores. Figure S1: Distribution of the ecosystem condition index values within the CSA. Figure S2: Crop (human nutrition) production service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S3: Biomass for energy service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. FigureS4: Crop (fodder) production service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S5: Livestock production service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S6: Timber service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S7: Fibers service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. FigureS8: Wood fuel service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S9: Wild food service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S10: Fish and seafood service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S11: Beach wrack and flotsam organic material service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S12: Ornamental service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S13: Drinking water service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S14: Abiotic energy service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potentialmatrix. Figure S15: Mineral production service potential maps using CLC (left) and ATKIS/InVeKoS (right) land cover data and the ES potential matrix. Figure S16: Groundwater recharge service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S17: Local climate regulation service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S18: Global climate regulation service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data andthe ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S19: Flood protection service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S20: Air quality service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S21: Erosion regulation (wind) service potential maps using CLC land coverdata and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S22: Erosion regulation (water) service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S23: Nutrient regulation service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S24: Water purification service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S25: Pest and disease control service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land coverdata and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S26: Pollination service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoSland cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S27: Recreation and tourism service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S28: Landscape esthetic and inspiration service potential maps using CLC land cover data and the ES potential matrix(left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S29: Knowledge systems service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S30: Cultural heritage service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data andthe ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S31: Regional identity service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data and the ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Figure S32: Natural heritage service potential maps using CLC land cover data and the ES potential matrix (left), ATKIS/InVeKoS land cover data andthe ES potential matrix (middle), ATKIS/InVeKoS land cover data, the ES potential matrix and ecosystem condition indicators (right). Table S2: Spatial agreement between ES potential maps based on CLC and ATKIS/InVeKoS datasets for three ES. Table S3: Spatial agreement between ES potential maps based on ATKIS/InVeKoS dataset only and ATKIS/InVeKoS combined with ecosystem condition indicators for three ES.

Author Contributions: Conceptualization, M.P., C.S.C. and B.B.; methodology, M.P.; writing—original draft preparation, M.P.; writing—review & editing, C.S.C., F.M., P.R. and B.B.; supervision, B.B. All authors have read and agreed to the published version of the manuscript.

Funding: This study was part of IMAGINE project (BiodivERsA) supported for Germany by the BMBF–Federal Ministry for Research and Education.

Acknowledgments: We thank Angie Faust for the English language check.

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

Abbreviations	**Definitions**
ATKIS	Authoritative Topographic and Cartographic Information
SystemBGR	Federal Institute for Geosciences and Natural Resources
CBD	Convention for Biologic Diversity
CICES	Common International Classification of Ecosystem
ServicesCLC	CORINE land cover
CSA	Case study area
EC	Ecosystem condition
EEA	European Environment Agency
ES	Ecosystem service
EU	European Union
FISBo	Soil Information System of the Federal Geosciences and Natural Resources (BGR)
InVeKoS	Integrated administration and control system

LTER	Long-term ecological research
LULC	Land use/land cover
MES	Mapping and assessment of ecosystems and their services
MMU	Minimum mapping unit
RLI	Red List Index
SIM	Similarity in means
SIP	Similarity in pattern
SIV	Similarity in variance
SOC	Soil and organic carbon
SSIM	Structural similarity index

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Chapter 4

A hierarchical framework for mapping pollination ecosystem service potential at the local scale

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Ecological Modelling (2021), 444, 109484

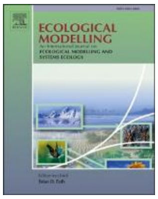
This Chapter focuses on quantifying, modelling and mapping pollination service potentials using hierarchical species distribution models (SDMs) and the Ecological Production Function (EPF) framework. With this study, we aimed at better understanding ecological processes underlying the delivery of specific ES and how bioclimatic variables, land cover and the presence of semi-natural habitats impact the distribution patterns of ESPs and thereby the delivery of ES.

Ecological Modelling 444 (2021) 109484

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



A hierarchical framework for mapping pollination ecosystem service potential at the local scale

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ARTICLE INFO

Keywords:
Species richness
Ensemble species distribution modelsWild
bee species
Ecosystem service providers
Species-specific habitat filter

ABSTRACT

Wild bees play a major role in the cultivation of crops for human use, in the reproduction of many wild plants andare a key component of biodiversity. Mainly due to human activities, wild bees, like other insects, face a rapid decline in Europe. Understanding species distribution can help to design efficient conservation measures. Species distribution can also be used to estimate pollination ecosystem service potential, which can benefit the pro- duction of crops relying on pollination and the reproduction of wild plant communities. The presence of pollinators depends on a combination of environmental and biotic factors, each playing a determining role at different spatial scales. We therefore developed a model composed as a hierarchical framework for environ- mental predictors: climatic data and Land Use/Land Cover (LULC) variables at the European scale and species-specific habitat information at the local scale. The model combines the advantages of two different existing approaches: pollinator species distribution predictions based on their environmental requirements and knowledge on bee species life-history traits and habitats. This paper presents the predicted distribution of twenty-five wild bee species of the *Andrena* genus in an agricultural region in Northern Germany. We used oilseed rape pollinators as a case study and compared the potential pollination services to the potential demand in the Case Study Area. The developed framework allows to determine the capacity of landscapes to support pollination ecosystem services from wild bees at the local scale, which can support the identification of vulnerable areas and the design of local scale measures for habitat improvement and for conservation. The hierarchical approach leaves potential for further adaptations in order to improve the prediction of wild bee species dynamics and factors influencing their spatial distribution.

1. Introduction

Pollination is a key ecosystem service, vital to both wild plants and cultivated crops (Klein et al., 2007). Gallai et al. (2009) estimated that 10% of the total economic value of food production in Europe depends upon insect pollination. There is growing evidence that wild bees play a significant role in crop pollination (Javorek et al., 2002; Greenleaf and Kremen 2006a; Klein et al., 2007; Bommarco et al., 2012; Garibaldiet al., 2013), and that the pollination service delivered by wild pollinators cannot entirely be substituted by honeybees (Brittain et al., 2013; Garibaldi et al., 2013). An increasing number of insect pollinators are in decline or threatened, mainly because of anthropogenic stressors such as environmental pollution, land use change and agricultural intensification but also climate change (Winfree et al., 2009; Potts et al., 2010;Cameron et al., 2011; Ollerton et al., 2014; Nieto et al., 2014). This decline of pollinating species will not only have an impact on agricultural productivity and resilience (IPBES 2016), it can also lead to a parallel decline of wild plant species (Biesmeijer et al., 2006), as globally estimated 85% of flowering plants (78% in temperate zones) are adaptedto animal pollination (Ollerton et al., 2011), mainly to bees (Potts et al., 2010). Therefore, ongoing declines in pollinator diversity may result in community cascade effects, i.e., the subsequent loss of other species that directly or indirectly rely upon extinct or declining species (Chapinet al., 1997). This in turn can have an impact on wild food, fibre and medicine supplies, as well as decrease the cultural and aesthetic values of the cultural

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https://doi.org/10.1016/j.ecolmodel.2021.109484
Received 17 August 2020; Received in revised form 27 January 2021; Accepted 28 January 2021

and aesthetic valuesof a landscape (IPBES 2016).

In light of these observations, there are increasing calls and efforts to conserve wild pollinator species and their habitats (IPBES 2016). An effective biodiversity conservation policy should provide a clear guidance to planning authorities on how to develop targeted species-specific conservation options for organisms that contribute to pollination ser-vices at relevant scales (Kremen et al., 2007). To this end, there is a need for better spatial assessments of pollination. Understanding spatial patterns of pollinators is also crucial for estimating their availability to pollinate cultivated crops and wild plants (Kremen et al., 2004), to facilitate monitoring and inform on the habitats and vulnerability of local pollinators (Kremen et al., 2007; Kremen and Chaplin-Kramer 2007).

Up to now, the main approaches for building pollinator ecosystem service maps are by using InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) (Sharp et al., 2016) and ESTIMAP (Ecosystem Service Mapping Tool) (Zulian et al., 2013). InVEST and ESTIMAP models are primarily based on expert judgements on the presence and preferences of pollinators (essentially nesting places and floral feeding resources). The main issues with expert-based knowledge are that this knowledge may strongly depend on their selections, experience and expertise (Polce et al., 2018; Lonsdorf et al., 2009), and therefore can be biased towards specific species or species groups. Fewer studies are based on Species Distribution Models (SDMs) and actual species records (Polce et al., 2013; Polce et al., 2018; Nogué et al., 2016). SDMs rely on the correlation between environmental variables and geo-localizedspecies records to determine the environmental variables that drive species presence and delineate potential species distribution (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Araújo and Guisan 2006). Contrary to SDMs, InVEST and ESTIMAP models do not allow to dynamically consider different environmental conditions (Lonsdorf et al., 2009; Zulian et al., 2013). When mapping pollination ecosystem service potential at national or sub-national scales, bioclimatic conditions can largely vary and be a major determinant of bee species occurrence. Conversely, existing pollination models based on SDMs are at relatively coarse resolution, constrained by occurrence data and environmental variables typically available at coarse spatial resolution. Especially in highly fragmented landscapes, this resolution may fail to cover important habitats such as hedgerows, small pastures and forests, and therefore obtain biased pollinator distribution maps. Thus, to improve our ability to predict pollinator diversity and the associated pollination ecosystem service, one possibility could be to combine the advantages of the two different approaches: species distribution predictions through SDMs and knowledge on bee species life-history traits and habitat requirements as implemented in InVEST and ESTIMAP frameworks.

The aim of this study is to develop a high-resolution pollinator species model to predict spatial patterns of pollination ecosystem services potential from wild bees at the local scale. Hereby we assume that pollinator species richness and landscape suitability are good proxies of pollination service potential. This is a common assumption in existing pollination models (Kremen et al., 2007; Lonsdorf et al., 2009; Zulianet al., 2013) and is supported by the fact that pollination quantity, quality and stability tend to increase in landscapes with a diverse pollinator community (Klein et al., 2007; Albrecht et al., 2012; Dainese et al., 2019). The model is used as a tool to provide clear guidance for potential users such as planning authorities on how to optimise conservation measures for wild bee conservation and to inform on how management decisions can affect pollination ecosystem services and therefore pollination-dependant crop productivity. We apply the modelin an agriculture-dominated case study area in northern Germany to test this approach at the local scale and its applicability for landscape management, using selected bee species as an example. The approach also allowed us to assess how and which environmental variables affect wild bee species distribution, as well as the role of life-history traits on their spatial distribution.

2. Materials and methods

2.1. Case study area (CSA)

The CSA is located in the region of the Bornhöved Lake District in the federal state of Schleswig-Holstein in Northern Germany (Fig. 1). The extent of the area is approximately 140 km^2. Agroecosystems dominate the landscape in a catchment area of five glacially formed and consecutively connected lakes. The CSA shows a suit of habitats with a high proportion of hedges and wall hedges that are characteristic in the province, shaping a highly diverse and fragmented landscape (see Fig. 1 and Fränzle et al. 2008). Only small settlements, following a north-south alignment, are located in the CSA.

2.2. Datasets

2.2.1. Bees

We selected species from the genus *Andrena*, also called mining bees, as they represent a highly various group including small bees to ones larger than honey bees, species that differ in seasonality or soil preference as well as specialists (oligolectic) and generalist (polylectic) species. This genus of bees is therefore a good representative of a broad range of bee species. From the *Andrena* genus, we selected species that were identified in the region and documented in the federal red list (van der Smissen 2001). This step accounts for historical and current dispersal limitations and helps to determine which species in the global source pool could have dispersed to the CSA (Guisan et al., 2017). The selected *Andrena* species are listed amongst the most important pollinators for crops in Europe, particularly of oilseed rape flowers and apple trees (Klein et al., 2007; Kleijn et al., 2015), or wild flowers (Westrich 2018). Plant families visited by each species are listed in Table 1 in the supplementary material. We obtained 125,681 presence-only records of twenty-six wild bees from the Global Biodiversity Information Facility[1] (GBIF). Occurrence records retrieved from GBIF were cleaned using the “CoordinateCleaner v.2.0–14′′ package (Zizka et al., 2019). Occurrences with sea coordinates, zero coordinates or without geographic coordinate, country mismatches, country centroids, outlier coordinates and coordinates assigned to biodiversity institutions were excluded. We also removed data older than 1950 as old records are more likely to be unreliable (Maldonado et al., 2015), data records with unprecise coordinates and duplicates. We also checked for taxonomic errors, including spelling mistakes and synonyms. To reduce model overfitting derived from spatial autocorrelation and overdominance of specific regions due to sampling bias, we then thinned the records using the package “spThin v.0.2.0′′ (Aiello-Lammens et al., 2015).

We only selected species that had more than 50 GBIF occurrencerecords, as this is a key criterion for SDM modelling quality (Guisan et al., 2017). After geographic and taxonomic cleaning, only 10,928 records of twenty-five wild bee species were retained for modelling (Table 1 in the supplementary material).

2.2.2. Environmental variables

We used bioclimatic and Land Use/Land Cover (LULC) data as environmental predictors (see Table 2 in the supplementary material for a complete list of the environmental variables). We first selected the main drivers of species ranges based on knowledge about mechanistic relationship between environmental variables and physiology of the targeted species. We further reduced the number of variables as too many variables increase the risk of overfitting and collinearity issuesbetween the variables (Dormann et al., 2013; Guisan et al., 2017). Collinearity refers to the non-independence of predictor variables and can be a problem for the

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[1] https://www.gbif.org/

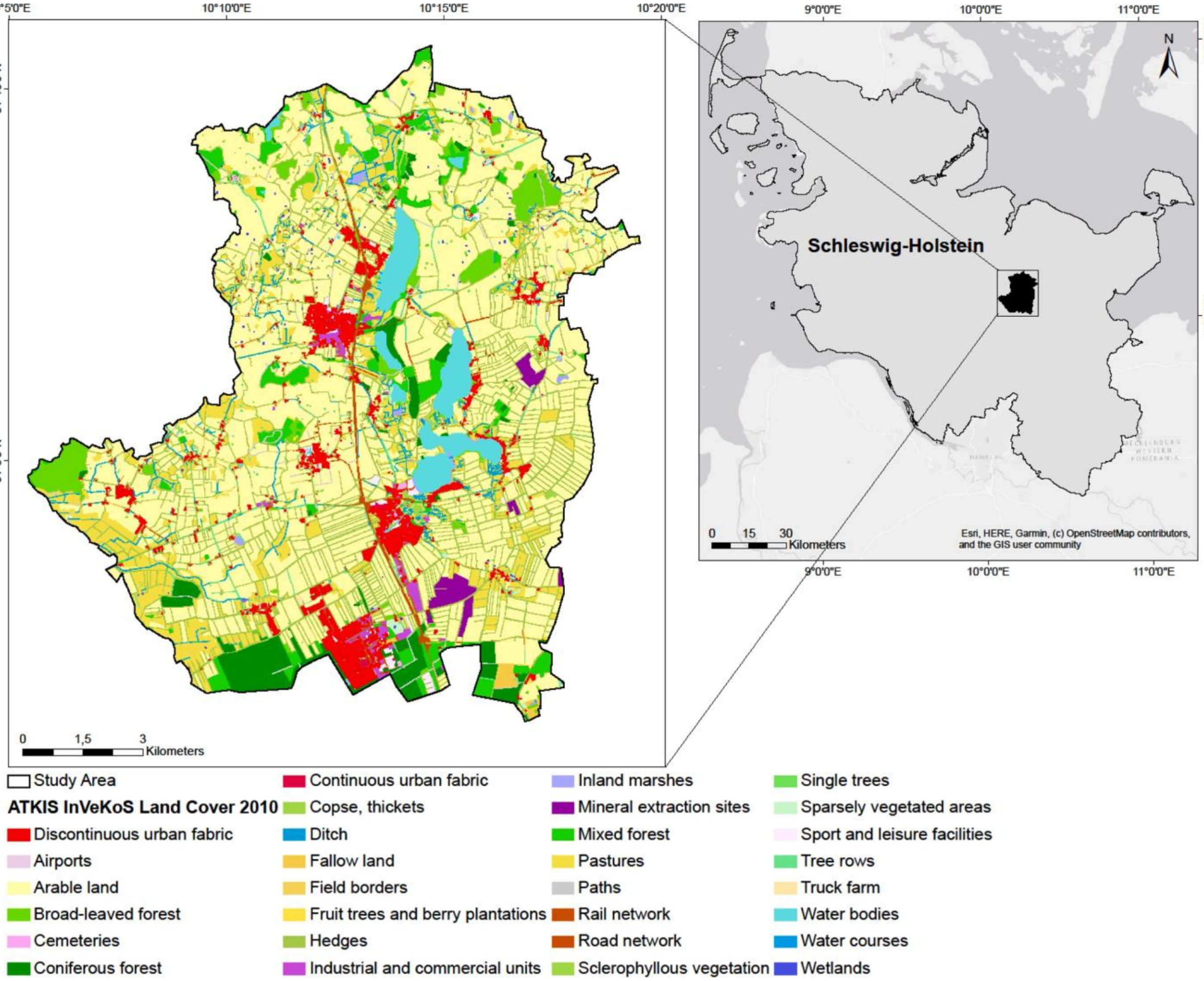

Fig. 1. Location of the study area in Northern Germany (on the right) and distribution of Land Use / Land Cover classes (AKTIS/InVeKoS (2010)) in the case studyarea (on the left).

parameter estimation as it inflates the variance of regression parameters and potentially leads to the wrong identification of relevant predictors. Therefore, reducing the number of environmental variables maximises the performance of SDMs and the accuracy of the predictions (Araujo and Guisan 2006). A Principal Component Analysis (PCA) was used to visualize the correlation between variables, to identify the main environmental gradients in the study area and to investigate the distribution of species in the environmental space (Guisan et al.,2017). We conducted our PCA using the "ade4 v.1.7–16'' package from R (Dray and Dufour 2007). We also analysed correlations between environmental variables with a Pearson analysis for all bioclimatic and LULC variables. Only the most relevant uncorrelated variables, i.e., with a Pearson's correlation coefficient below 0.7, were finally selected (Dormann et al., 2013).

The bioclimatic variables were first selected based on their impact on diurnal foraging activity of bees, nesting success and plants availability. During active months, low temperatures and high precipitation values reduce the number of foraging days and consequently potentiallydecrease bee fitness (Westrich 2018). High precipitation values probably impact the nesting success for ground nesters (Bystriakova et al., 2018). Extreme temperature and precipitation also indirectly affect bees by impacting the bloom of plants and therefore resource availability (Nieto et al., 2014). Climatic data were retrieved from WorldClim[2] on a 30 second resolution raster grids (~1 km^2 at the equator) from WorldClim 2.0 (Fick and Hijmans 2017). From the 19 available climatic variables, we first selected the variables expected to be the most causal for the species distribution: Bio_02 (Mean Diurnal Range), Bio_5 (Max Temperature of Warmest Month), Bio_6 (Min Temperature of Coldest Month), Bio_7 (Temperature Annual Range, Bio_5 - Bio_6), Bio_8 (Mean Temperature of Wettest Quarter), Bio_10 (Mean Temperature of Warmest Quarter), Bio_11 (Mean Temperature of Coldest Quarter), Bio_14 (Precipitation of Driest Month), Bio_16 (Precipitation of Wettest Quarter), Bio_18 (Precipitation of Warmest Quarter) and Bio_19 (Precipitation of Coldest Quarter). The results of the PCA indicated that from the nine pre-selected bioclimatic variables, eight were strongly correlated (Bio_5, Bio_6, Bio_10 and Bio_11, Bio_14 and Bio_18 as well as Bio_19 and Bio_16) and one (Bio_8) did not significantly contribute to the overall environmental variation (see Fig. 1 in the supplementary material). We selected Bio_19, Bio_11, Bio_2, Bio_7 and Bio_14 for the modelling, as they are good variables for discriminating between beespecies and the rest of the environment.

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[2] http://worldclim.org/version2

In temperate zones, wild bee species distributions are influenced by the proportion of heathland, woodland, grassland and urban areas coverages at the landscape scale (Senapathi et al., 2015). As major threats to wild bees in Europe, agricultural intensification and expansion, pollution and urban sprawl will generally have a negatively impact wild bee species distribution (Nieto et al., 2014). For this study, LULC data was derived from the CORINE (Coordination of Information on the Environment) Land Cover 2018 dataset[3], with a 100 m resolution. This dataset is produced by the European Environmental Agency (EEA) and is composed of 44 different LULC classes belonging to the five main land cover categories artificial surfaces, agricultural, forest, semi-natural areas, wetlands or water bodies. We used the hierarchical level 3 from CORINE and first aggregated the data in 1 km * 1 km grid cells, representing the percentage cover of each LULC per 1 km * 1 km grid. This was a necessary first step to generate a clean data structure for modelling (all predictors having the same resolution). The resolution of the predicted results is the same as the one of the environmental variables (1 km * 1 km). We first selected 15 LULC classes based on their ecological relevance: Continuous urban fabric, discontinuous urban fabric, road and rail networks and associated land, non-irrigated arable land, pastures, complex cultivation patterns, broad-leaved forest, coniferous forest, mixed forest, natural grasslands, moors and heathland, transitional woodland-shrub, sparsely vegetated areas, water courses and water bodies. We run the complete model a first time to select the most important variables for the select wild bee species distribution. This ledto the selection of the following LULC variables: discontinuous urbanfabric, non-irrigated arable land, pastures, coniferous forest, sparsely vegetated areas, water courses and water bodies. The selected LULC variables are neither correlated within each other nor with the selected bioclimatic variables (see Pearson correlation coefficients in Table 3 in supplementary material).

In total, five bioclimatic variables and seven LULC classes were selected for modelling the potential distribution of the twenty-five bee species.

2.2.3. Habitat filter variables

We used the ATKIS (version 2012, Authoritative Topographic and Cartographic Information System), the official topographic information system for Germany and the InVeKoS (version 2010, Integrated Administration and Control System) datasets to build our species- specific habitat filters. The ATKIS dataset is originally mapped at a scale of 1:25.000 and describes 182 object classes that belong to artificial surfaces, traffic, vegetated areas (mainly agricultural, forest and natural areas), water bodies and relief (such as dams, cliffs, dunes). The InVeKoS dataset was used to obtain landscape elements such as hedge- rows and tree rows for the CSA. For both datasets, the spatial resolution depends on the feature classes and has a MMU between 0.1 and 1 hectare (Bach et al., 2006). The ATKIS/InVeKoS datasets was used to map bee species habitat as described by Westrich (2018). To our knowledge, it is the most appropriate way to map bee species habitat at a high thematical and spatial resolution in our CSA. Though the latest generation of satellite products may allow to map LULC at a high resolution and to describe the presence of landscape elements at European scale, this data is not available yet. We created a habitat filter for each of the twenty-five selected bee species, by keeping only the LULC classes described as potential habitats (Table 4 in the supplementary material).

2.3. Model calibration and evaluation

2.3.1. Conceptual model

We aimed at developing a species-centered approach based on the Ecosystem Services Providers (ESP) concept, i.e., species, functional groups, species communities, or habitats that produce ecosystem services (Kremen et al., 2007). In our model, the ESP are wild bees that provide pollination ecosystem services. The conceptual framework (Fig. 2) is inspired by the Ecological Production Function framework from Kremen et al. (2007). Key elements for species geographical distribution depend on the spatial scale of the influencing factors (Pearson and Dawson 2003; Thuiller 2004; Milbau et al., 2009; Hortal et al., 2010). At the global scale, species occurrence is governed by bioclimatic and land cover variables (Fig. 2a) (Hegland et al., 2009). For bee species, distribution drivers at the global scale are not yet well understood (Bystriakova et al., 2018), while local determinants are relatively well known and mainly depend on the presence of nesting places and floral resources at the local scale, which define the habitat of a species (Fig. 2b) (Westrich 2018). The analysis of the role of different environmental drivers at their operating scales is required to appropriately predict wild bee occurrences at the local scale. We therefore use a hierarchical framework that builds on the work of Milbau et al. (2009): environmental drivers operating at large scales are used to predict species distribution using SDMs, and the outputs are combined with a species-specific habitat suitability filter to refine the suitability maps at the local scale. The pollination efficiency of each species depends on life-history traits, such as morphology and behaviour (Willcox et al.,2017). One important trait for the pollination of crops is the foraging range (Fig. 2c), because it determines the distance over which pollen can be transported and if crop fields or target plants are reachable for the different species. The pollination potential is defined as the sum of each predicted species probability of presence combined with foraging distances. The pollination ecosystem service potential on crop fields was restricted to the probability of presence of crop pollinators on potential pollination-dependant fields (Fig. 2d).

2.3.2. Species distribution model

Species distribution modelling was carried out with the “biomod2 v.3.4.6'' library (Thuiller et al., 2016) implemented in R (Version 4.0.3) (R Core Team 2017). All maps were created using ArcGIS (Version 10.6.1).

Occurrence data from GBIF are typically presence-only data, with no recorded absence data, whereas the algorithms used for modelling need presence-absence points, so pseudo-absence points were generated with the following approach: several sets of pseudo-absence data were generated to prevent sampling bias and to be able to test the effect ofeach pseudo-absence selection on the predictive ability of the model. Following Phillips et al. (2009), we restricted the selection of the background points in a 10 km buffered convex hull around the GBIF *Andrena* records to reflect species sampling bias. One thousand pseudo-absence data points were sampled randomly from the back- ground region and we repeated the random selection ten times to build a ten-fold internal cross-validation of the models (Phillips et al., 2009; Barbet-Massin et al., 2012).

We chose to combine different algorithms with ensemble modelling as no statistical tools will *per se* perform better than any other (Elith and Leathwick 2009; Aguirre-Gutiérrez et al., 2013; Araújo et al., 2019) and as predictions based on an ensemble of several algorithms are often more robust than predictions derived from a single model (Araújo and New 2007; Araújo et al., 2019). For each bee species model, we used three different algorithms: Generalized Linear Model (GLM), a flexible regression model allowing to handle non-normally distributed response variables, Flexible Discriminant Analysis (FDA), a flexible classification approach derived from Linear Discriminant Analysis methods and Random Forest, a bagging approach. To train the SDMs and test their predictive performances, we used a cross-validation with a random subset of 70% of the points to calibrate the model for every single species, while the remaining 30% of the points were used for validation. Each single model was run on the training data and evaluated on the test data using performance evaluation metrics. This process was repeated four times with different partitioning of the original dataset into a training and a test set. Cross-validation was used to decrease bias in the predictive performance of the measuring models (Pearce and Ferrier 2000).

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[3] https://land.copernicus.eu/pan-european/corine-land-cover/clc2018

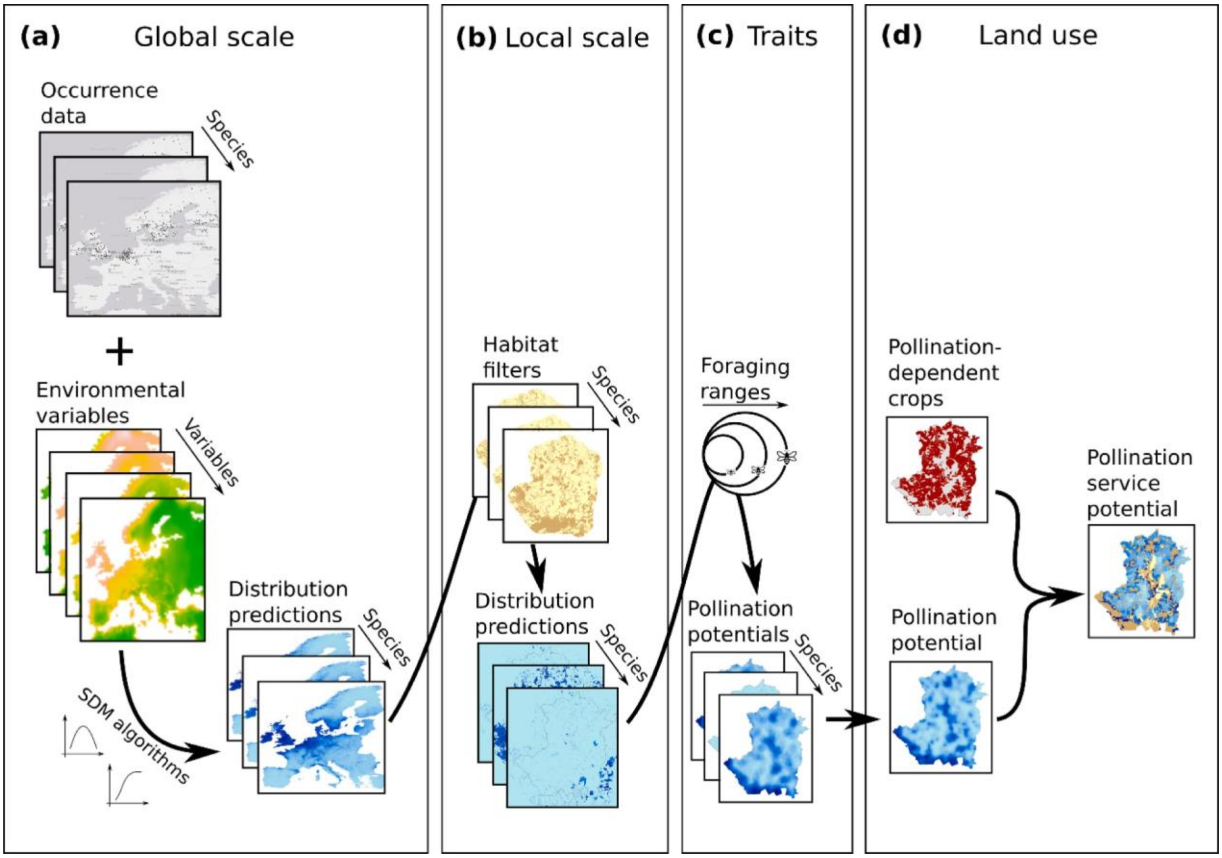

Fig. 2. Flow chart representing the different steps of the hierarchical modelling approach to predict pollination potential at the local scale.

We used different performance evaluation metrics: Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot, True Skills Statistics (TSS) and the continuous Boyce index (CBI). AUC is a threshold-independent model evaluation indicator (Franklin 2010), which continuously discriminates between suitable and unsuitable habitats, independently of prevalence of target species (Elith and Burgman 2002). It plots the commission error against omission error and ranges between 0.5 and 1, where 1 represents a perfect discrimination between presence and absence, and 0.5 represents a random fit. TSS is a threshold-dependant measure of model accuracy and, contrary to AUC,is based on binary predictions of predicted suitability/unsuitability for each species (Allouche et al., 2006). It ranges from -1 to 1, with +1 indicating perfect agreement between predictions and observations, and 0 or less indicating an agreement no better than a random classification (Zhang et al., 2015). This metric is negatively related to species prevalence (Allouche et al., 2006). Contrary to AUC and TSS, CBI does not require absence data and is therefore considered as more appropriate when working with presence-only data. The metric measures howobserved presences are distributed across the gradient of predicted presences and how this differs from a random distribution. It also varies from -1 to 1, where positive values indicate a good agreement between predictions and the distribution of presences in the evaluation dataset, values close to zero indicate predictions not different from a random distribution and negative values indicate incorrect models (Hirzel et al., 2006).

One of the main challenges in modelling pollination potential is that each pollinator species has its specific potential geographical range and habitat needs, so each species needs to be modelled independently. For each bee species, a total of 120 models was built (using three algorithms, four cross-validations to sample test and training data and ten pseudo-absences samplings). Only models with a TSS greater or equal to 0.6 were kept to build the final ensemble (Landis and Koch 1977). Ensemble predictions were calculated as weighted averages of single-model pre- dictions, with weights assigned to each modelling technique using the TSS (Allouche et al., 2006).

To ensure transparency and reproducibility of our SDMs, we included an Overview, Data, Model, Assessment, and Prediction (ODMAP) protocol from Zurell et al. (2020) in the supplementary material.

2.3.3. *Habitat filter*

The next step was to combine the SDM ensemble models with the corresponding habitat filters for each modelled bee species into a unique predicted distribution (or environmental suitability) map for the CSA(Fig. 2b). To do so, for each species and each grid cell of the CSA, we multiplied the species distribution prediction and the binary habitat filter values. The resulting maps represent the suitability of the area to support the different bee species, according to its environmental conditions and the presence of potential habitats for each species.

2.3.4. *Foraging range*

As bees are central place foragers, their foraging ranges determine their capacity to pollinate and to potentially increase the yield of adjacent crop fields. The foraging ranges of the species were added to the model to determine the final pollination potential map (Fig. 2c). Foraging distances are species-specific and are a function of the inter- tegular distance (i.e., the distance between the wing-attachment points on either side of the thorax) (Greenleaf et al., 2007). Kendall et al. (2019) implemented the "pollimetry v.1.0.1" library, which allows to calculate foraging distances based on intertegular measurements of bees and provide the resulting database intertegular measurements of 4035 bee specimens. We used this package in R to estimate the average foraging range of the twenty-five selected bee species. When no data were found, we used the average of all foraging ranges over the *Andrena* genus. Foraging range values are presented in Table 5 in the supplementary material. Using the “raster v3.4–5′′ package (Hijmans et al., 2013), we then implemented a circular moving window, with a focalcorresponding to the average foraging distance of each bee species. For each grid cell of the CSA, the pollination potentials were computed based on the foraging ranges and the suitability of the area to support the different bee species.

2.3.5. Relative pollination potential

The total pollination potential of the CSA was calculated as the sumof the pollination potential of each species, determined in the previousstep. We made the assumption that local species communities are made of species with the same environmental requirements and we neglected macroecological controls on community assembly such as competition and synergies between species (Guisan and Rahbek 2011). We chose to work with occurrence probability maps and not with binary presence/absence maps, as Calabrese et al. (2014) and D’Amen et al. (2015) showed that the addition of predictions of occurrence probabilities from individual SDMs is preferable to setting arbitrary thresholds to obtain binary predictions and then combining those into a stacked-SDM, as this tend to be biased and overpredict of species richness.

The resulting map represents the relative pollination potential of the area, i.e., the potential of the area to sustain pollination from the selected *Andrena* species.

2.3.6. Comparison with independent field data

In the CSA, flower visiting insects were collected using one yellow pan trap in 12 rapeseed fields between May 4th to June 6th 2018. Traps were set up at one border of each field, close to a near-natural habitat (such as hedgerows or forests), with their tops approximately even with the surrounding oilseed rape flowers. The traps were filled with diluted detergent solution and emptied weekly. All bees were identified to species level. The trap locations were selected to cover the landscape diversity in the CSA: from locations surrounded by a landscape with a high proportion of near-natural habitats to locations with a low pro-portion of near-natural habitats.

We used linear regression to assess whether the pollination model outputs reflect the pollinator community abundance and species richness collected in the field. We compared the abundance and richness of oilseed rape pollinators from the *Andrena* genus from the collected data with the predicted pollination potential. We also compared *Andrena* species richness from the collected data with the predicted richness of *Andrena* species obtained with the model (the sum of all the predicted suitability using the SDMs and the habitat filters, Fig. 2b in the work- flow). For this comparison, we calculated the mean predicted species richness for all pixels within a radius of 200, 300 and 500 m radius of trap locations.

3. Results

3.1. Model evaluation

The evaluation scores of all ensemble models were high to very high (ROC between 0.892 and 0.978, TSS between 0.623 and 0.887 and CBI between 0.965 and 1), which means that the predictive accuracies of the models were good to very good. An overview of all these performances measures can be found in Table 7 in the supplementary material.

The importance of each predictor for each species model varied with the tested algorithms and modelled species. Bioclimatic variables indicated a higher percentage of the data variances than LULC variables.Bio_2 (Mean Diurnal Range), Bio_11 (Mean Temperature of Coldest Quarter) and Bio_7 (Temperature Annual Range) appear to be generally the most important variables, followed by Bio_19 (Precipitation of Coldest Quarter) and Bio_14 (Precipitation of Driest Month). LULC variables have a more minor importance for the models and generally only few categories are relevant for each species. Discontinuous urban fabric is overall the most important LULC variable, followed by non- irrigated arable land and sparsely vegetated areas (Table 6 in the supplementary material).

3.2. Species distribution models

Figs. 3 and 4 illustrate the different results for two species (*Andrena barbilabris* and *Andrena carantonica*). The predicted presence of each species is determined through a SDM at the European scale (Figs. 3 and 4 (B)) based on occurrence data (Figs. 3 and 4(A)). Even at the local scaleof the CSA, we obtained different distribution predictions for each species. For instance, the model predicted that overall, the area is slightly more suitable for *A. carantonica* than for *A. barbilabris* (Figs. 3 and 4(C)). Habitat filtering was done with a buffer of 2 km around the CSA to ac- count for foraging distances and the possibility that bees can nest outside and forage inside the CSA (Figs. 3 and 4(D)). The differences in the finalpredicted presence of species were also due to habitat preferences of each species: For instance, *A. carantonica* has a wider range of potential habitats and a broader distribution over the CSA than *A. barbilabris*. *A.carantonica* has a wider foraging range than *A. barbilabris* (700 m compared to 200 m), which also explains the differences in species respective pollination potential in the final maps (Figs. 3 and 4(E)).

3.3. Potential pollination map for the CSA

The model predicted the CSA as suitable for all the target species. The predicted pollination service potential (sum of the pollination potentialof all target wild bee species) scores from 0 (none of the modelled species is potentially present) to 15 (highest predicted scores when adding the pollination service potential of the twenty-five wild bee species) for each grid cell (see Fig. 2 in the supplementary material). Areas where none of the species is potentially present have no potential pollination ecosystem service performed by the selected and modelled species, whereas a high predicted landscape suitability and wild bee species richness increase the pollination service potential of the area.

Fig. 5 compares the predicted spatial patterns of oilseed rape pollinators and the potential pollination ecosystem service demand for oilseed rape (the main pollination-dependant crop in the CSA), estimated with the ATKIS/InVeKoS “arable land” LULC class. The locationof rapeseed fields generally changes annually, as a result of crop rotation, changing market prices and changes in political schemes and subsidies. The demand for pollination ecosystem services will therefore change annually and can potentially occur on all arable fields. This iswhy we did not directly map rapeseed fields and assumed that it could potentially grow on every arable field. For this analysis, we restrictedthe pool of modelled wild bee species to oilseed rape flowers visitors (as documented in Table 1 in the supplementary material). Our model predicted that most of the fields have a low pollination potential and the mean pollination potential value on arable fields was 1.5. The model predicted low mean pollination ecosystem service potentials particularly the North-Eastern part of the CSA (e.g., in Fig. 5(C)). Fields with relatively high mean pollination ecosystem service potentials are more evenly distributed over the CSA.

3.4. Comparison with independent field data

Yellow pan traps captured 801 individual bees from 42 different species. From the collected wild bees, 681 were from the genus *Andrena*, from 19 different species. Form the genus *Andrena*, 576 individuals were known oilseed rape flower visitors, from 9 different species. Abundance and richness of oilseed rape visitors from the genus *Andrena* increased with the predicted pollination service potential (r = 0.28, d.f. = 10, p = 0.07) and (r = 0.29, d.f. = 10, p = 0.07), however not significantly(Fig. 6(a) and (b)). Oilseed rape visitor richness increased with the mean predicted pollinator richness within a radius of 500 m (r = 0.28, d.f. =10, p

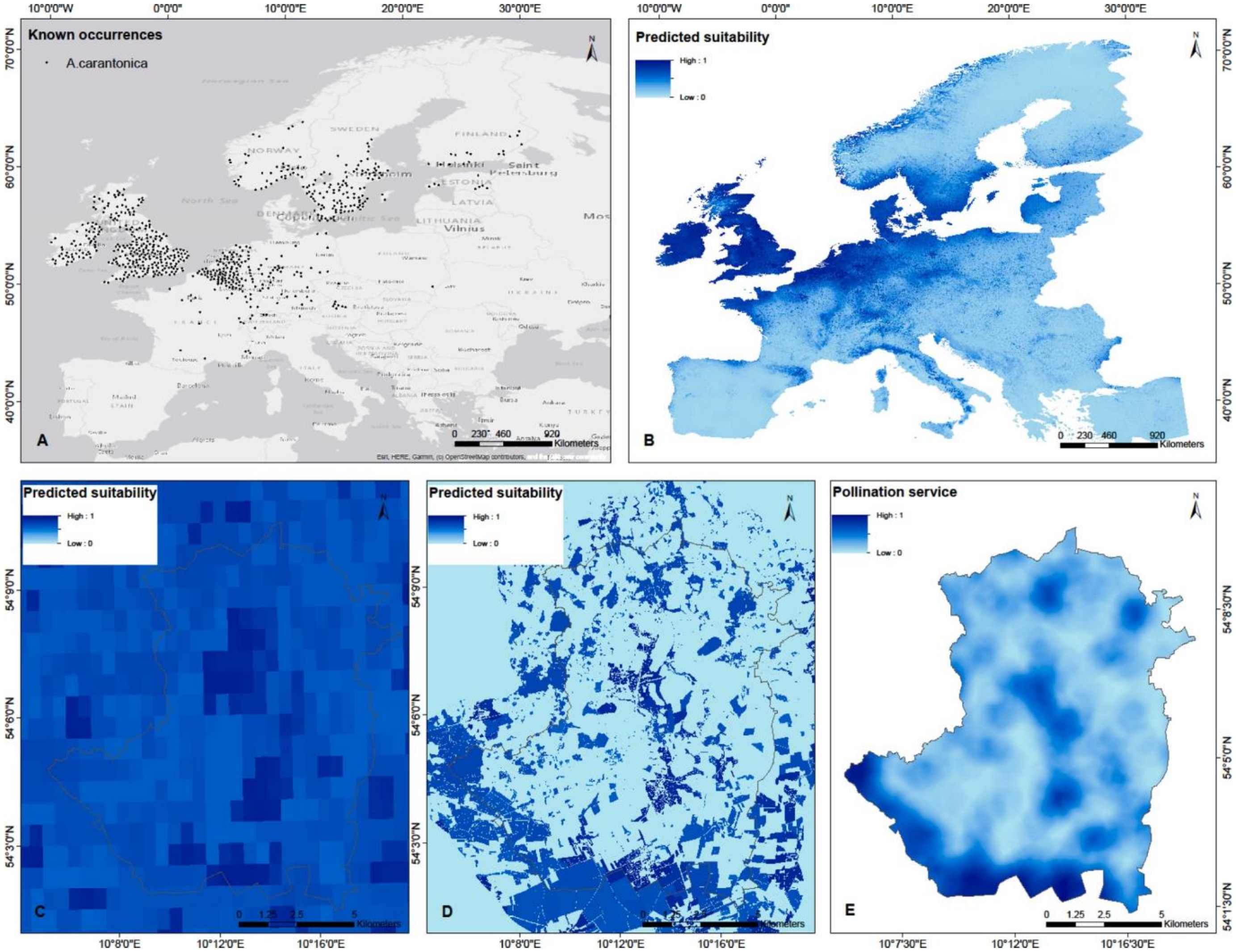

Fig. 3. Examples of species distribution model outputs for A. carantonica. (A): Occurrence points, retrieved from the GBIF database and cleaned, (B): predicted probability of presence at the European level (ensemble model of the best performing algorithms), (C): Zoom of the predicted probability of presence covering the CSA, (D): predicted probability of presence on potential habitats (SDM results X habitat filter; including buffer around the CSA), (E): predicted pollination ecosystem service potential by A. carantonica in the CSA.

$= 0.07$, not shown here), 300 m ($r = 0.38$, d.f. $= 10$, $p = 0.03$) and 200 m ($r = 0.48$, d.f. $= 10$, $p = 0.01$) (Fig. 6(c) and (d)).

4. Discussion

We have predicted the current potential occurrence of twenty-five selected bee species at the local scale in order to estimate the potential pollination ecosystem service supply for pollination-dependantcrops and wild plants. The aim was to develop a model based on peer-reviewed knowledge rather than on expert-judgement, adapted to the region of interest and its bioclimatic conditions and with consideration to the availability of foraging resources and nesting places, for which a fine resolution is needed. One further novelty of the developed methodis that it combines environmental drivers at larger and local spatial scales and thereby goes beyond existing pollination models, which typically focus on one scale, despite the importance of integrating environmental drivers at multiple geographical scales (Milbau et al., 2009; Mateo et al., 2019b).

4.1. *Modelling pollination service potential*

SDMs results highlighted the role of bioclimatic factors in bee species occurrence at continental to local scales, as previously illustrated by Polce et al., (2013); Nogué et al., (2016); Polce et al., (2018) and Bystriakova et al., (2018). This is indicated by the predicted suitability maps (Figs. 3b & 4b): SDMs predicted that the suitability for *A. carantonica* and *A. barbilabris* is highly variable across Europe countries and we also obtained different predictions at the local scale (Figs. 3c & 4c). As the ESTIMAP and InVEST models only express the relative suitability for pollinators in terms of availability of floral resources and nesting sites (Lonsdorf et al., 2009; Zulian et al., 2013), they neglect the variability of bee species distributions due to bioclimatic factors. To our knowledge, no study has yet assessed these models in regard to the use or non-use bioclimatic factors. Furthermore, SDMs provide an effective alternative to local expert opinion on species potential occurrence (Gastón et al., 2014) and can be used to discriminate present from absent species in a given location. In addition, as the modelling framework allows to assess the relative importance of environmental variables on different species, it can be also used to analyse the impact of climate and land cover changes on wild bee species and future pollination service potential.

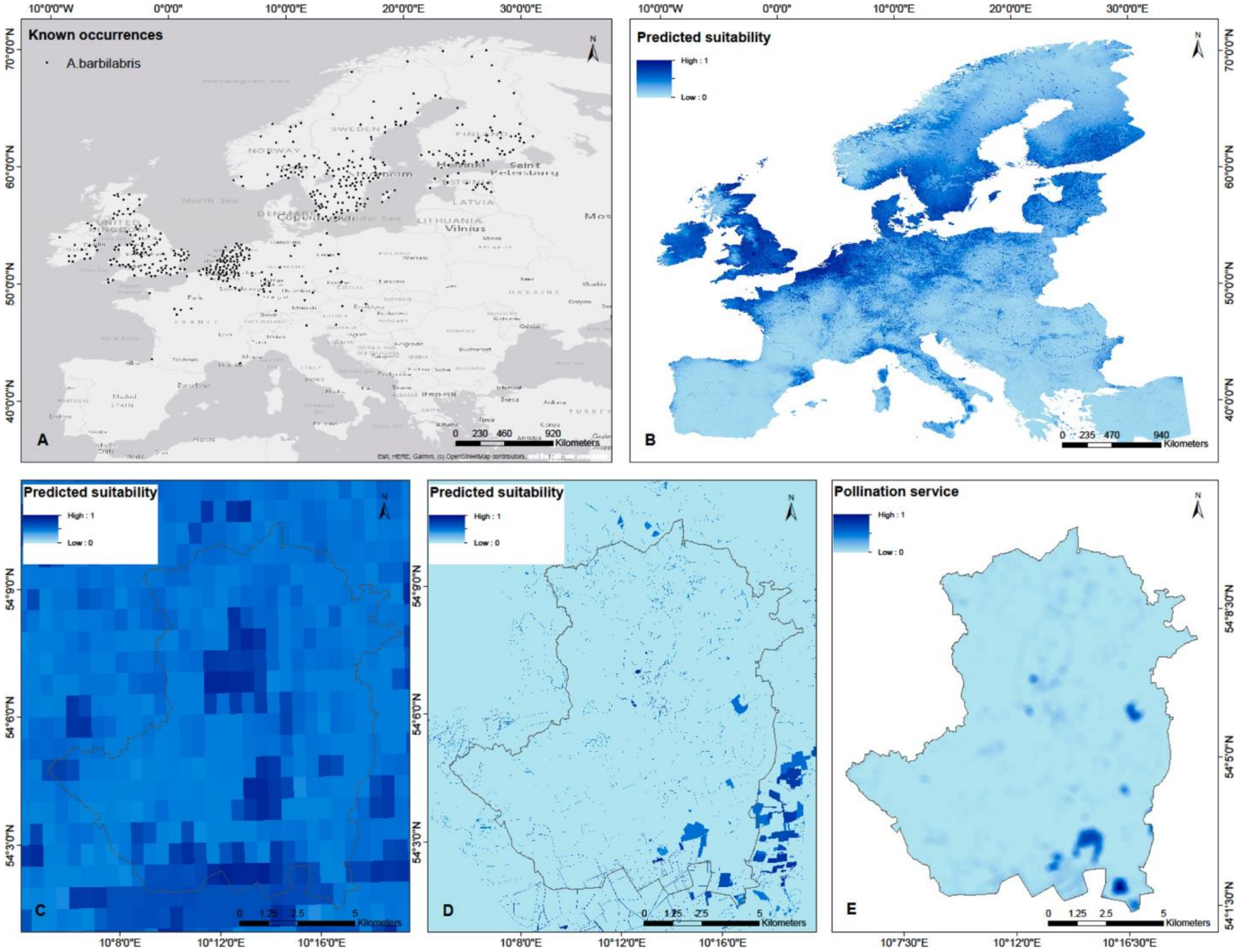

Fig. 4. Species distribution model outputs for A. barbilabris. (A): Occurrence points, retrieved from the GBIF database and cleaned, (B): predicted probability of presence at the European level (ensemble model of the best performing algorithms), (C): Zoom of the predicted probability of presence covering the CSA, (D): predicted probability of presence on potential habitats (SDM results X habitat filter; including buffer around the CSA), (E): predicted pollination ecosystem service potential by A. barbilabris in the CSA.

As they do not account for natural and semi-natural areas, previous pollination (or wild bee species distribution) models based on SDMs also probably overpredict the distribution of bee species at the local scale (Polce et al., 2013; Nogué et al., 2016; Polce et al., 2018; Bystriakova et al., 2018). These models may therefore significantly overpredict the pollination potential and minimize areas where pollination demand exceeds pollination service potential, as only specific areas in croplands provide suitable habitats for wild bee species (mainly natural and semi-natural habitats) (Westrich 2018). This is particularly problematic when pollination-dependant crops are isolated from natural and semi-natural habitats (Ricketts et al., 2008; Garibaldi et al., 2011). The importance of the presence of natural and semi-natural areas at small spatial scales within agricultural landscapes for wild pollinator species has been described in many studies (Gathmann and Tscharntke 2002; Zurbuchen et al., 2010; Ricketts et al., 2008; Kennedy et al., 2013) and is also supported by our results. This is indicated by the differences between the predicted suitability and pollination potential maps (Figs. 3 & 4): our results of SDMs predict that the whole CSA is highly suitable for *A. carantonica* and *A. barbilabris*, whereas their final suitable areas are much more restricted when accounting for habitat availability. This is consistent with Fournier et al., (2017) and Hattab et al., (2014), which also found that adding species-specific habitat filters greatly refined habitat suitability for terrestrial and marine species. As it integrates information on drivers operating across different scales, our multi-scale approach should provide more accurate predictions and a better understanding of processes underlying species distribution compared to single-scale models (Pearson et al., 2004; Mateo et al., 2019b; Mateo et al., 2019a; Bellamy et al., 2020; Fournier et al., 2017).

Despite the low number of sampling sites and the restricted sampling period during the mass-flowering of oilseed rape, our model correlated fairly well with the data observed in the field. The model was able to predict a significant proportion of the variation in oilseed rape pollinator richness from independent data. Oilseed rape pollinator richness andabundance from the collected data were also correlated with the predicted pollination service potential, however with no significance. This analysis can be considered as a first approach to evaluating the model results, but not yet a validation of our model due to the small number of sampling sites and the absence of replication.

4.2. *Limitations and uncertainties of the study*

The presented approach comes with several modelling limitations. First, the performance of each SDM is constrained by the quantity and quality of the GBIF occurrence data. In principle, the performance of each SDM can be

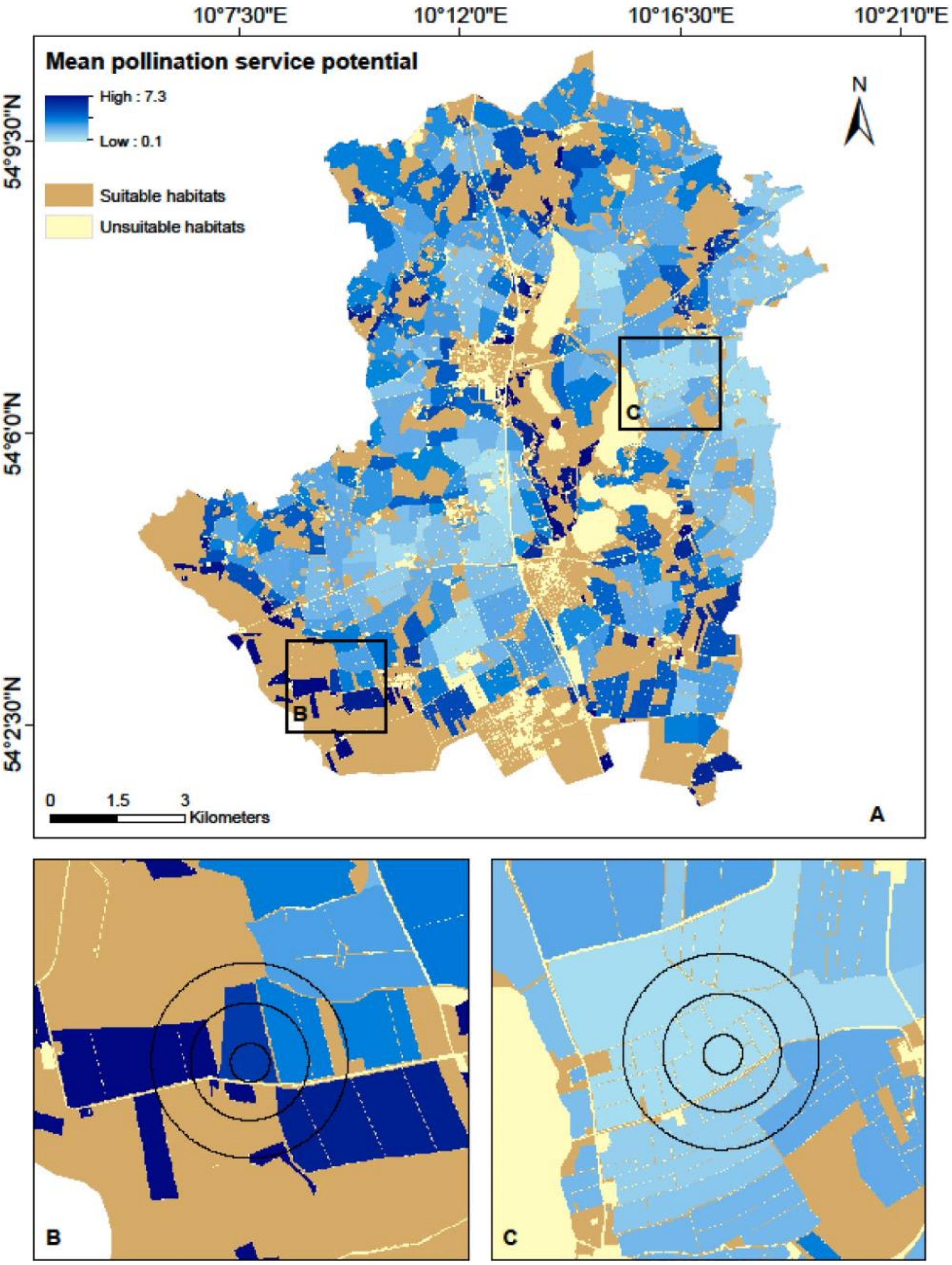

Fig. 5. Predicted mean pollination potential on arable lands (A) and zoom over two contrasting pollination service potential results (B and C). Brown areas represent potential suitable habitats for the different bee species. Light yellow areas represent unsuitable habitats other than arable lands. Arable lands are marked with a gradient from light to dark blue, depending on the predicted mean pollination service potential for each parcel of the CSA (the mean is calculated over each parcel). In (B), the landscape has a larger proportion of potential habitats such as grasslands and forests, whereas in (C), the landscape is largely dominated by arable lands. In (C), the mean pollination potentials tend to be lower than in (B) (values between 0.9 and 6.2 in (B); 0.2 and 4.2 in (C)).
The circles represent the principal foraging ranges of the selected bee species (100, 300 and 500 m radius), so the principal distances around fields within which the presence of habitats for pollinators can increase pollination ecosystem service supply.

improved by including more species occurrence data. For the selected bee species, GBIF occurrence data are particularly biased towards higher occurrences in Northern European countries including Great Britain, Sweden, Belgium and Germany, which may make the outputs of the SDMs less reliable for regions with very different bioclimatic conditions such as Southern European countries. This is however less problematic in the studied CSA, located in Northern Germany.

Second, our model might overpredict single species occurrences because there is no limit on the number of species that can occupy a given area, i.e., the carrying capacity of ecosystems is not considered in SDM approaches (Graham and Hijmans 2006; Thuiller et al., 2015). This is particularly the case when interactions between species (competition, parasitism, mutualism, predator-prey) strongly influence species co-occurrences and can exclude species from a community. For instance, honeybees have been reported to negatively impact the presence of wild bees because of their density and their outstanding foraging capacity (Thomson 2004; Hudewenz and Klein 2013), although this is debatable (Greenleaf and Kremen 2006b; Westrich 2018). One way to account for biotic interactions in SDMs is to test models' residual for evidence of species interaction using Joint Species Distribution Models (jSDMs) (Pollock et al., 2014). Using jSDMs instead of SDMs may increase the explanatory power when modelling pollinator communities. However,when restricted to relatively few species, the present model should not lead to an overprediction of the local pollination potential.

Our habitat filter is based on the work from Westrich (2018), which gathered knowledge on wild bees in Germany based on more than 3000 scientific publications. As the habitat preference of wild bee species may be different in other countries, the habitat filter should be adapted to local characteristics when using the model in other regions of the world.

We found that two precipitation variables and three temperature-related variables were the most important for predicting the potential distribution of bee species over Europe: Precipitation of the Coldest Quarter and of the Driest Month, Temperature Annual Range, Mean Temperature of Coldest Quarter and Mean Diurnal Range.

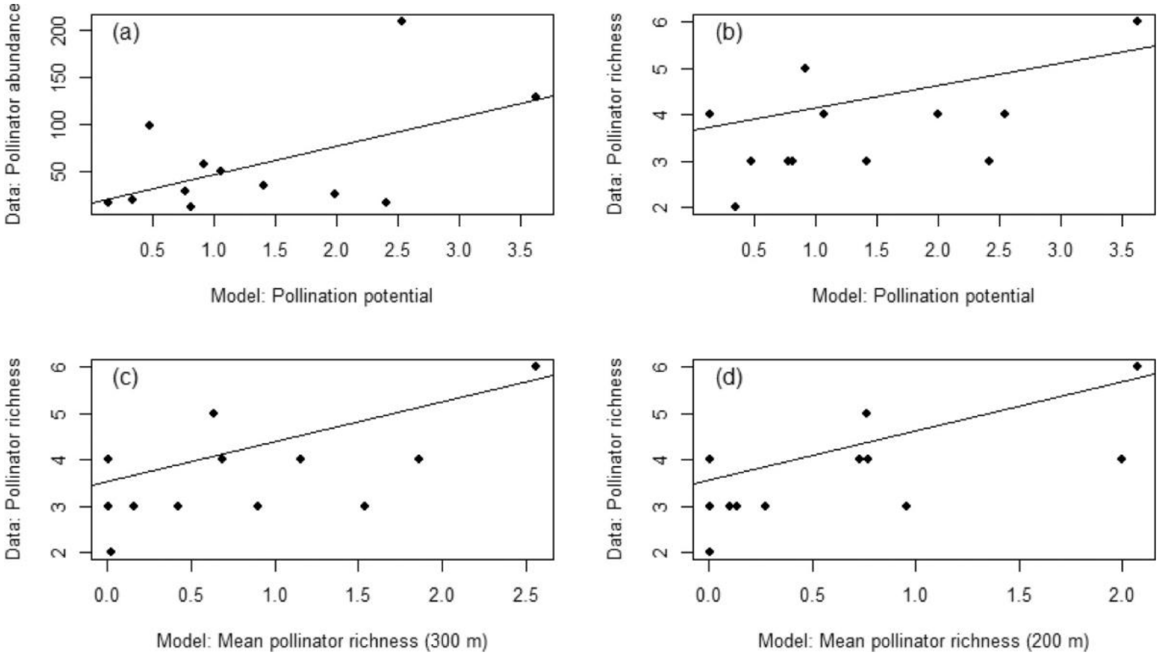

Fig. 6. Linear regressions with one independent dataset from the CSA: between oilseed rape pollinator abundance and the predicted pollination potential (a), between oilseed rape pollinator richness and the predicted pollination potential (b), between oilseed rape pollinator richness and the mean predicted oilseed rape pollinator richness for a radius of 300 m (c) and 200 m (d) around the pan trap locations.

These variables all have a direct or indirect ecological implication that can be explained. Precipitation and temperature extremes affect nesting suitability, foraging behaviour and resource availability. Low temperature and high precipitation values might have a higher impact on the presence of bees during their active season (principally spring and early summer), by directly reducing their foraging capacity. Instead of using bioclimatic variables from WorldClim, SDM predictions might be improved by using temperature and precipitation values restricted to each respective bee-active season. We found that LULC variables have a much lower impact on species distribution, except discontinuous urban fabric, non-irrigated arable land and sparsely vegetated areas for some species and depending on the algorithm. These results on the relative importance of environmental data for predicting bee species distribution are comparable to Polce et al., (2013) but not Bystriakova et al., (2018) nor Polce et al., (2018). This may be due to the selected bee species, as the latter two studies were calibrated with Bumblebee species or bees of the subfamily Colletinae, whereas the study from Polce et al., (2013)was calibrated with species from different genera, including some *Andrena* species. Besides, Polce et al., (2013) found that the use of pesticides plays a significant role in bee distribution. As there is growing evidence that pesticides inputs can have a considerable negative impact on wild bee species (Brittain et al., 2010; Whitehorn et al., 2012), this variable should be used when available to refine the different SDMs.

Effective pollination depends on the pollination effectiveness or performance of each species, which in turn depends on a broad range of factors, e.g., pollinator morphology and behaviour, flower visitation rates, pollen deposition but also plant health (Willcox et al., 2017). There is growing evidence that not all species are equally important for the pollination of a given crop (Kleijn et al., 2015; Winfree et al., 2015)or wild plant species (Gorenflo et al., 2017). Empirical data linking yield gain specifically to one pollinator taxon are however still scarce (but see Rader et al., (2009) and Jauker et al., (2011)), so we did not include information about pollination efficiency of each wild bee species in our model. Furthermore, there are a wide range of community-level factors that may influence pollination efficiency, such as species interactions and niche complementarity (Willcox et al., 2017). Instead, we assumed that the pollination ecosystem service potential of an area increases with the likelihood of the presence of bees and bee species richness, which is supported by Klein et al., (2009), Garibaldi et al., (2011) and Woodcocket al., (2019). Accounting for functional diversity and specifically choosing bee species with a high functional divergence (characterised by non-overlapping traits) could however greatly improve the informative value of pollination models and allows to ultimately link crop pollination service potential to service provision and contribution to crop yield, seed quality and eventually economic return (Woodcocket al., 2019; Gagic et al., 2015). Building on Woodcock et al., (2019), the framework could be further improved by adding an extra step converting species probability of presence into a functional divergence index (i.e., a composite index derived from species effect traits that play an important role for the pollination of the considered crops), whenever this data is available. To do this, the function divergence index from Woodcock et al., (2019) or a similar composite of traits influencing species pollination efficiency could be included in step (c) (Fig. 2) of the framework, along with the foraging range, a trait which is already accounted for in the model. Similarly, including information about temporal dynamics, particularly about bee flight seasons can further increase the robustness of the model predictions. This could be done by adding flighting season filters (similar to the habitat filters) between step (b) and (c) (Fig. 2) of the framework and running the model for each month of the crop flowering season to estimate the monthly pollination service potential throughout the entire crop flowering season. This will allow to assess whether the entire crop flowering time is covered by a high pollination potential or if there is a temporal mismatch between ES demand and potential.

Lastly, the presented pollination potential maps are based on solely one genus (*Andrena*) and twenty-five species, whereas around 300 species have been observed in the region – of which only 110 species are not threatened by extinction nor are already extinct (van der Smissen 2001). As we selected species from the genus *Andrena* and only species that are soil-nesting and solitary, the results certainly do not represent each single bee species occurring in the region. For a better wild bee species richness assessment, other genera should be included in the model. For instance, above-ground nesting bees and species with different degrees of sociality are not represented in our model. Including bees with these characteristics could have an impact on the resulting pollination potential maps, if sociality and nesting requirements play a major role in species distribution. The selected bees are nevertheless suitable for pollination potential modelling, as they represent a highly variable group due to their varied size, seasonality, soil preference for nesting and foraging behaviour and as the vast majority of wild bees are soil-nesting and solitary (Westrich 2018).

4.3. Applications

The pollination potential maps in the studied CSA can help to assess the needs for practical conservation measures to promote insect pollinators in agri-environmental schemes. Spatially explicit maps of the pollination potential in comparison to maps of pollination demand will allow the identification of areas where pollination service is deficient. The resulting maps can support land management recommendations such as where to prioritize habitat conservation measures in agricultural landscapes to sustain biodiversity, ecosystem functions and services that support crop production. One advantage of the developed model is the combination of SDMs and species-specific habitat filters. This can help to develop relevant habitats for species, for which large-scale factors such as climatic parameters are also suitable. For example, in Fig. 4 (C), the dark blue zones indicate a high suitability for *A. barbilabris*. However, as there are only few potential habitats for this species at these spots, the species cannot colonise a large part of these suitable areas. These areas could thus be potential targets for *A. barbilabris* conservation measures, such as the inclusion of fallow in the crop-rotation pattern. Conservation measures such as hedgerows, field margins and flower strips have been shown to have a positive and significant effect on wild bee abundance and diversity (M'Gonigle et al., 2015), particularly for bumblebees (Pywell et al., 2005; Carvell et al., 2011; Pywell et al., 2012). This demonstrates the importance of these habitats at the small scale for pollinator community conservation. Furthermore, Pywell et al., (2012) highlighted the importance of using ecological knowledge of targeted species when designing conservation measures and showed that species-specific measures are much more efficient and sustain a higher species richness than generalized conventional conservation measures. As climatic factors have a significant effect on the distribution of bees, climate change will certainly affect bee distribution in the future and disrupt plant–pollinator interactions (Memmott et al., 2007; Biesmeijer et al., 2006). Our results show that the consideration of climatic factors (and therefore climate change) is essential when developing conservation measures for the long term, for pollinator biodiversity and to preserve plant-pollinator interactions.

5. Conclusions

To our knowledge, this is the first work that developed a framework that predicts geographical patterns of pollinators based on SDM and multi-scale environmental drivers to predict pollination ecosystem ser vice potential at the local scale. The results of the different models show that the framework can be adapted for a local scale assessment. This approach allowed us to predict the pollination potential from mining bee species and to identify areas with high or low pollination ecosystem services potential. The comparison with independent samples showed good agreement between the model outcomes and species occurrence data collected in the field. The developed model can support land-use decisions but also help to identify conservation measures and areas for prioritizing species conservation planning. This method is transferable to other European regions and other countries in the World, provided that they have enough species occurrence data. It can also be used to investigate the effect of climate and land-use changes on pollinators' distribution and pollination potential and help to implement mitigation measures for vulnerable areas and species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was part of the IMAGINE project (BiodivERsA) supported in Germany by the BMBF – Federal Ministry of Research and Education. We are grateful to Igor Oehlschläger and Uta Hoffmann for species identification. We thank Angie Faust for the English language check.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109484.

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Chapter 5

Modelling potential natural pest control ecosystem services provided by arthropods in agricultural landscapes

Perennes, M., Diekötter, T., Hoffmann, H., Martin, E. A., Schöder B. and Burkhard, B.
Agriculture, Ecosystems & Environment (2023), 342, 108250

This Chapter focuses on quantifying, modelling and mapping natural pest control service potentials based on the Ecological Production Function (EPF) framework, using hierarchical species distribution models (SDMs) and analysing species interactions. With this study, we aimed at better understanding ecological processes underlying the delivery of natural pest control ES and how bioclimatic variables and landscape complexity impact the distribution patterns of ESPs and thereby the delivery of ES.

Agriculture, Ecosystems and Environment 342 (2023) 108250

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

Modelling potential natural pest control ecosystem services provided by arthropods in agricultural landscapes

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ARTICLE INFO

Keywords:
Ensemble species distribution models
Joint species distribution models
Natural enemies
Hierarchical models
Biological control Landscape
complexity Arthropod
community Species richness

ABSTRACT

Natural pest control has the potential to reduce pesticide use. Therefore, it has an essential role to play in the transition towards a more sustainable agriculture. For the prediction of natural pest control, it is essential to understand the distribution of the species providing this ecosystem service. The presence of pests and natural enemies depends on a combination of abiotic and biotic factors, each playing a determining role at different spatial scales. We developed a hierarchical model composed of environmental predictors including bioclimatic and land use variables at the European scale, as well as landscape complexity and biotic interactions at the landscape scale. This paper presents the predicted distribution of 111 species from seven different arthropod families (two pest aphid species and their natural enemy species) in an agricultural region in northern Germany. The hierarchical framework allows determining the capacity of landscapes to support pest control ecosystem services provided by arthropods at the local scale and informs on vulnerable areas or potential mismatches between natural pest control demand and supply. Thereby it can support the design of local scale measures for habitat improvement, biodiversity conservation and the increase of ecosystem services supply. The hierarchical approach can be adapted to other agroecosystems and leaves potential for further adaptations to improve the prediction of pests and their natural enemy distribution, dynamics and factors influencing their spatial distribution.

1. Introduction

Pests are defined as species that compete with humans for resources. They can be responsible for substantial agricultural losses despite the widespread use of pesticides (Oerke, 2006). The deleterious impacts of pesticide use on human health, its toxicity for non-target organisms and the induced disturbance on ecological communities, which can favour the emergence of new pests (DeBach and Rosen, 1991) and disrupt ecosystem services essential to agricultural production (Chagnon et al., 2015) have become a major environmental issue (Bommarco et al., 2013). Consequently, there is an increasing pressure to reduce pesticide inputs while minimizing agricultural losses due to pests. One approach is to rely on natural pest control, i.e., control of pests by their natural enemies and land use management (Naylor and Ehrlich, 1997). However, replacing insecticide use by natural pest control requires understanding the mechanisms underlying pest outbreaks and their control. In this regard, spatially explicit tools are needed to predict natural pest control potential, potential mismatches between pest control demand and supply and to inform on how it can be affected by planning and land management decisions (Daily et al., 2009; Groot et al., 2010; Maes et al., 2012; Kleijn et al., 2019). The current knowledge on the different ecological processes influencing the delivery of natural pest control ecosystem services (ES) in agroecosystems is however fragmented (Jonsson et al., 2014; Holland et al., 2017), (but see Haan et al., 2020 for

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https://doi.org/10.1016/j.agee.2022.108250
Received 17 May 2022; Received in revised form 25 September 2022; Accepted 26 October 2022

a recent review on our current understanding on the effect of landscape on pest control), and there is currently no widely accepted and applicable tool to assess, map and predict this ecosystem service (Englund et al., 2017; Alexandridis et al., 2021).

In this study, we aimed to model and predict the potential for natural pest control ES by arthropods using hierarchical, mechanistic and multi-trophic models, combining and synthesizing prior knowledge on the main factors that shape local species distribution and pest control potential. We focused on natural pest control of aphids by arthropod natural enemies, an important but still poorly quantified ecosystem service (Landis et al., 2008; Tschumi et al., 2015), mainly because it differs widely among landscapes, agroecosystems and local contexts (Tscharntke et al., 2005; Jonsson et al., 2014; Karp et al., 2018). Reasons for this variability include a variety of factors, such as differences in temperature, precipitation, land use and management, the structure and composition of the landscapes as well as biotic interactions. Each of these factors plays a role at different spatial scales: distributions at global to regional scales are shaped by factors that vary slowly across space, such as bioclimatic variables, whereas predictors influencing a species' mobility, resource distribution or biotic interactions are important at finer scales (Pearson and Dawson, 2003; Pearson et al., 2004; Thuiller et al., 2004; Wisz et al., 2013; Mateo et al., 2019). In this regard, hierarchical modelling approaches are an appropriate way to account for environmental factors driving species distribution and associated ecosystem services at different scales (Pearson et al., 2004; Gallien et al., 2012; Fournier et al., 2017; Mateo et al., 2019; Bellamy et al., 2020).

Another challenge when modelling natural pest control is that this service is the result of mutual interactions among at least three trophic levels: the primary producers, the pests, the natural enemy communities (Wilby and Thomas, 2002; Tscharntke et al., 2012), and interactions between enemies which may even constrain pest control (Duffy et al., 2007; Martin et al., 2013; Tscharntke et al., 2016; Karp et al., 2018). To address this latter issue, we assessed the co-occurrence patterns of natural enemy species using joint Species Distribution Models (jSDMs, Pollock et al., 2014). Hereby, we analysed the assemblage of the natural enemy community by identifying which species tend to co-occur and whether species interactions or environmental factors are the main drivers of the observed co-occurrence patterns.

As pest control mechanisms differ with the agroecosystem type, we did not attempt to develop a global model that would fit all agro-ecosystems (e.g., Alexandridis et al. 2022). We focused on arthropod species playing a role in the natural pest control of cereal aphids, which dominate the herbivore community of many crop systems in temperate regions (Schmidt et al., 2003; Dedryver et al., 2010). We applied the model in a region of northern Germany (Schleswig-Holstein). We assumed that a high natural enemy species richness enhances natural pest control ecosystem service potential. A higher species richness may enhance pest control ecosystem services through complementarity, niche partitioning, facilitation, and a higher probability of having efficient predators included in a species-rich community (Letourneau et al., 2009; Cardinale et al., 2012). This assumption is supported by two meta-analyses by Letourneau et al. (2009) and Dainese et al. (2019), although the strength of the relationship between species richness and pest control tends to vary substantially among studies (Karp et al., 2018; Kleijn et al., 2019).

With the work presented in this paper, we aimed at developing a natural pest control ecosystem service potential model framework that could be adapted to other agroecosystems and new knowledge on ecological processes. Using the framework, we assessed how abiotic and biotic factors affect the spatial distribution of cereal aphids and their natural enemies at different spatial scales. Thereby we investigated if interactions between natural enemies can reduce pest control potential. Model performance was assessed using independent field data. Finally, we investigated the spatial (a)synchrony between aphids and their natural enemies in a study area in northern Germany.

2. Materials and methods

2.1. Conceptual framework and model workflow

We aimed at quantifying the potential of an exemplary landscape to support aphids and aphids' natural enemies and thereby its natural pest control ecosystem service potential in a spatially explicit way. We assumed that natural enemy richness enhances pest suppression in agroecosystems. Our model was built on the ecological production function framework presented by Jonsson et al. (2014), a mechanistic model for natural pest control of cereal aphids and based on the Ecosystem Service Providers (ESP) concept by Kremen et al. (2007) and Luck et al. (2009). ESP are biodiversity elements that provide a specific ecosystem service. Jonsson's framework defines all ecological processes as well as abiotic and biotic interactions that need to be considered when modelling natural pest control at the landscape and local scales. This framework was integrated in a hierarchical approach at two different spatial scales, as key elements for species geographical distribution depend on the spatial scale of the influencing factors and are assumed to operate hierarchically (Pearson and Dawson, 2003; Thuiller, 2004; Milbau et al., 2009; Hortal et al., 2010). First, we considered Species Distribution Models (SDMs) fitted at the regional scale using bioclimatic predictors to assess the distribution and realized niche of aphids and their natural enemies (Fig. 1). SDMs rely on the correlation between environmental variables and geo-localized species records to determine the environmental variables that drive species presence and delineate potential species distribution (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009; Araújo and Guisan, 2006). We then considered jSDMs fitted at the landscape scale to account for landscape complexity (i.e., landscape configuration and composition) (Martin et al., 2019) and biotic interactions (Martin et al., 2013; Tscharntke et al., 2016) (see Section 2.4). jSDMs also help determining potential assemblages of the natural enemy community. The pest control ecosystem service is defined as the reduction by biological interactions of the incidence of species that consume and reduce the production of food, material or energy (Haines-Young and Potschin-Young, 2018). The ES is therefore determined by the spatial overlap of pest control potential (i.e., the natural enemies) and the demand (i.e., the fields dedicated to the production of food, material or energy that can be infested by aphids). Here, we defined pest control potential as the sum of the probabilities of presence of each predicted natural enemy species, after accounting for intraguild predation. The pest control ecosystem service potential was then determined by the spatial overlap of the pest control potential with the potential ecosystem service demand, i.e. the presence of crop fields (Fig. 1).

2.2. Species data

In Germany, one of the main pests for cultivated cereal crops are aphid species (mainly *Sitobion avenae*, *Metopolophium dirhodum,* and *Rhopalosiphum padi*) (Schmidt et al., 2003; Thies et al., 2005). Aphid populations are preyed on by a complex community of arthropods including generalist ground-dwelling natural enemies, more specialized vegetation-dwelling predators, and flying parasitoids. Abundant natural enemies of aphids in agricultural landscapes are ground beetles (Lang, 2003; Schweiger et al., 2005; Diekötter et al., 2010), rove beetles (Schmidt et al., 2003), wolf and sheet-web spiders (Schmidt et al., 2003, 2008; Schmidt and Tscharntke, 2005; Schweiger et al., 2005; Bosem Baillod et al., 2017; Redlich et al., 2018), lady beetles (Bosem Baillod et al., 2017; Redlich et al., 2018), syrphids (Schweiger et al., 2005; Bosem Baillod et al., 2017; Redlich et al., 2018), chrysophids (Bosem Baillod et al., 2017), and parasitoids (Schmidt et al., 2003; Snyder and Ives, 2003; Thies et al., 2005).

For the regional scale models, presence-only records of aphid and natural enemy species were gathered from the Global Biodiversity Information Facility (GBIF) (GBIF, 2021b, 2021a). Occurrences were

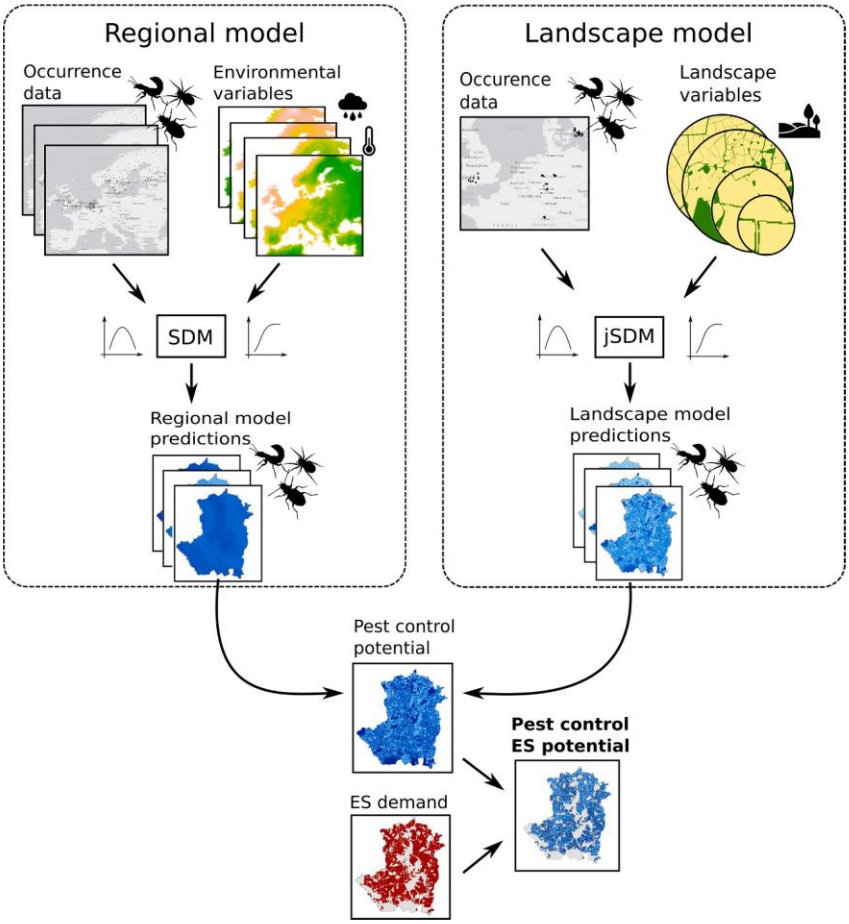

Fig. 1. Flow chart representing the different steps of the hierarchical modelling approach to predict natural pest control ecosystem service potential at the local scale based on regional scale SDMs, landscape scale jSDMs and the potential ecosystem service demand.

retrieved at the European geographical extent. Occurrence records retrieved from GBIF were cleaned using the "CoordinateCleaner v.2.0–14" package in R (Zizka et al., 2019). We excluded occurrences with sea and other water body coordinates, zero coordinates or without geographic coordinates, country mismatches, country centroids, outlier coordinates, coordinates assigned to biodiversity institutions, records with unprecise coordinates and duplicates. As old records are more likely to be unreliable (Maldonado et al., 2015), we only selected data between 1979 and 2013 to match the time extent of environmental variables. We also checked for taxonomic errors, including spelling mistakes and synonyms. To reduce model overfitting derived from spatial autocorrelation and overdominance of specific regions due to sampling bias, we then thinned the records using the package "spThin v.0.2.0" (Aiello-Lammens et al., 2015). We only selected species that had more than 50 GBIF occurrence records, to assure a sufficient sample size for accurate model fitting (Wisz et al., 2008; Guisan et al., 2017). After geographic and taxonomic cleaning, records of 111 species were retained for modelling (see Table S1 in the supplementary material S1). Due to a lack of data on many natural enemy species, it was not possible to apply the model to parasitoid species. For the same reason, only two aphid species, (*Rhopalosiphum padi* and *Sitobion avenae*) were included in the model.

For the landscape scale models, we used the dataset published by Martin et al. (2019), which represents a large collection of European studies measuring arthropod abundance in crop fields. The original dataset was composed by studies that included observations of pollinator, pest and natural enemy abundance across a gradient of surrounding landscape composition and configuration. It also includes landscape variables such as the percentage of arable and semi-natural habitat around each sampling plot at a high spatial resolution (see Martin et al., 2019 for more details). From this dataset, we selected data on aphids and their natural enemy abundance collected in cereal crop fields. From these, we only selected species that had more than 30 occurrence data in GBIF (corresponding to the regional scale selection). We selected datasets which had landscape data covering at least 1 km radius around sampling points as it has been identified as a relevant scale to understand landscape complexity effects and trophic interactions of natural enemy species (Thies and Tscharntke, 1999; Thies et al., 2005; Rusch et al., 2016; Dainese et al., 2019). As landscape variables, we only selected the percentage of semi-natural habitats (SNH) and edge density at 100 m to 1 km radius around sites. To ensure reliable model parameter estimation, only species with prevalence of at least 5% in all sampling plots were retained for statistical analyses. After applying prevalence criteria, six studies, 186 sampling plots and 111 species were retained for statistical analyses. The data were organized as a binary presence/absence matrix indicating the presence (1) or absence(0) of a particular species for each plot.

We used an independent opportunistic stratified sampling strategy to evaluate the performance of the regional, landscape and hierarchical models using field data. The sampling sites were located in Schleswig-Holstein, the northernmost federal state of Germany, bordered by the North Sea to the West and by the Baltic Sea to the East (Fig. 2a). This federal state has an area of approximately 15’800 km^2 (Statistische Ämter des Bundes und der Länder, 2018). Agriculture is the predominant land use (non-irrigated landscapes and pastures, Fig. 2b). It is also characterised by relatively small cultivated fields and forests and

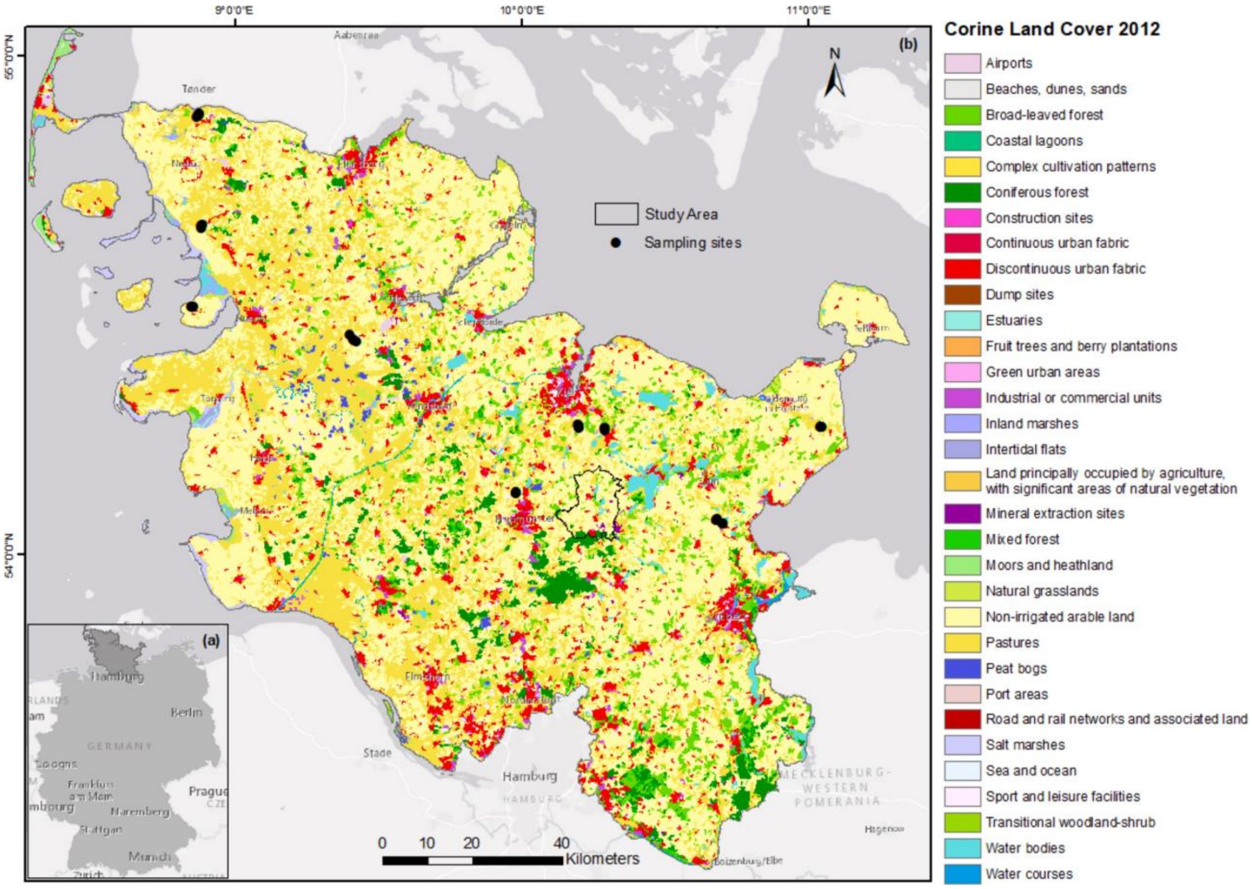

Fig. 2. Location of the study area and of the sampling sites in northern Germany (a) and distribution of Land Use / Land Cover classes (b) (Data source: CORINE Land Cover 2012).

overall, a highly diverse and fragmented landscape. It has a sub-oceanic climate, with mean annual temperature around 8,4 °C and mean annual precipitation values around 760 mm (Anon, 2020). The sampling locations were selected to cover the landscape diversity in Schleswig-Holstein: from locations surrounded by a landscape with a comparably high proportion of semi-natural habitats to locations with a lower proportion of semi-natural habitats (Fig. 2b). Full methods and results of sampling are reported in Hoffmann et al. (2021), but shortly: the presence and abundance of spiders, ground and rove beetles were recorded using pitfall traps in 20 sampling plots for three years. The species were sampled from end of May until mid-July 2017–2019 using three pitfall traps per sampling plot and two plots per site (one in flower strips, one in the adjacent arable fields).

From all the species sampled by Hoffmann et al. (2021), 100 species corresponded to the species modelled for our study and were used to evaluate the performance of the hierarchical models (spiders, ground and rove beetles species but no aphid, lady beetle, damsel bug nor green lacewing species).

2.3. Environmental variables

We selected two sets of environmental variables with different extents and resolutions, one for each considered scale: the regional scale and the landscape scale.

For the regional scale, we selected bioclimatic variables based on knowledge about the mechanistic relationship between environmental variables and the physiology of the targeted species (Araújo et al., 2019). At regional scales, arthropod populations are mainly affected by variations in temperature, precipitation patterns, and vegetation cover (Netherer and Schopf, 2010; Settele et al., 2014; Giezendanner et al., 2020; Mammola et al., 2020). In temperate areas, longer warm seasons and mild winters without frost, tend to facilitate the proliferation of arthropods, while they generally suffer from extreme rainfall and warming events (Bale et al., 2002; van Nouhuys and Lei, 2004; Harmon et al., 2009; Bale and Hayward, 2010; Settele et al., 2014). An increase in temperature towards species optima will generally promote arthropod growth and survival rates by accelerating development stages and/or by allowing additional generations within a year (Bale et al., 2002; Rouault et al., 2006; Halsch et al., 2021). Temperature optima vary among species, depending on each species' thermal tolerance and heat/frost sensitivity, the life stage at which they experience high/low temperatures and their capacity to adapt to or flee unfavourable environmental conditions (Bale et al., 2002; Kruse et al., 2008; Schmitz and Barton, 2014). We therefore selected the following variables from CHELSA (Karger et al., 2017) to characterize the geographical range of the selected species: Annual mean temperature (Bio_1), Max temperature warmest month (Bio_5), Min temperature coldest month (Bio_6), Mean temperature wettest quarter (Bio_8), Mean temperature driest quarter (Bio_9), Mean temperature warmest quarter (Bio_10), Mean temperature coldest quarter (Bio_11), Precipitation wettest quarter (Bio_16), Precipitation driest quarter (Bio_17), Precipitation warmest quarter (Bio_18), Precipitation coldest quarter (Bio_19), Normalized Different Vegetation Index in summer (NDVI_summer), Growing degree days (GTS0, GTS5, GTS10) and Number of frost days (NFD). Degree days are the sum of all monthly temperature values greater than a given threshold temperature (here 0, 5 and 10 °C) multiplied by the total number of days and NDVI is an index of vegetation productivity.

These variables were retrieved from CHELSA V1.2 at a resolution of 30 arc-seconds (~1 km² at the equator) (Karger et al., 2017, 2018). These environmental variables were standardized (so that the mean of observed values is 0 and the standard deviation is 1) to maximise uniformity. To reduce multicollinearity, we then reduced the number of variables selected: We assessed univariate variable importance for each predictor using Generalized Linear Models (GLM) with linear and quadratic terms in a five-fold cross-validation and assessed the percentage of explained deviance for each variable (Zurell et al., 2020b). We then ran a pairwise Spearman correlation analysis. In case of highly correlated variables ($|r| < 0.7$), we removed the variables with the lower univariate importance value (Dormann et al., 2013; Zurell et al., 2020b). We obtained a final set of seven ecologically meaningful variables for arthropods in temperate climates, which we used for model calibration at the regional scale: GTS5, Bio_5, Bio_9, Bio_18, Bio_19, NDVI_summer and NFD.

At the landscape scale, arthropod species distribution is mainly driven by the landscape composition, commonly described as the amount of semi-natural habitats (SNH) in a given area, and by the landscape configuration, which can be characterized by its edge density (ED) (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Veres et al., 2013; Holland et al., 2017; Martin et al., 2019; Kleijn et al., 2019). Changes in species' host, predator and parasite populations also impact their distribution (Netherer and Schopf, 2010; Settele et al., 2014). Both pest populations and their enemies can profit from complex landscapes with high amounts of SNH or high edge density, as they usually provide a higher availability of overwintering habitats, shelters and alternative food resources (Thies et al., 2005; Roschewitz et al., 2005; Holland et al., 2016; Tamburini et al., 2020). Many aphid species exhibit complex life-histories involving multiple host plants (for instance on *Rosa* ssp., *Prunus padus* or on perennial grasses (Powell and Bale, 2005; Honek et al., 2018), and they may profit from complex landscapes (Thies et al.,2005, 2011; Östman et al., 2003; Schmidt et al., 2003). However, during mild winters, aphids are able to survive on winter cereals, independently of the presence of overwintering host plants and this might partly explain why pest abundance shows no consistent relationship to landscape complexity (Caballero-Lopez et al., 2012; Veres et al., 2013; Bosem Baillod et al., 2017; Elliott et al., 2018; Ulina et al., 2019). Besides, fine-grained landscapes with high edge density should facilitate exchanges between SNH and crops and therefore enhance pest and natural enemy richness (Hendrickx et al., 2007; Holzschuh et al., 2010; Fahrig et al., 2011; Tscharntke et al., 2012; Blitzer et al., 2012; Haddad et al., 2017; Martin et al., 2019; Sirami et al., 2019; Haan et al., 2020). Landscape composition (share of SNH) and landscape configuration (ED) may contribute additively or interactively to natural enemy abundance and richness (Martin et al., 2019; Haan et al., 2020).

As harvesting and soil cultivation eradicate a high share of species living in arable fields, recolonization of fields by pests and their natural enemies mainly comes from the surrounding habitats and crops (Blitzer et al., 2012). The effect of landscape complexity on natural enemy populations in fields is therefore assumed to decrease with increasing distance from such habitats (Tscharntke et al., 2016; Holland et al., 2016; Miguet et al., 2017). Each species is likely to experience landscape complexity at different scales (Thies et al., 2005), depending on traits such as body size, foraging range and specialization (Östman et al., 2001; Thies et al., 2005). From Martin et al. (2019), we included landscape variables (% of SNH and ED) from 100 m to 1 km radius around sampling plots (which include 250 and 500 m radius as well). This spatial extent corresponds to the typical foraging distance of most arthropod natural enemies (Rusch et al., 2016; Dainese et al., 2019). Prior to modelling, the variables were standardized to maximise uniformity. Similar to the regional variable selection, we first assessed the univariate variable importance of each predictor to reduce the number of variables in the model. As the plots are spatially nested (with random effects), we assessed univariate variable importance for each predictor using Generalised Linear Mixed Models (GLMMs) with linear and quadratic terms in a spatial block five-fold cross-validation design. We then ran a Spearman pairwise correlation analysis to detect multicollinearity. In case of variables with a correlation value greater than $|0.7|$, we removed the variable with the lower univariate importance value (Dormann et al., 2013). Predictor variable ranking varied with species. However, as jSDMs require a unique set of predictor variables, we then selected the variables with the highest mean cross-validated univariate importance for all species. We obtained a final set of four ecologically meaningful and not highly correlated ($|r| < 0.7$) variables for arthropods at the landscape scale: proportion of SNH within 100 m (SNH_100), proportion of SNH within 250 m (SNH_250), proportion of SNH within 1 km (SNH_1000) and ED at 1 km radius (ED_1000).

2.4. *Regional models*

For the regional models, species distribution modelling was carried out with the biomod2 (v.3.4.6) package (Thuiller et al., 2016). Occurrence data from GBIF are typically presence-only data, with no recorded absence data, whereas the algorithms used for modelling need presence-absence points, so pseudo-absence points were generated with the following approach: several sets of pseudo-absence data were generated to prevent sampling bias and to be able to test the effect of each pseudo-absence selection on the predictive ability of the model. Following Phillips et al. (2009), we restricted the selection of the background points in a 10 km buffered convex hull around the GBIF species records to reflect species sampling bias. One thousand pseudo-absence data points were sampled randomly from the back-ground region (which kept prevalence > 0.01 and < 0.9 see Table S1 in the supplementary material S1), and we repeated the random selection ten times to build a ten-fold internal cross-validation of the models (Phillips et al., 2009; Barbet-Massin et al., 2012).

Following Araújo et al. (2019), SDMs were fitted using an ensemble approach with three different algorithms: Generalized Linear Models (GLM), Boosted Regression Trees (BRT) and Random Forests (RF). GLMs were fitted with linear and quadratic terms and using AICc (Zurell et al., 2020b). BRTs were estimated with 6000 trees, an interaction depth of 3, a bag fraction of 0.5 and a shrinkage of 0.01 (Elith et al., 2008; Guisan et al., 2017). Random forests were fitted with 1000 trees, and a minimum node size of 20 (Zurell et al., 2020b). To train the SDMs and test their predictive performances, we used a cross-validation with a random subset of 70% of the points to calibrate the model for every single species, while the remaining 30% of the points were used for validation. Each single model was run on the training data and evaluated on the test data using performance evaluation metrics (explained below). This process was repeated four times with different partitioning of the original dataset into a training and a test set. Cross-validation was used to decrease bias in the predictive performance of the measuring models (Pearce and Ferrier, 2000).

We used different evaluation metrics to evaluate the performance of the regional models: Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot, True Skills Statistics (TSS), and the continuous Boyce index (CBI). AUC/ROC is a threshold-independent model evaluation indicator (Franklin, 2010), which continuously discriminates between suitable and unsuitable habitats, independently of prevalence of target species (Elith et al., 2002). It plots the commission error against omission error and ranges between 0.5 and 1, where 1 represents a perfect discrimination between presence and absence, and 0.5 represents a random fit. TSS is a threshold-dependent measure of model accuracy and, contrary to AUC/ROC, is based on binary predictions of predicted suitability/unsuitability for each species (Allouche et al., 2006). It ranges from − 1 to + 1, with + 1 indicating perfect agreement between predictions and observations, and 0 or less indicating an agreement no better than a random classification (Zhang et al., 2015). The CBI measures how observed presences are distributed across the gradient of predicted presences and how this differs from a random distribution. It also varies from − 1 to + 1, where positive values indicate a good agreement between predictions and the distribution of presences in the evaluation dataset, values close to zero indicate predictions not different from a random distribution and negative values indicate incorrect models.

For each species, a total of 120 models was built (using three algorithms, four cross-validations to sample test and training data and ten pseudo-absences samplings). Only models with a TSS greater or equal to 0.6 were kept to build the final ensemble (Landis and Koch, 1977). Ensemble predictions were calculated as weighted averages of single-model predictions, with weights assigned to each modelling technique using the TSS (Allouche et al., 2006).

2.5. Landscape models

In addition to bioclimatic and landscape factors, natural enemy communities are also structured by biotic interactions such as mutualism, parasitism and facilitation or competition (Gilman et al., 2010). For instance, it has been shown that the pest control ecosystem service potential of an area can be impeded by interactions among natural enemy populations, such as intraguild predation but also behavioural interferences (Ives et al., 2005; Straub et al., 2008; Birkhofer et al., 2011; Martin et al., 2013; Rusch et al., 2013). Facilitation has also been reported, for example between lady beetles and ground beetles, leading to more effective aphid suppression (Losey and Denno, 1998). As SDMs do not explicitly consider biotic interactions (Kissling et al., 2012; Wisz et al., 2013), jSDMs have been developed to account for biotic interactions in SDMs and model community ecology. jSDMs estimate the effect of biotic interactions after assessing alternative explanations for species' co-occurrence patterns due to environmental factors. These interactions are modelled in jSDMs by measuring the covariance of the models' residuals, after environmental factors have been controlled for (Pollock et al., 2014; Warton et al., 2015; Ovaskainen et al., 2017; Dormann et al., 2018). jSDMs are thus composed of two stages (Warton et al., 2015; Wilkinson et al., 2019). Negative residual correlations suggest that species have a negative interaction (for instance if the species are competitors or predators/preys). Positive residual correlations suggest that the species potentially facilitate each other's occurrence (D'Amen et al., 2018).

We fitted a jSDM with the Hmsc (v.3.0–11) package (Tikhonov et al., 2020), which is based on the hierarchical modelling of species communities (HMSC) framework from Ovaskainen et al. (2017). This package allows the specification of nested study designs (through random effects as spatial latent variables), large species communities and reasonable computation times compared to other jSDM packages (Norberg et al., 2019; Wilkinson et al., 2019). We fitted probit-models (binomial error distribution for presence-absence data) using both linear and quadratic terms of the selected landscape variables, with random effects on sites and datasets. Each model was built using height Markov Chain Monte Carlo (MCMC) chains. Each chain was run for 30, 000 iterations, out of which the first 5000 were removed as burn-in and the remaining ones were thinned by 50 to yield 500 posterior samples per chain, and thus 4000 posterior samples in total. We checked convergence using the Gelman–Rubin convergence diagnostic (Gelman and Rubin, 1992) and trace plots (Plummer et al., 2006). For each model, we computed the matrix of pairwise species associations and classified estimates as having high statistical support if their 95% credible interval did not include zero. Posterior distributions with 95% highest posterior density (HPD) intervals not overlapping zero were interpreted as evidence for non-random association within a species pair. The predictive model performance of the different models was assessed using AUC/ROC and TSS using two-fold cross-validation. We also assessed variable importance and decomposed the explained variance (Tjur's R^2 values) into fixed effects (landscapes predictors) and random effects (sites and datasets) through variance partitioning analysis (Ovaskainen et al., 2017; Tikhonov et al., 2019). The overall performance of the models was evaluated by averaging AUC/ROC and TSS values across species.

2.6. Hierarchical models

The gridded layers generated by the regional models (SDMs, 1 km × 1 km) were disaggregated to the pixel size of the landscape models (jSDMs, 100 m × 100 m) using bilinear interpolation. Following Bellamy et al. (2020), the hierarchical models for each species were generated by multiplying the prediction values of the two gridded layers on a pixel-by-pixel basis. The hierarchical models were evaluated with independent field data (i.e., data that were not used to train the regional and landscape models) using generalized linear mixed models (GLMM) ("LME4" package (Bates et al., 2014)) to account for the nested structure of the sampling design. The performance of the models was evaluated based on deviance explained by the regional, landscape and hierarchical models' habitat suitability predictions.

We then used the hierarchical model results to determine natural pest control service potential and investigate the spatial (a)synchrony between pest control demand and potential in a study area located in the region of the Bornhöved Lake District (Fig. 2b), in Schleswig-Holstein. The extent of the area is approximately 140 km^2. The study area is characterised by a catchment area of five glacially formed and consecutively connected lakes and a few settlements within an agricultural landscape (Fränzle et al., 2008).

Statistical analysis, SDMs and jSDMs were implemented in R 4.0.3 (R Core Team, 2020). All maps were created using ArcGIS 10.6.1. To ensure transparency and reproducibility of our models, we include an Overview, Data, Model, Assessment, and Prediction (ODMAP) protocol following Zurell et al. (2020a) in the supplementary material S2.

3. Results

The evaluation scores of all ensemble models at the regional scale were high to very high (AUC/ROC: 0.935 ± 0.020, TSS: 0.734 ± 0.063 and CBI: 0.983 ± 0.025). An overview of all performance measures for each species included in the analysis can be found in Table S1. The importance of each predictor for each species regional model varied highly with algorithms and modelled species. Number of frost days (NFD) and Maximum temperature of warmest month (Bio_5) were overall the most important variables explaining arthropod species occurrence, followed by Growing degree days above 5 °C (GDD5) and Mean temperature of driest quarter (Bio_9). An overview of variable importance for each species and each algorithm can be found in Table S2. Partial dependence plots can be found in Fig. S1.

The jSDM models converged well and most of the species showed statistically significant responses to most of the landscape variables (Fig. S2). Significant negative responses to the squared effects of SNH and ED at 1 km were observed for most of the species (corresponding to a slightly 'hump-shaped' relationships, but which do not appear when species are aggregated by families/orders, see partial dependence plots in Fig. S4). This suggests an optimum percentage of SNH and ED value at 1 km for most of the species. Similar responses were observed for the percentage of SNH at 100 m but for fewer species: 25% of the species showed a positive response to SNH_100, 13% an optimum value, which maximized occurrence probability and 3% of the species showed a negative response to SNH_100. Almost half of the species had a significant negative response to the effect of SNH_250 and 16% of the species had a significant positive response to the squared effects of SNH_250. The predictive performance (based on cross-validation) of the jSDM models was overall good: the mean AUC/ROC value was 0.86 (SD: 0.10), mean TSS was 0.54 (SD: 0.25) and the mean RTjur2 value was 0.37 (SD: 0.23). See Tables S3 and S4 in the supplementary material for the evaluation metrics of each species. Variance partitioning results indicated that the random effect associated with the datasets themselves was the most important predictor of species occurrence (79.4%), followed by landscape variables (17.2%) and the random effect associated with the sampling sites (4.4%). Landscape variable importance varied considerably between species (see Fig. 3, Fig. S3 and Table S4). Overall, the proportion of semi-natural habitat (SNH_1000) and the edge density (ED_1000) at 1 km radius were the most important landscape variables for the arthropod species composition and explained 11.7% of the explained variance. Landscape variables explained a higher percentage of the explained variance for ground beetles, followed by spiders, rove beetles, lady beetles, and aphids. Variable importance and explained variance of each species can be found in Table S4.

Most species pairs did not present a significant residual correlation (i. e., 95% HPD intervals of residual correlations that exclude zero), which would have indicated non-random species associations after accounting for environmental effects (Fig. 4). Most natural enemies covaried positively (significant positive residual species correlations showed in red in Fig. 4). Only some spiders covaried negatively with some ground and lady beetle species (significant negative residual correlations showed in blue in Fig. 4). Aphids covaried negatively with many natural enemy species, particularly spiders.

We evaluated the regional, landscape and hierarchical models (combining results from the models at the regional and landscape scales) using the independent field data (see Section 2.3). The hierarchical model's habitat suitability predictions explained 16% of the variation in species richness and 18% of the variation in species abundance observed in the independent field data (see Table S5). Particularly, the hierarchical models better explained the variation in ground beetle and spider species richness, as well as rove beetle abundance. However, ground beetle abundance was better explained by the landscape models (Variance explained: 0.23 vs. 0.17), and spider abundance respectively rove beetle species richness were better explained by the regional models alone than by the hierarchical models (Variance explained: 0.13 vs. 0.01 respectively. 0.05 vs. 0.02).

As expected, the regional and landscape model outputs showed substantially different habitat suitability patterns and the suitable area predicted by the regional models for each species was greater than the one predicted by the landscape models (see for instance the predicted habitat suitability from the different models for the spider *Erigone dentipalpis* and the ground beetle *Anchomenus dorsalis*, Fig. 5).

Fig. 6a displays the predicted natural pest control ecosystem service potential on cereal fields across the study area. The ecosystem service potential values are mapped at a 100 m resolution and reached a maximum value of 16.3 and a minimum value of 4.9 (with 0 = minimum potential and 109 = theoretical maximum potential). Areas predicted as not suitable for the modelled natural enemy species have no natural pest control ecosystem service potential (performed by the modelled species), whereas a high predicted habitat suitability for a broad range of natural enemy species increases the pest control service potential of the area. Our model predicted an overall low pest control potential on crop fields (mean pest control potential value of 10.6). More heterogeneous agricultural areas, characterized by relatively small fields and a high share of SNH, have higher pest control potential values, whereas larger fields have a lower natural pest control service potential (Fig. 6a).

The landscape models predicted that the landscape complexity (i.e., proportion of SNH and ED, see Fig. S5) has a (small) positive effect on aphids' abundance. This was, however, not observed in the pest distribution map (Fig. 6b) and is probably the result of natural enemy suppression (see negative residual correlations between natural enemies and pests, Fig. 4), particularly in areas with small fields (e.g., Eastern

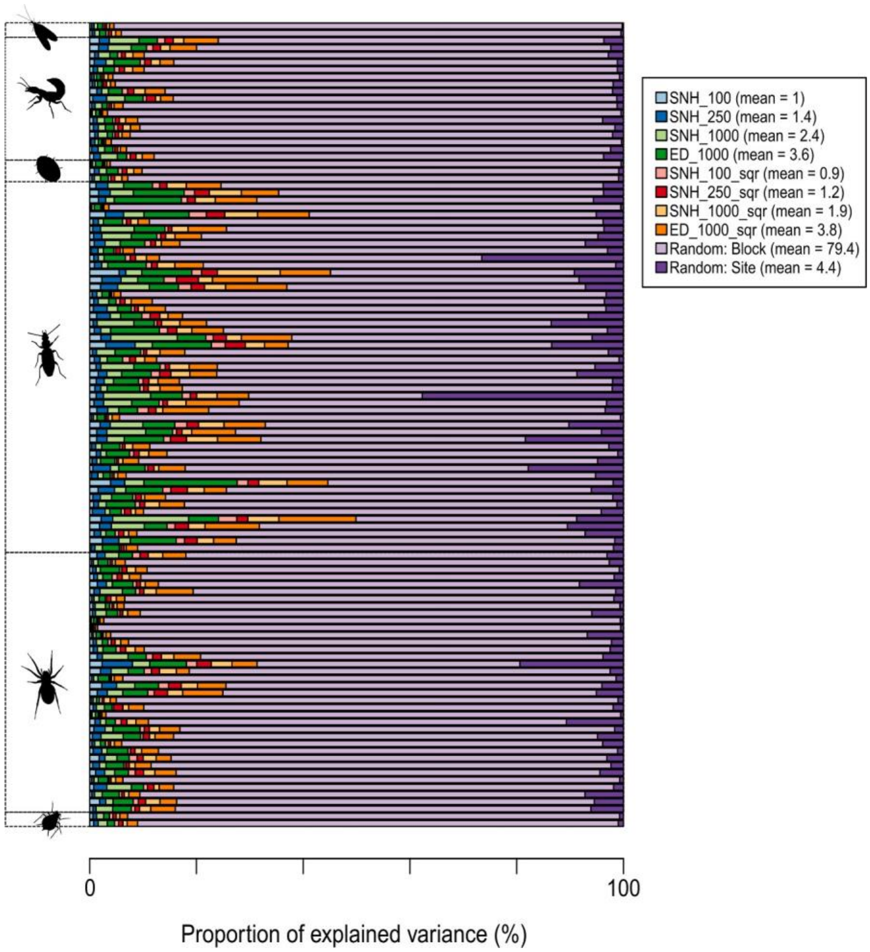

Fig. 3. Outputs of the variance partitioning analysis for each species. Species are grouped by families/orders to which they belong (Bottom to top: aphids, spiders, ground beetles, lady beetles, rove beetles and others (common green lacewings and damsel bugs)). The variance explained by each landscape variable, by the spatial location of each dataset (random factor: Block) and by the spatial location of the site, which also yields the species association matrix (random factor: Site) are represented with barplots.

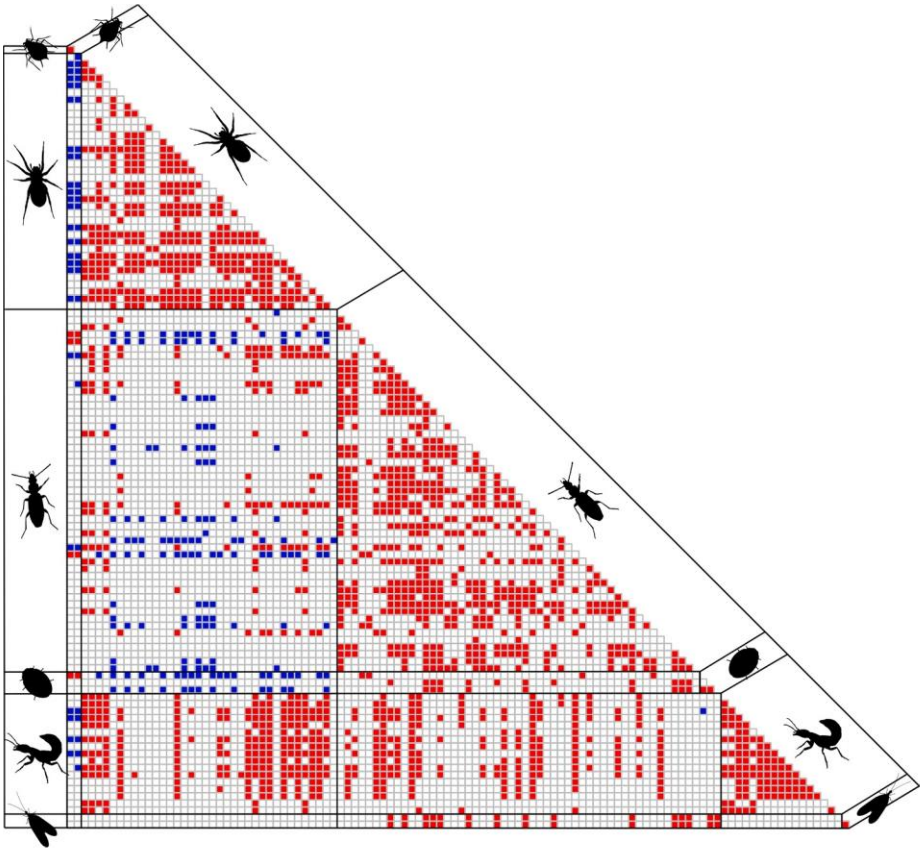

Fig. 4. Residual correlations among arthropods species. Species were ordered by families (top to bottom: aphids, spiders, ground beetles, lady beetles, rove beetles and others (common green lacewings and damsel bugs)). Only values with high statistical support are shown in the figure, in red for positive residual correlations and blue for negative residual correlations.

part of the study area, see Fig. S6). Overall, the hierarchical models predicted a low suitability for aphids for the whole study area (Fig. 6b), except in larger crop fields.

4. Discussion

This study presented a new approach to model natural pest control ecosystem service potential of aphids in cereals focusing on the arthropod natural enemy community. The use of a hierarchical model allows to assess how different factors at different scales influence natural enemy distribution. These are novel findings, as most previous models focus on environmental variables at a single scale (i.e. at regional or landscape scale) and neglect biotic interactions (e.g., Civantos et al., 2012, Jonsson et al., 2014, and Rega et al., 2018). The presented framework to model and predict pest control ecosystem service potential at the local scale can be adapted to different pests, agroecosystems and regions and is meant to evolve with new knowledge about ecological processes underlying pest control.

The principal advantages of the presented framework are to combine two different research fields (biogeography and landscape ecology), which are usually considered separately (but see Bellamy et al., 2020 and Perennes et al., 2021) and the use of independent field data to assess the hierarchical model performance and reliability (Fiedling and Bell, 1997; Schröder and Richter, 1999). Landscape models only assess if the local ecological conditions are suitable for the targeted species, but they can fail to represent the realized climatic niche of species and their transferability is questionable (Thuiller et al., 2004; Petitpierre et al., 2016). Regional models are expected to better capture the realized climatic niche of the targeted species, but they tend to overpredict suitable areas for the species at the landscape scale as they are unable to reflect fine-scale ecological processes influencing spatial species distribution patterns at the local scale (Fournier et al., 2017; Bellamy et al., 2020; Perennes et al., 2021). This is also what our results indicate and for each modelled species, the predicted suitable areas by the regional SDMs were larger than that of the landscape SDMs (Fig. 5). Hierarchical SDMs jointly consider regional and landscape drivers of species distributions, account for the hierarchical habitat selection process and can thus overcome the limitations that separate landscape and regional SDMs have and should provide more accurate and realistic predictions (Lindenmayer, 2000; Whittingham et al., 2007; Zeller et al., 2017; Mateo et al., 2019; Bellamy et al., 2020).

This study demonstrates, with the help of a study area in northern Germany, how hierarchical SDM approaches can be used to model pest control ecosystem services. Assessing how bioclimatic variables can affect pest and natural enemy species distribution is essential to determine the impact of global climate change on pest control and therefore crop production. Particularly, global climate change can affect pest and natural enemy phenology (Thomson, 2010), promote range expansion or shift, disturb current space and time synchrony between presence and abundance of pests and their natural enemies and favour the emergence of new pests (Schmitz and Barton, 2014) and lead to significant yield losses (Civantos et al., 2012; Deutsch et al., 2018). Anticipation of climate change effects on pest control can therefore help to adapt land management to mitigate yield losses while limiting the use of and reliance on pesticides.

A combination of bioclimatic and biotic variables with a landscape context was found to be affecting pest and natural enemy species distribution. Our results highlight the importance of bioclimatic variables

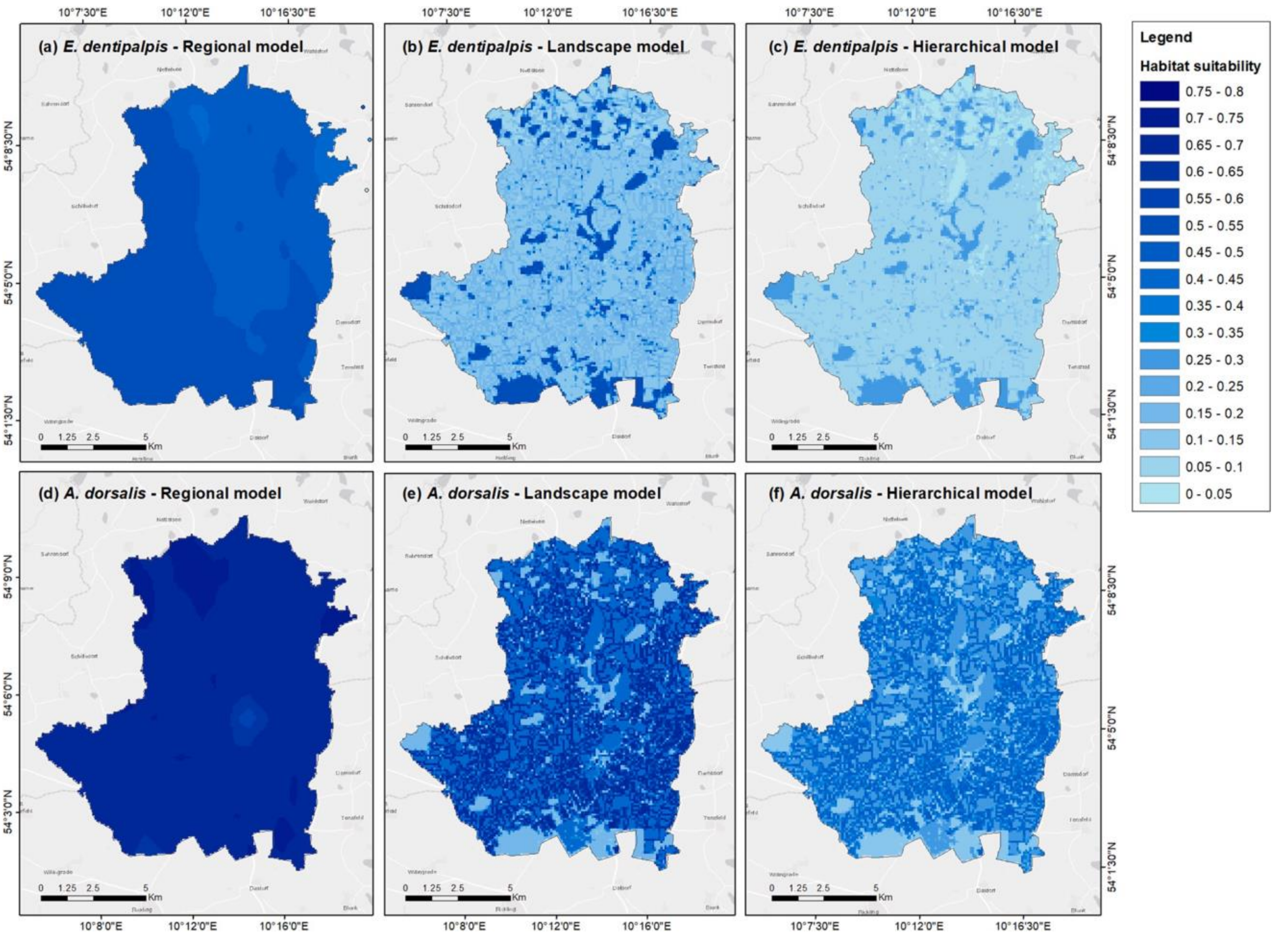

Fig. 5. Prediction maps for a spider species (*Erigone dentipalpis*) and a ground beetle species (*Anchomenus dorsalis*). (a) and (d) are the predictions retrieved with the regional models, (b) and (e) predictions from the landscape models and (c) and (f) the final predictions from the hierarchical models. The maps from the regional model were rescaled to fit the spatial resolution of the landscape models.

in arthropod species distribution, which is consistent with Ulrich and Fiera (2009), Hortal et al. (2010), Kotze et al. (2011), and Giezendanner et al. (2020). The variables "Number of frost days" (NFD) and "Maximum temperature warmest month" (Bio_5), followed by "Growing degree days above 5 °C" (GTS5) and "Mean temperature driest quarter" (Bio_9) exhibited the highest relative contribution to the models for most of the species, in line with Titeux et al. (2009), Harrington et al. (2007), Barredo et al. (2015), Pellissier et al. (2013), and Cerasoli et al. (2020). At the regional scale, species distributions are mainly limited by frost (or frost sensitivity), temperatures in summer (or heat sensitivity) and mean temperature in spring, i.e., during the development stage of most of the species (see Fig. S1). Similarly to Ulrich and Fiera (2009) but contrarily to Titeux et al. (2009), we found that precipitation is not one of the main influencing factors for species occurrences in the study region. Model evaluation scores were high for most of the species but were lowest for ubiquitous species, with a broad ecological range such as *Haplodrassus signifier, Carabus violaceus, Pisaura mirabilis, Harpalus latus,* and *Alopecosa pulverulenta*. It has been shown that species with these characteristics tend to be harder to model and retrieve poorer or more unreliable predictions (mainly because of their low specificity) (Mateo et al., 2019; Mammola et al., 2020; Vermeiren et al., 2020).

At the landscape scale, we found that landscape complexity (i.e., % of SNH and ED) is an important driver of natural enemy richness, in line with Dainese et al. (2019), Kleijn et al. (2019) and Martin et al. (2019). Results in the literature are, however, often inconsistent for single species or families: for instance for lady beetles (Puech et al., 2015; Woltz and Landis, 2014; Dominik et al., 2018), spiders (Schmidt et al., 2008; Gallé et al., 2018; Li et al., 2018) and ground beetles (Puech et al., 2015; Gallé et al., 2018). We found that the relationship between species occurrence and the landscape complexity is highly species-specific but most of the considered species were positively influenced by landscape complexity, mainly at the highest measured radius of 1 km around the sampling plots. While many empirical studies measure landscape metrics in the 1 km radius (or less) around the sampling plots (Chaplin-Kramer et al., 2011; Dainese et al., 2019), landscape variables have been shown to influence species occurrence up to 3 km radius (Holland et al., 2016; Martin et al., 2019), particularly for spiders (Schmidt et al., 2008) and lady beetles (Holland et al., 2016). Similarly, other landscape variables might have significant effects on natural enemy species (e.g., the proportion of cropland, forest or grassland (Jonsson et al., 2014)). Landscape complexity variables at any spatial scale are typically highly correlated with other spatial scales and disentangling their single effect on species richness is therefore challenging. We thus cannot entirely exclude that the observed species responses to landscape complexity are also due to other landscape variables or to effects at broader scales (Jackson and Fahrig, 2015).

Our results also highlight the role of species interactions in arthropod communities in agroecosystems. We found that many of the natural enemy species considered showed a negative correlation with aphids, suggesting that the natural enemy community reduces the occurrence of aphids (predator-prey interactions). This can be the consequence of additive or synergetic effects between individual species, which cannot

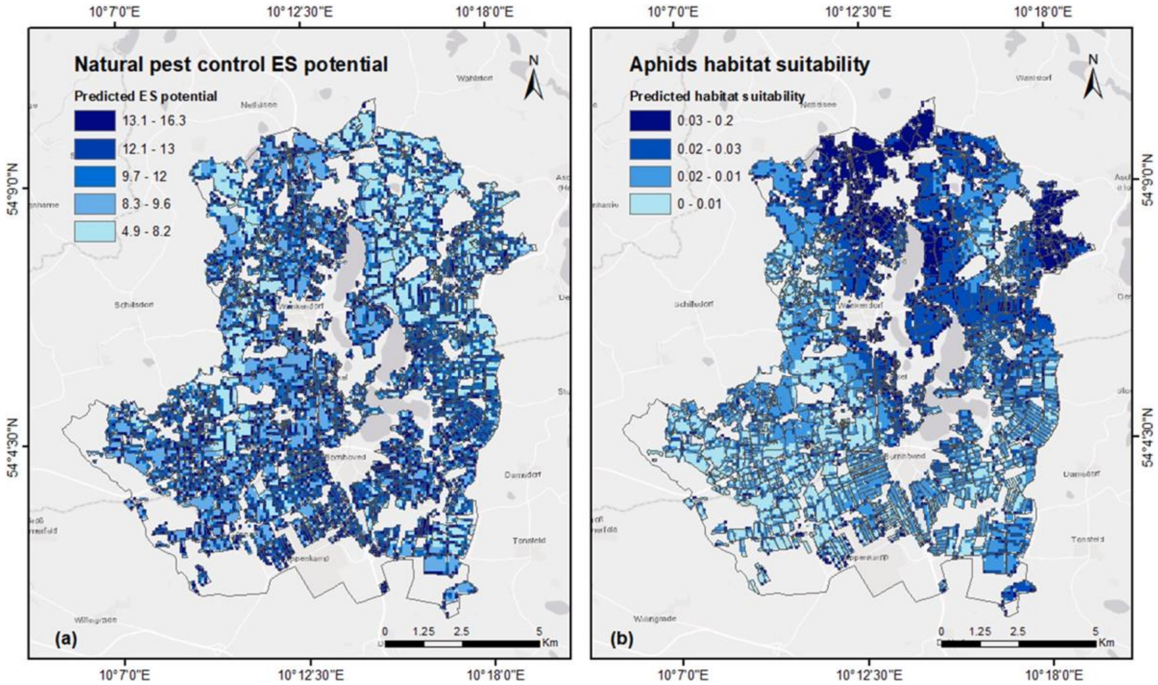

Fig. 6. Natural pest control ecosystem service potential (a) and predicted suitability for aphids (b) in the study area. Crop fields are marked with a gradient from light to dark blue, depending on the predicted natural pest control ecosystem service potential (resp. Predicted suitability of the area for aphids) for each parcel of the study area.

be disentangled using jSDMs. The residual negative correlation between natural enemies and pests is consistent with empirical studies (for instance from Rusch et al., 2013 and Liere et al., 2015) and the synthesis from Dainese et al. (2019). However, other meta-analyses and reviews reported the influence of natural enemy richness on pest suppression as not significant or inconsistent (Bianchi et al., 2006; Letourneau et al., 2009; Tscharntke et al., 2016). Our results indicate that not explicitly considering abiotic variables and species interactions can partly explain the differences in the links between landscape complexity, arthropod richness and pest suppression observed in the literature.

Many natural enemy species did not significantly influence each other and most of the significant correlations were positive indicating potential facilitation between natural enemy species. Significant negative residuals were mostly found between spiders and ground beetles species pairs. This is in line with empirical studies: For instance, facilitation between lady and ground beetles has been reported (Losey and Denno, 1998). Ground beetles are known to feed on spiders (Roubinet et al., 2017; Lang, 2003). Spiders are generally not ground-beetle-predators and tend to avoid them. For instance, Snyder and Wise (1999) found that when lycosid spiders were present with ground beetles, no intraguild predation took place, but spiders altered their feeding habitats and/or emigrated. In the literature, other cases of competitive interactions between natural enemies have been reported, which we did not observe in our results: for instance between lady beetles (Hoogendoorn and Heimpel, 2004; Cardinale et al., 2006), particularly between introduced lady beetle species (*Harmonia axyridis*) and native ones (*Coccinella septempunctata*) (Alyokhin and Sewell, 2004; Snyder et al., 2004). Spiders have been shown to frequently prey on other spiders (Lang, 2003; Davey et al., 2013; Raso et al., 2014; Roubinet et al., 2017) or to have other antagonistic behaviour (Wilby et al., 2005; Straub and Snyder, 2006), whereas only positive correlations between spiders were found in our models. These differences between residual correlations and other empirical studies can be explained by a lack of observational studies across multiple taxa as existing studies are generally limited to simple systems including few species (Thies et al., 2011). However, residual correlations can support but do not infer species interactions (Dormann et al., 2018; Warton et al., 2015) as co-occurrence patterns can also be due to missing environmental predictors influencing species similarly (Pollock et al., 2014; Zurell et al., 2018). Moreover, species interactions have been shown to be scale-dependent (Barner et al., 2018; Mod et al., 2020; Sander et al., 2017; König et al., 2021) and some responses described in the literature might be only detectable at broader or finer spatial scales. Nevertheless, the species interactions detected by the jSDMs are globally supported by empirical studies and are therefore likely to be reliable.

4.1. Uncertainties and potential future framework improvements and future research

A potential future improvement of the presented framework would be to assess the actual benefit, i.e., how the presence of natural enemies influences crop yield. This was not done in the proposed framework as there are still considerable knowledge gaps on the different mechanisms involved in pest control ecosystem service delivery (Holland et al., 2017, 2020). The relationships between natural enemies and pest densities, crop damage and yield decrease are context-dependent and underlying processes remain mostly unexplained as only relatively few studies have quantified the effects of natural enemies on pest reduction or crop production (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Crop yield is primarily affected by land management decisions including agrochemical inputs, crop variety and water availability (Tscharntke et al., 2016) and extricating the influence of natural enemies is challenging.

Because of the lack of data on species abundance, we only modelled species occurrence and richness. Beside species richness, natural enemy abundance also plays a key role in natural pest control services (Dainese et al., 2019). Effective pest control also depends on temporal synchronisation between pest populations and their natural enemies as aphids and their arthropod predators have short life cycles and a significant inter-annual variation in abundance (Roschewitz et al., 2005; Iuliano and Gratton, 2020). Moreover, each natural enemy species may not have the same importance for pest control, depending on its voracity and its degree of specification (Letourneau et al., 2009). During early stage of aphid colonization, parasitoids may deliver a more efficient pest control service than other natural enemies, mainly due to a good synchronisation in time and space between aphids and their parasitoids (Schmidt et al., 2003). However, parasitism rates are often too low to influence aphid outbreaks after the colonization stage (Roschewitz et al., 2005). During the aphid population growth phase, other aphid-specific predators (particularly syrphids and lady beetles) may be the main factor influencing aphid population reduction (Östman et al., 2003; Winder et al., 2005). Generalist predators such as rove beetles, ground beetles and spiders contribute continuously to aphid density reduction, however at relatively low rates compared to specialist predators (Nienstedt and Poehling, 2004; Harwood et al., 2005). Including information on species abundance, predator-prey populations temporal synchronisation and pest control efficiency according to aphid consumption rates represent three desirable future improvements of the presented model. Similarly, improving knowledge on inter and intra-guild predation mechanisms would greatly help to better understand the role of species richness in pest control (Roubinet et al., 2017). We mainly found facilitation interactions between natural enemy species, without being able to disentangle complementary, additive and synergistic interactions between species. This would imply to characterize resource partitioning and complementary foraging modes, which probably depend on diversity in natural enemy habitat preferences, phenology, body size and foraging behaviour (Schmidt et al., 2008; Thies et al., 2011; Martin et al., 2015; Dainese et al., 2017; Perez-Alvarez et al., 2021). Besides, species interactions might depend on environmental factors (Crain et al., 2008; Garnier et al., 2017). For instance, the intensity of intra- and interguild predation is probably affected by landscape simplification (Birkhofer et al., 2011), which can, in specific cases, lead to pest control disruption (Martin et al., 2013; Jonsson et al., 2017; Perez-Alvarez et al., 2019). These aspects were not included in the presented modelling framework because of their complexity but could greatly increase the reliability and transferability of natural pest control service potential models.

A model is always a simplified version of complex phenomena occurring in the real world. Here we focused only on some properties of real agroecosystems. Despite the simplifications we made, the model predictions appear reliable and supported by comparison with independent field data. The developed framework therefore provides a useful tool for pest control conservation decisions and to predict the magnitude of pest control mismatch in crop fields.

5. Conclusions

To our knowledge, this is the first framework that uses a hierarchical modelling approach, integrating climate, landscape and species interactions, to map natural pest control ecosystem service potential at the landscape scale. The developed modelling framework synthesizes the knowledge on the relationships between environmental variables, landscape complexity, and the distribution of aphids and their natural enemies. The aim of the presented framework is to provide spatially-explicit natural pest control service potential information to support decision-making processes at different scales. As hierarchical SDMs generate a more complete understanding of species distributions and communities, they should therefore provide more accurate predictions and support more effective land-management decisions. Effective measures to sustain natural pest control have the potential to play a key role in shifting towards a more sustainable agriculture by decreasing the use of pesticides while maintaining crop yield.

There are multiple potential applications for the presented model, among them to identify areas with a potential mismatch between pest control demand and existing ecosystem service potential or to guide the design of effective measures to enhance pest control potential, particularly in the frame of agri-environmental schemes or Green Infrastructure as defined by the EU Biodiversity Strategy to 2020. The developed model framework can also be used to assess, anticipate and mitigate the effects of climate change on natural pest control, which is essential in maintaining future crop yields and increasing agriculture sustainability in a changing environment. Our capacity to rely on natural enemies for pest management highly depends on our understanding of the ecological processes underlying it and the presented model contributes to this objective.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

This study was partly funded by the BiodivERsA project "IMAGINE", supported in Germany by the BMBF – Federal Ministry for Research and Education. M.P. was supported by a grant from the Graduate Academy of the Leibniz University of Hannover.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108250.

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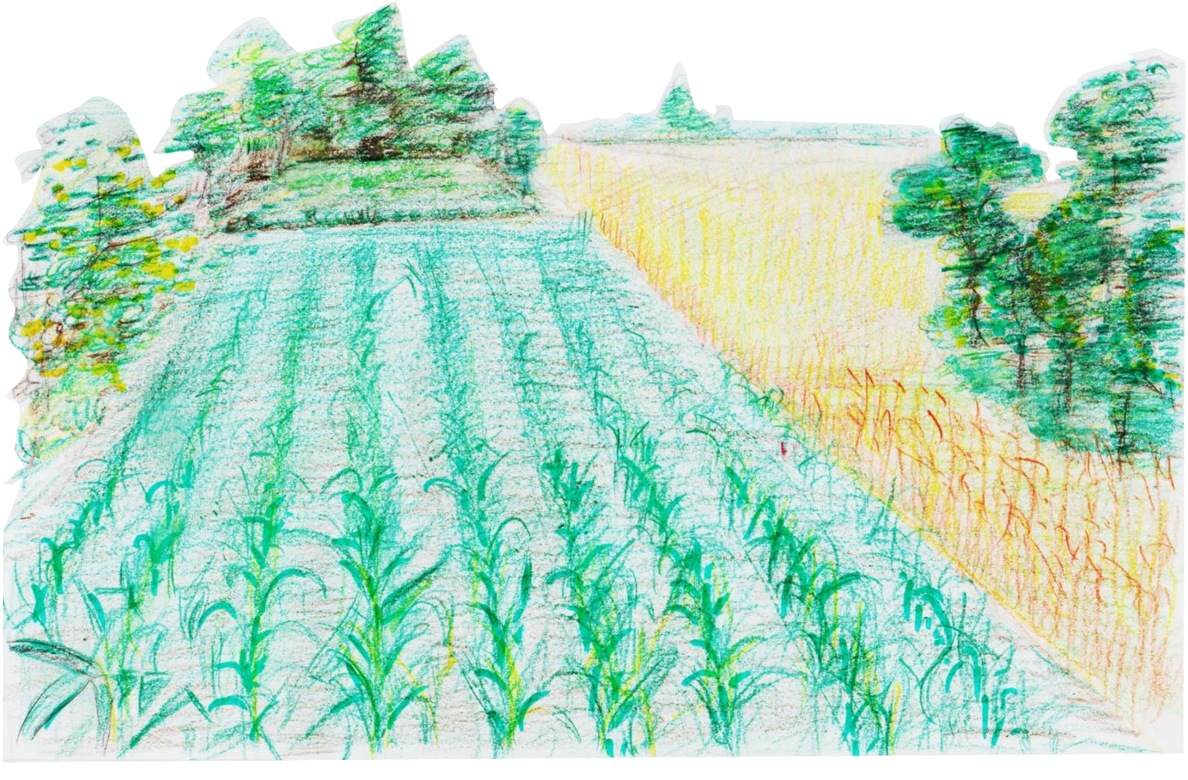
Chapter 6

Synthesis



6 Synthesis

Ecosystems are being degraded at an alarming rate, with direct consequences on human health and well-being (IPBES, 2019). In agricultural landscapes, agricultural intensity is accompanied by high biodiversity decline rates, which is and will be intensified by climate change (Pereira et al., 2010; IPBES, 2019; Raven and Wagner, 2021). This has cascading effects on ecosystem functioning and services (Cardinale et al., 2012; IPBES, 2019), and potentially will have dramatic consequences on agriculture production, as it relies on the delivery of various ES (Aizen et al., 2009; Bommarco et al., 2013; Gagic et al., 2015). Particularly, it is widely acknowledged that the decline in arthropods can compromise the capacity of ecosystems to deliver ES (Ross et al., 2021) and translate into lower crop production and yields (Reilly et al., 2020). Achieving efficient and productive agriculture, while conserving biodiversity and a wide range of ES is therefore a major current challenge, with a high priority on the political and research agendas (Bommarco et al., 2013; Landis, 2017). ES have become an increasingly popular concept to illustrate the consequences of ecosystem degradation and biodiversity loss on people's lives (Braat and Groot, 2012; Potschin and Haines-Young, 2016). Ecological and ES research conducted over the last decades is providing concepts aiming to guide the design of multifunctional and sustainable agricultural landscapes (Rossing et al., 2007; Renting et al., 2009; Duru et al., 2015). This thesis contributes to this research field and aims at providing an integrated approach to assess and map ES in an agricultural landscape in northern Germany. This thesis particularly focuses on pollination and natural pest control ES, compiling and analysing previous knowledge on ecological processes underpinning these specific ES. The findings of this thesis show the advantages and disadvantages of several ES assessment approaches and help to select appropriate methods to support land use decision-making at the local scale. The outputs of the different ES mappings also support the assessment of the capacities of different ecosystems to deliver specific ES, understanding the impacts of land use decisions on ecosystems. They can thereby improve the design of biodiversity and ES measures in agricultural landscapes.

The central question of this thesis was to assess whether and how different ES assessment methods influence the predictions of ES potential, aiming at finding the appropriate level of information needed for ES assessment at the local scale. Specifically, this thesis aimed to answer the following research questions:

5) Does a high spatial resolution and the integration of ecosystem condition information affect the ES assessment and can patterns between different ES and ES categories be detected? How can the employed method affect the resulting maps?
6) How do biotic and abiotic factors affect pollinator and natural enemy species distributions and their associated ES potentials? What are the implications for an ES assessment in the case study area?
7) Do we observe spatial asynchrony between ES potential and demand for pollination and natural pest control in the selected case study area?
8) What conclusions can be drawn for practical applications in landscape management to optimise ES delivery and particularly the conservation measures for wild bee and natural enemy species?

These research questions are answered and discussed in the following Section (Section 6.1). The remaining challenges and uncertainties in modelling and mapping ES are presented in Section 6.2.

Sections 6.3 and 6.4 present the contributions of this thesis to the ES modelling research and the implications for planning, management and decision-making.

6.1 Main results

6.1.1 Spatial resolution, model complexity and ecosystem service potentials

According to the ES matrix assessment alone (tier 1), the case study area (CSA) has a relatively high capacity to provide a wide range of ES, for all ES categories. The CSA is however characterised by an overall low ecosystem condition, especially for agricultural ecosystems of which the CSA is mainly composed (see Figure 1). This is mainly explained by a low Red List Index (RLI) status and trend and low Soil Organic Carbon (SOC) values in agricultural ecosystems. Especially, agroecosystems are the only ecosystems to have a negative RLI status, i.e., the status of the species living in these habitats is overall worsening. In other ecosystem types, species in the RLIs are recovering, especially in forest and freshwater habitats. This is consistent with an improvement in water quality in the past two decades (European Environmental Agency, 2012) and an overall improvement in the management of European forests (European Environmental Agency, 2008). Fragmentation affects all ecosystems equally. Under the assumption that the capacity of ecosystems to deliver a broad range of ES relies on their good condition, considering ecosystem condition in the ES assessment significantly decreased the capacity of the CSA to provide a wide range of ES (tier 2).

With different spatial resolutions and levels of detail, the resulting ES maps showed different spatial patterns. Particularly, provisioning services seem to be overestimated when using a coarse spatial resolution, whereas regulation and maintenance services tend to be underestimated when using a coarse spatial resolution. This is mainly because landscape elements are not appropriately mapped when using a coarse resolution. Cultural services are less affected by spatial resolution than provisioning, regulation and maintenance services. The overall ES assessment for the whole CSA showed a high congruence in the mapping outputs using the two different resolutions. It was also observed that, especially for cultural, regulation and maintenance ES, not accounting for ecosystem condition makes a significant difference in the mapping results. This means that using the ES matrix approach only based on LULC tends to retrieve incomplete assessments as it does not sufficiently capture spatial heterogeneity due to ecosystem condition in ES potentials. These results are coherent with previous studies on provisioning ES (Kandziora et al., 2013b), nutrient regulation services (Bicking et al., 2018; Bicking et al., 2019) and multiple services (van der Biest et al., 2015). Besides LULC, soil properties, local biodiversity and the landscape configuration are important parameters to consider when mapping ecosystems and ES.

The expert-based assessment highlighted the importance of the smaller landscape elements (such as hedgerows and field borders) in the delivery of a broad range of ES, particularly regulation and maintenance services. However, as landscape elements are usually relatively small, their importance at the landscape scale is not well-captured by mapping methods based on LULC data-based look-up table approaches. Typically, spatial spillover-effects or interactions between different LULC classes are not accounted for and the capacity of landscape elements to deliver ES to adjacent fields is ignored.

At tier 3, a hierarchical, multi-scale assessment was conducted, building on the Ecological Production Function (EPF) and using species distribution models (SDMs). The scales of the assessment were determined by ecological processes determining the distribution of the different species: regional scale for biogeographical niches, whereas habitat filter and biotic interactions were assessed at a finer spatial resolution. The two developed approaches were based on existing knowledge of ecological processes underlying the provision of pollination and natural pest control ES potentials. This should increase the reliability and accuracy of the results compared to tier 1 and 2 approaches (Lavorel et al., 2017). Contrarily to the first two tier models, the developed modelling frameworks allow for exchanges between ecosystems and characterize the spillover-effect between semi-natural habitats (SNH) and agricultural fields. This spillover-effect was determined based on species richness and species life-history traits such as foraging strategies and flying ranges. Model performance was evaluated by comparing model predictions to independent in-field collected data. The pollination potential model performed rather well when compared with in-field sampled data, even if a high proportion of the in-field species richness variation remained unexplained. The natural pest control potential model performance depended on the taxon; spiders and ground beetles were overall better predicted than other species.

6.1.2 Pollination and natural pest control service ES potentials' main drivers

At tier 1 (Chapter 3), the main drivers of ES supply were hypothesized to be LULC classes. The capacity of each LULC class to deliver ES potentials was then determined by experts using the ES matrix approach. According to the expert assessment, the main LULC classes sustaining pollination and natural pest control service ES potentials in the CSA are SNH (such as heathlands), forests, fallows, orchards and landscape elements (such as hedgerows). At tier 2 (Chapter 3), ecosystem condition was assumed to be essential for the delivery of these ES (Maes et al., 2018). Fragmentation, soil quality and biodiversity (here used to estimate ecosystem condition) have been shown to largely influence the delivery of pollination and natural pest control ES (Kandziora et al., 2013a; Adhikari and Hartemink, 2016; Maes et al., 2018).

At the tier 3 level (Chapters 4 and 5), it was shown that bioclimatic variables are important predictors of wild bees and natural enemy species occurrence. Bioclimatic variables determine the presence or absence of each species based on their physiological tolerance. For wild bees, precipitation and temperature variables, particularly during spring, were found to be the main drivers of species presence. For pests and natural enemies, frost, growing degree days and temperature during spring and summer were found to be determinant for most of the species. Besides, the presence of habitats is often used as a proxy for ESPs and ES (e.g., Lonsdorf et al. (2009), Jonsson et al. (2014), Zulian et al. (2013) and Rega et al. (2018)). For wild bees, a habitat filter at the local scale combined with foraging ranges was used to refine the ecological niche of each species at the local scale. For pests and natural enemies, the importance of landscape complexity (proportion of SNH and edge density) was tested for each species. Landscape complexity at 1 km and 100 m radii were found to be important predictors for species occurrences. The relationships between the presence of species and the percentage of SNH and edge density were found to be hump-shaped. This suggests an optimum percentage of SNH and edge density, which is coherent with the intermediate landscape-complexity theory (Tscharntke et al., 2012b).

The results also demonstrated the importance to assess the role of biotic interactions in shaping natural pest control enemy communities. jSDMs results described mainly positive biotic interactions between natural enemies and negative interactions between pest and natural enemy species. This tends to demonstrate that the whole natural enemy species community reduces the occurrence of pest and that intra- and interguild interactions do not disrupt the natural pest control ES potential. This result should be however carefully interpreted and would need to be further investigated by empirical studies explaining the mechanisms behind species co-occurrence patterns.

6.1.3 Pollination and natural pest control ecosystem service spatial patterns

Most pollination and natural pest control ESPs are to some extent dependent on the presence of SNH such as forests, heathlands and hedgerows. Satisfying the ES demand on arable fields, therefore, requires a flow from the SNH into the arable fields during the crops' flowering or growing period. This flow is determined by the capacity of the ESPs to move from the SNH to the fields, which is in turn determined by foraging behaviour, overwintering strategies and dispersal capacity of pollinator and natural enemy species. The dispersal capacity of arthropod species is restricted to a few metres or kilometres, mainly depending on their body size (Bianchi et al., 2006; Greenleaf et al., 2007; Ekroos et al., 2013; Steffan-Dewenter et al., 2002; Shackelford et al., 2013). The CSA is characterised by a relatively high share of SNH. Still, at the tier 3 level (Chapters 4 and 5), the model predicted important spatial mismatches between pollination and natural pest control potentials and demands, with an overall low mean pollination and natural pest control ES potentials on arable fields. This is comparable to other ES models at the local scale (Lonsdorf et al., 2009; Fernandes et al., 2020). Potential explanations for the predicted spatial mismatches are: there is a need for more SNH in the CSA and, probably, more importantly, a need for a better design of SNH at the landscape scale, with smaller fields (i.e., a higher edge density) to account for the low dispersal capacity of most of the ESPs (Tscharntke et al., 2005; Hendrickx et al., 2007; Tscharntke et al., 2012b). Another possible explanation for the predicted low pollination ES potential in some parts of the CSA is the relatively low local SNH diversity when a higher SNH diversity could support a higher bee species richness (Westrich, 2018; Bartual et al., 2019).

6.1.4 Conclusions for practical applications in landscape management

One of the main goals of ES mapping and modelling is to inform and assist decision-makers in making more sustainable land management decisions and policies, by reducing pressures on ecosystems or by restoring, enhancing or protecting ecosystems (Burkhard and Maes, 2017). Although there are still knowledge and data gaps (see Chapter 6.2), the outputs from the modelling approaches can be used to support landscape management decisions. The ecosystem condition and ES potential maps (tiers 1, 2 and 3) can inform on how land use and management decisions affect ecosystems and the delivery of multiple ES in the CSA. ES potential maps (tier 3) can help to design suitable ecosystem restoration or conservation measures and thereby improve different ES potentials.

Particularly, the pollination and natural pest control ES potential maps in the studied CSA (tier 3) can help to assess the needs for practical conservation measures to promote pollinators and natural enemy species in agri-environmental schemes (AES). Spatially explicit maps of ES potential in comparison to maps of ES demand allow the identification of areas where ecosystem service potentials are deficient (= areas of unmet demand). The resulting maps can support land management recommendations, such as where to prioritize habitat conservation measures in agricultural landscapes to sustain biodiversity, ecosystem functions and services and thereby crop production. The combination of SDMs and species-specific habitat filters or effects of landscape complexity on species can help to develop relevant ecological measures for specific species, for which global-scale bioclimatic conditions are also suitable. Species-specific measures have been shown to be much more efficient and sustain a higher species richness than generalized conventional conservation measures (Pywell et al., 2012). As each species has different bioclimatic and habitat needs, designing landscapes that will support a high ESPs diversity and resilient communities require considering the amount and configuration of SNH at the landscape scale as well as the geographical context, as all these factors together will influence the presence of specific species at the local scale. Moreover, as bioclimatic factors have a significant effect on the distribution of arthropods, climate change is and will affect species diversity and their distribution, at increasing rates in the near future. Biodiversity-friendly agricultural management and SNH can mitigate the detrimental effects of climate change on species richness and abundance (Outhwaite et al., 2022) and considering the combined effects of land use and climate on species communities is essential when developing conservation measures for the long term (Wilson et al., 2007).

The pollination and natural pest control ES models indicated that land use decisions at the plot scale has consequences at broader spatial scales through spillover-effects between different ecosystems: many ESPs can move over larger distances than single SNH or single fields and therefore ecological measures implemented by one farmer can benefit a neighbouring farm as well. This highlights the importance of the coordination of the ecological measures at the landscape scale to optimise efforts, to achieve multifunctional landscapes and sustainable land use management in agricultural landscapes (Tscharntke et al., 2005; 2012a). Overall, the findings of this thesis call for better conservation of ecosystems and particularly of SNH for (climate-)resilient agricultural production, implying land use management changes and changes in agricultural practices.

6.2 Challenges and uncertainties when modelling ecosystem services

This thesis emphasized the complexity of quantifying and mapping ES, dealing with ecosystem complexity and the lack of appropriate spatially-explicit data for ES quantification. Understanding how ecosystem components and functions determine ES delivery and how ecosystems can be affected by anthropogenic, biotic and abiotic factors is a prerequisite to designing robust ecological measures and therefore for a shift towards a more sustainable land use (Kremen, 2005; Maes et al., 2012a; Lavorel et al., 2017). However, many processes affecting the delivery of ES are not well explored and quantifying ES potential is still a challenge for many ES (Martínez-Harms and Balvanera, 2012; Harrison et al., 2014). Besides, the lack of data at the suitable spatial and temporal resolutions is still an obstacle to accurately assess and map many ES (Eigenbrod et al., 2010). Indicators and simple models help to overcome knowledge and data scarcity but are usually associated with important uncertainties (Eigenbrod et al., 2010; Egoh et al., 2012; Schulp et al., 2014a). Uncertainties may also arise from the selected assessment methods (Hou et al., 2013). Modelling uncertainties are also inherent to the complexity of ecological systems and processes (Hou et al., 2013). Ecological processes are characterised by a large number of different components, that interact with each other in various ways, at various scales and often show non-linear dynamics (Bond and Chase, 2002; Harrison et al., 2014). Besides, ecological processes are directly and indirectly impacted by external variables and feedback loops, at different scales (Chave, 2013; Heffernan et al., 2014; Miyasaka et al., 2017). This complexity also explains why, even after long years of research, there is still a lack of knowledge about the different processes and dynamics underlying the ES supply. Therefore, modelling and mapping ES imply making simplifications, assumptions and dealing with uncertainties, which one has to be aware of when presenting and using the results.

The first approaches (Chapter 3) apply rather simple methods, including expert-based assessments and the use of indicators. This approach allows to assess multiple ES potentials and the importance of ecosystem condition for mapping ES. The ES matrix approach has many advantages, amongst others, it allows for a rapid assessment at various spatial scales and is highly adapted in case of data scarcity (Jacobs et al., 2015; Roche and Campagne, 2019). It allows a consistent assessment of multiple ES, which is essential to account for trade-offs between ES and when studying landscape multifunctionality. Besides, it can easily be combined with other information, such as socioeconomic variables when available (Vihervaara et al., 2010). The main critics of the ES matrix approach are: the evaluations are based on experience and personal beliefs (Jacobs et al., 2015), even though this bias can be limited through expert selection and increasing expertise and background variability between experts (Jacobs et al., 2015; Campagne et al., 2017). Moreover, LULC-based methods generally do not account for the capacity of ES to be delivered by nearby LULC elements (Vrebos et al., 2015) and are unable to account for the spatial heterogeneity of biophysical processes (Eigenbrod et al., 2010). This can be particularly an issue for maintenance and regulation services sustained by SNH, such as pollination and natural pest control potentials. The approaches used at the tier 2 level (Chapter 3) rely on the assumption that good ecosystem conditions indicate an ecosystem capable to provide a broad range of services in a sustainable way (Balvanera et al., 2006; Maes et al., 2018). Uncertainties of these approaches come from 1) a general lack of spatially explicit data that could allow to map and assess ecosystem condition with a high accuracy and reliability (Erhard et al. 2017), particularly affecting the local scale, for which a fine spatial resolution is suitable, 2) lack of knowledge on how ecosystem condition impacts the delivery of ES, even if some ES have been shown to be more dependent on a good condition than others (Harrison et al., 2014). Applications of tier 1 and 2 methods are still constrained by the availability of suitable data at the needed resolution. For instance, while the importance of ecosystem pressures such as land use change and degradation, pollution and over-exploitation to determine ecosystem condition is well known, data on different pressures at suitably fine resolution (i.e., here the plot scale) for the extent of the CSA are typically not available.

The approaches used at tier 3 rely on the main assumption that pollination and natural pest control ES are provided by the presence and richness of ESPs (Chapters 4 and 5). This assumption is debatable (Kleijn et al., 2015), but several mechanisms can explain how species richness can contribute to a higher ES delivery, amongst them the functional complementarity and redundancy (Hooper et al., 2005; Tscharntke et al., 2005). Functional complementarity implies that species richness can increase the ES delivery by increasing the functional diversity of the species pool. For example, an increase in bee species richness can increase the pollination ES potential by increasing the trait diversity of the species community (such as body size or daily-activity patterns) (Hoehn et al., 2008). Functional redundancy assumes that several species have a similar role within an ecosystem, and implies that the loss of species due to environmental changes can be compensated by the remaining species, hereby enhancing the ES stability (Tscharntke et al., 2005; Oliver et al., 2015). There is increasing evidence that besides species richness, specific traits are determinant factors for the delivery of many ES (Bello et al., 2010; Lavorel et al., 2011; Hanisch et al., 2020). For specific ES, the relationships between traits and ES have already been quantified through empirical evidence: trait approaches have been for instance used to assess nutrient regulation (Bouskill et al., 2012; Pommier et al., 2018) and fodder production on grasslands (Grigulis et al., 2013). This approach could also be explored for pollination and natural pest control ES to better quantify the relationship between ESPs and ES.

The approaches developed in Chapters 4 and 5 build on SDMs. In general, uncertainties in SDMs can result from data deficiency and from errors in the specification of the models (Zurell et al., 2020a). Deficiency in species occurrence data mainly occurs when the data are temporally or spatially biased or the sample is too small (Phillips et al., 2009; Merow et al., 2014). There is an exponential increase in species presence data availability from species record portals. The global biodiversity information facility (GBIF) is currently the largest biodiversity database with over 1.6 billion species occurrences and growing daily (GBIF, 2021), reducing the issue of dealing with small samples. Data stored in this platform, however, come from a wide array of sources (e.g., citizen science networks, natural history museums and scientific surveys) and are therefore of varying quality (Maldonado et al., 2015). Data quality is improving as an increasing amount of data from biodiversity platforms are going through a peer-review process before publication, to check for taxonomic identification and georeferencing (GBIF, 2021). However, this practice is not yet common and will still be a challenge in the future, mainly because of the lack of taxonomic specialists. A first step to reduce species data uncertainty is to standardise (i.e., data cleaning) the occurrence data retrieved from species occurrence portals. This includes identifying erroneous or imprecise data such as temporal and spatial outliers, with high coordinate uncertainty or sea coordinates for terrestrial species (Zizka et al., 2020). Occurrence data can also be compared to previous knowledge about the species occurrence, such as IUCN distribution maps, when available. In the case of the studies presented here, IUCN distribution maps were available for some of the wild bee species but not for most of the other arthropod species, so comparison with distribution maps provided by the IUCN was done only for wild bee species.

An important bias in species occurrence can come from spatial autocorrelation of data as species data are usually not evenly spatially distributed, even in rather well-studied areas such as European countries. There is a huge discrepancy in available data depending on the region of the World and between countries. Arthropod data for instance were more common in northern European countries than in the southern European countries, whereas arthropod biodiversity should be higher in southern countries, particularly in the Mediterranean countries (Nieto et al., 2014). SDMs can generally deal with biased occurrence data, but models can be improved with data availability in data-poor regions (El-Gabbas and Dormann, 2018). This can only be solved by increasing the sampling effort and higher data sharing from data-scarce regions. Another common issue when using data from biodiversity platforms is the lack of absence data. Absence data is generally hard to determine for mobile species, even using in-field samplings. Pseudo-absence data was therefore used in the models developed in Chapters 4 and 5. Pseudo-absence data proved to be useful and adapted (Barbet-Massin et al., 2012), “true” absence data could however significantly improve SDMs performance (Lobo et al., 2010).

Errors of specification of SDMs result from errors in predictor variables, using variables that are not proximal and do not explain the distribution of the species and missing variables. Predictor variables were selected through sophisticated processes in Chapters 4 and 5, combining existing knowledge about the modelled species and different statistical approaches. The choice of potential variables was however here again determined by data availability and resolution. For instance, microclimate has been shown to be determinant for arthropod occurrence (Austin 2002), but microclimate data are very scarce and were not available for the selected CSA. It was therefore not included in the developed models. Advances in remote-sensing technology will increasingly provide the necessary resources to determine microclimatic conditions and help to model micro-habitats. Furthermore, the number of variables in SDMs was restricted by occurrence data availability (Guisan et al., 2017). This can become an issue when assessing community assemblages (Chapter 5), as jSDMs imply the use of the same set of variables for all modelled species. If the proximal predictors are not the same for all species in the community, this can decrease the model performance compared to a species-specific model. However, species-specific models are unable to account for species co-occurrence and biotic interactions, whereas assessing co-occurrence can improve the performance and accuracy of the models (Harris and Warton, 2015).

Besides, in addition to deterministic factors, species occurrence and assemblages are also determined by stochastic processes such as random colonisation and extinction (Chase and Myers, 2011). This can induce variation among species occurrence and assemblages under otherwise identical conditions, which by definition will remain unexplained. Uncertainties can also come from algorithm selection (Elith et al., 2006). In Chapters 4 and 5, different SDM algorithms were used to quantify the relations between species and predictors and combined through ensemble frameworks, decreasing model uncertainty (Araújo and New, 2007). Finally, the models were developed by following current standards (Araújo et al., 2019; Zurell et al., 2020a), improving the robustness and reliability of the predictions and increasing the transparency of the models.

A common challenge for all modelling approaches is the difficulty to assess the accuracy and reliability of the predictions, which usually implies to evaluate the predictive performance of the models, and comparing predictions with other models or independent data (Araújo and Guisan, 2006; Ochoa and Urbina-Cardona, 2017). ES assessment and predictions are rarely compared with in-field data, mainly because of the low data availability but also because there is a general difficulty to quantify ES (Seppelt et al., 2011; Crossman et al., 2013; Lavorel et al., 2017). In Chapter 3, the overall accuracy of the ES assessment was not assessed, mainly due to the limited availability of measured or reference values in the CSA. In Chapters 4 and 5, species occurrence probability predictions were compared with species data collected in the field. This evaluation process was data and resource intensive and was only possible for some species. This is nevertheless an advantage of the approaches presented in Chapters 4 and 5, as the performance of comparable approaches is rarely assessed (e.g., Civantos et al. (2012), Zulian et al. (2013), Polce et al. (2013), Nogué et al. (2016), Rega et al. (2018) but see Lonsdorf et al. (2009)). Prediction evaluation using independent data is particularly important to assess model performance when transferred to different locations (Yates et al., 2018). However, model performance when compared with in-field sampled data can also depend on the design of the data sampling and the species modelled (Tsoar et al., 2007; Newbold et al., 2010; Marshall et al., 2015) and is particularly challenging for models covering large extents. How methods to collect data can influence the collected data has also been demonstrated by Westphal et al. (2008). Some species are harder to detect than others. Besides, sampling can be spatially biased and/or not perfectly adapted to the seasonality of all species. Similarly, our model performance varied with species and taxon, for instance, spider and ground-beetles species tended to be better predicted and achieved higher model performance than rove beetles when compared to in-field collected data, whereas this is not observed when using cross-validation assessment methods.

6.3 Conceptual and methodological contributions

In Chapter 3, how spatial scale and modelling complexity can influence ES modelling outputs at the local scale was analysed. There are many ways to compare maps, i.e., the spatial patterns of the different mapping outputs (Long and Robertson, 2018). To date, the mainly used approach for comparing ES mapping outputs is to assess the degree of correlation (e.g., van der Biest et al., 2015; Roche and Campagne, 2019). Besides correlation, differences in variation and local abundance are also important to consider when comparing mapped results (Zulian et al., 2018). The structural similarity index (SSIM) allows to consider the local magnitude and spatial structure of the underlying data, as well as spatial dependencies between neighbouring cells when comparing maps (Jones et al., 2016).

The SSIM index was therefore selected to compare ES mapping outputs from tiers 1 and 2. ES maps based on different ES assessment methods (such as primary data and land use proxies) are often highly correlated (Chapter 3, Roche and Campagne, 2019). This implies that LULC data-based assessments are useful for mapping ES patterns at coarser scales, such as ES hotspots and coldspots. However, methods using land use proxies often fail to correctly determine local high and low abundances of ES (Chapter 3 and Eigenbrod et al., 2010) and to correctly predict the local ES variance (Chapter 3 and Zulian et al., 2018). More work is needed to explore if the benefits of improving ES mapping outreach the costs of misidentifying important areas for ES conservation (Eigenbrod et al., 2010).

Up to now, the main approaches for building ES maps following the ESP approach are primarily based on expert judgements on the potential presence and habitat preference of ESPs (see Section 1.3.5). This is particularly the case for pollinators and pollination. These approaches are therefore associated with typical expert-based approach issues and biases (Lonsdorf et al., 2009; Polce et al., 2013; Jacobs et al., 2015), such as the difficulty to find taxonomical (entomological) expertise at the desired spatial and temporal scales. Fewer studies are based on empirical data or use ecological niche modelling theories to determine ESP species occurrence drivers and limiting factors. SDMs are one suitable method to determine the ecological niche of the targeted species and to determine if the environmental conditions in the study area of interest are suitable for the targeted species. SDMs have the advantage to build on actual data records and thereby can provide an effective alternative to local expert knowledge on species' potential occurrence or absence in a given location (Chapters 4 and 5, Polce et al., 2013, Gastón et al., 2014). Existing SDMs are however usually fitted at relatively coarse resolution, constrained by occurrence data and environmental variables, typically available at rather coarse spatial resolution. Bioclimatic conditions are the main determinant of species occurrence at national and broader scales, but this resolution is not adapted to map ESPs occurrence at the local scale (Chapters 4 and 5). Particularly in highly fragmented landscapes, this resolution may fail to cover important habitats such as hedgerows, small pastures and forests, and therefore obtain biased species distribution maps (Polce et al., 2013; Nogué et al., 2016; Marshall et al., 2021). To tackle these issues and increase the ESP approach’s realism, a hierarchical framework was applied to account for the different assembly processes that determine where species occur at different scales following Soberón and Peterson (2005) (Chapters 4 and 5). Hereby, it was assumed that: 1) abiotic environmental conditions outline the physiological limits under which species can persist and are determinant at global or regional scales, 2) biotic variables determine the resource availability, nesting and overwintering places as well as potential refugees from disturbances at finer scales and 3) biotic interactions, such as predation and competition can further limit the presence of species at local scales. Thus, combining the advantages of the two different approaches (the ecological niche concept at biogeographical scale and landscape ecology theories at the landscape scale) should improve our ability to predict species occurrence and the associated ES. This approach helped to build modelling frameworks based on knowledge of life cycle requirements of the modelled species at different spatial scales, increasing the reliability of the model outputs. This thesis showed the potential of using SDMs for ES assessment and the need for species-specific approaches when modelling pollination and natural pest control potentials. Assessing and understanding spatial patterns of species distribution provide information on where and why species are present or absent, which is essential to design adapted conservation measures and assess potential threats of extinction for each species (Rodríguez et al., 2007; Guisan et al., 2013). In addition, as the modelling framework allows to assess the relative importance of environmental variables on different species, it can also be used to analyse the impact of climate and land cover changes on ESP species and their associated ES potentials.

ES mapping and assessment methods are constantly improved and applied to different scopes. However, the proliferation of ES mapping methods can also be contra-productive and can render the selection of a suitable ES assessment method particularly tedious (Willemen et al., 2015). The appropriate method depends on the decision-making process at stake and the intended audience (Grêt-Regamey et al., 2015). For instance, in highly fragmented landscapes, with a high share of linear elements and small habitats, the spatial heterogeneity cannot be captured by coarse spatial resolution data (Chapter 3). However, a high spatial resolution can be misleading when working at national or regional scales and the results may not be serviceable for or understood by decision-makers. Using LULC as a proxy has been criticised because of its simplicity (Chapter 3, Eigenbrod et al., 2010), it is however useful because of its availability and high spatial coverage. Besides, this proxy is highly suitable to distinguish which ES can and cannot be sustained at the landscape scale (Chapter 3, Burkhard et al., 2009; Maes et al., 2012a; Burkhard et al., 2014). For instance, at all tiers (Chapters 3, 4 and 5), the presence of SNH is one of pollination and natural pest control ES main drivers. Using simple approaches such as ES matrix assessments and LULC-data-based assessments are therefore suitable for awareness raising, particularly on the importance of habitats and SNH for the delivery of multiple ES. Besides, they can provide a comprehensive assessment of multiple ES, when most ES studies focus on few ES (Chapter 3; Seppelt et al., 2011). Land use-based assessments are however not adapted to design specific policies as important variables are missing and such assessments do not include the spillover potentials between different ecosystems (Chapters 4 and 5). The influence of biotic variables, ecosystem condition and landscape configuration is typically ignored when using land use-based assessments. Besides, the complexity of species-habitat relationships is also not well addressed. These approaches, therefore, imply a loss of information in ES quantification. Recommendations for land use management such as the implementation of effective AES, therefore, require assessing spatial patterns with a high spatial resolution and model complexity. More complex models are however more resource-intensive and modelling outputs are not free from assumptions and uncertainties (see Chapter 6.2). The importance of scale and modelling complexity required may depend on the ES at stake (Chapter 3; Kremen and Ostfeld, 2005) and complex methods may be only required to assess regulation and maintenance ES, whereas provisioning and cultural ES assessment should be less dependent on an extensive understanding of ecological processes (Villamagna et al., 2013).

Supporting decision-making for ES and biodiversity conservation at the local scale requires robust assessments based on evidence of ecological processes, with a high reliability, to avoid false predictions and ineffective conservation measures (Guisan and Thuiller, 2005; Schröter et al., 2015). However, because of the inherent complexity of natural systems and a general lack of knowledge on how biodiversity supports different ES, this is not always feasible (see Chapter 6.2). In practice, there is generally a trade-off between the feasibility and accuracy of the analyses of complex systems. Besides, analyses are often limited by resource availability (of data, human resource and knowledge). This thesis highlighted the issue of data availability at a fine spatial resolution, particularly affecting how ecosystem condition was assessed. The different ES mapping and assessment methods applied for this thesis are not exclusive and can be coupled to take advantage of the different approaches and limit the uncertainties of the mapping outputs. This thesis presented different methods from three different tier levels following Grêt-Regamey et al. (2015) and the different approaches should be considered together to support land management decisions (Figure 4). Particularly, combining data-driven approaches (such as SDMs) with expert knowledge increases the reliability of model predictions for ecological complex systems with (expert) knowledge gaps and patchy ecological data. Increasing the reliability and accuracy of the model results potentially also increases the efficiency of land management solutions, adapted to current and future situations (Schwartz, 2012). Using different approaches is also needed to address different decision-making issues and processes that can affect a particular area (Grêt-Regamey et al., 2015; Dunford et al., 2017). Besides, the different methods were developed within an adaptive framework, that could be adapted to new knowledge on the relationships between biodiversity and ES and to environmental changes in the CSA.

6.4 Outlook

6.4.1 Biodiversity and ecosystem services conservation in agricultural landscapes

Achieving sustainable and productive agriculture, while conserving a wide range of ES, is a global challenge (Tscharntke et al., 2012a; Landis, 2017; Vanbergen et al., 2020). Different farming approaches can help to achieve more sustainable agricultural systems whilst preserving agricultural production (Vanbergen et al., 2020). Ecological intensification or maximising nature-based ecosystem processes in support of agricultural production is one promising management approach (Bommarco et al., 2013; Kleijn et al., 2019; Vanbergen et al., 2020). The transition to a more ecological intensive agriculture requires adapting farming management practices and is still a challenge (IPBES 2019). Knowledge gaps on the effect of ecological intensification on farm yields and profitability are one of the barriers to a shift to more nature-friendly agriculture systems (IPBES, 2019; Vanbergen et al., 2020). Particularly, the relationships between biodiversity, ES and crop production are still not well understood (Cardinale et al., 2012; Harrison et al., 2014; Ricketts et al., 2016), making it hard to predict the overall impacts of a shift towards an ecological intensification, especially if different measures are implemented.

A key challenge for managing ES is to determine synergies and trade-offs between multiple ES within and across landscapes (Duncan et al., 2015). Some studies showed a trade-off between the intensive production of agricultural goods and other ES (Power, 2010; Maes et al., 2012a; Raudsepp-Hearne et al., 2010). Implementing ecological measures can therefore imply yield reductions, at least in the short term. There are however also examples of enhanced crop production and yield assurance when applying ecological intensification measures (Blaauw and Isaacs, 2014; Pywell et al., 2015), highlighting the potential synergies between natural pest control, pollination and crop yields (Rusch et al., 2016; Garibaldi et al., 2018). Besides, many ES are similarly affected by the same drivers of change (e.g., land use change, habitat degradation, pollution and over-exploitation) and/or are underpinned by analogous ecological processes (e.g., soil formation, water and nutrient cycles) and biodiversity aspects (Raudsepp-Hearne et al., 2010; Maes et al., 2012b). Determining potential synergies between different ES can be a strong argument for ES conservation and support land-management decisions towards multifunctional landscapes. It however requires a higher quantitative understanding of the different mechanisms and interlinkages between multiple ecosystem processes and ES at different scales.

Besides these knowledge gaps, there are well-known social barriers to shifting to a more ecological agriculture model (Vanbergen et al., 2020). These aspects were not directly analysed during this thesis. However, this thesis was part of the BiodivERsA project IMAGINE, which involved ES experts and local stakeholders. For instance, local stakeholders' social values for a better management of green infrastructure (including natural and semi-natural habitats) were analysed, focusing on the social and ecological aspects they would like to see prioritised. The results of the social valuation analysis showed that, despite potential social frictions regarding the management of green infrastructure, the local stakeholders have a common understanding of the importance of biodiversity in agricultural production (Roche, 2021). The different local stakeholders were clearly in favour of a better biodiversity conservation and called for better design of agricultural production systems, explicitly considering biodiversity and ES conservation (Roche, 2021). The research presented in this thesis provides information to decision-makers in the CSA on how to design a multifunctional landscape, with a focus on pollination and natural pest control ES and therefore could support decision-makers in a shift towards a better management of green infrastructures.

In agricultural landscapes, conservation measures are often implemented through AES from the CAP. However, the effectiveness of AES for biodiversity and ES conservation is still questioned (Concepción et al., 2008; Batáry et al., 2011; 2015). Reasons suggested to explain the low effectiveness of individual AES measures is the lack of planning and coordination at the landscape scale (Concepción et al., 2012; Gonthier et al., 2014), along with the intermediate landscape-complexity theory (Tscharntke et al., 2012b). According to this theory, AES will not increase biodiversity in both the simplest and the most complex landscapes, because of the non-linear relationships between landscape complexity and species richness. This thesis showed the importance of compositional and configuration complexity of the landscape to sustain ESPs and ES and that species and communities often experience and are impacted by their environment at different scales. SNH diversity is also crucial to sustain a wide diversity of species, particularly wild bees (Concepción et al., 2012; Senapathi et al., 2015). The low effectiveness of AES measures can be therefore also due to a lack of consideration of the complexity of species' life cycles and needs. If specific AES are effective at sustaining specific species depends on the targeted species‘ life-history traits and ecological needs such as nesting and feeding preferences. In addition, species respond to their environment at different spatial and temporal scales.

Effective conservation measures, therefore, need to be guided by scientific knowledge of species suitable ecological niches and to be coordinated at the landscape scale. AES are currently based on voluntary agreements with farmers and are therefore mostly applied at field scales, without coordination nor cooperation at the landscape scale. AES therefore often translate into the patchy distribution of temporal and individual measures, whereas species communities and ecological processes require perennial measures, designed at a broader scale (Concepción et al., 2008). The design of AES measures at the landscape scales, as it should optimise efforts and benefits, should be a strong argument for cooperation in the implementation of AES. The adoption of landscape scale strategies implies a social shift towards shared efforts and long-term interests of several stakeholders, that may differ from their immediate individual costs and benefits (Barnaud et al., 2018). Farmers have different beliefs, interests and capacities to adapt their management to promote multifunctional landscapes, making it difficult to build shared objectives at the landscape scale (Smith and Sullivan, 2014). The number of farmers that are potentially involved and the diversity of farming systems increase the complexity of the social system when the needed changes rely on the spatial and temporal consistency of nature-friendly farming practices.

The research presented in this thesis showed the importance of conservation and management of biodiversity for the conservation of regulation and maintenance ES. The analysis was restricted to a few ESPs, i.e., *Andrena* wild bees for pollination and some arthropod species for natural pest control, but other species have been shown to play a significant role in ES delivery: birds, bats and other insects for pollination services (Rader et al., 2016), mammals, birds and bats for natural pest control services (Maas et al., 2016), but also fungi, earthworms and nematodes for soil formation and nutrient regulation (Nielsen et al., 2015), among others. In addition, a large diversity of species, populations and communities is essential for the delivery of a wide range of ES and a sustainable agricultural production (Hooper et al., 2005; Bommarco et al., 2013; Letourneau et al., 2009; Dainese et al., 2019; Woodcock et al., 2019; Senapathi et al., 2021). Each species has a specific ecological niche, suitable habitat and dispersal capacity and therefore their conservation and the conservation of the associated ES is quite a complex issue. Besides, as species are differently affected by bioclimatic variables, global change will not affect each species or group of species the same way. Some management measures might favour some species over others, and might in the end not benefit the overall biodiversity nor ES delivery. There is still a lack of consensus on how to maximise the benefits of land management options such as AES measures for biodiversity conservation and to restore or sustain ES delivery (Duru et al., 2015). The results of this analysis can nevertheless support a better design of AES measures at the local and landscape scale. The shift towards a more sustainable agricultural management should ideally be associated with other land management changes, which were not addressed in this thesis, such as a reduction of the use of pesticides and fertilisers (Gallé et al., 2019). This shift implies an important change in practices, from simplified agroecosystems, where many ecological processes have been replaced by human inputs to less predictable and controllable systems, relying on a complex network of ecological processes (Vanbergen et al., 2020).

6.4.2 Future research

The previous discussion leads to the formulation of three major recommendations for needed research and efforts to improve ES modelling and mapping. This includes: 1) increasing the availability and resolution of data on ecosystem pressure and condition indicators, species occurrence, and environmental variables at a high spatial resolution, 2) increasing the realism of ES models and 3) developing methods for validation of ES models and mapping efforts.

Information on LULC management at a high spatial resolution will help to better quantify provisioning ES and to better assess the condition of different ecosystems. For example, farming management and practices highly influence soil quality, species diversity at different scales as well as the ecological status of neighbouring water bodies. Organic farming (generally characterised by lower pesticide and fertilizer inputs) (Happe et al., 2018; Muneret et al., 2018; Gallé et al., 2019), crop rotation and diversification (Marrec et al., 2017) and reduced tillage (Rowen et al., 2020) can support higher arthropod diversity. Accounting for land use management types might therefore increase the accuracy of ES modelling, particularly at the tier 2 and 3 levels, where this information should be included as ecosystem condition indicators or environmental variables determining the habitat suitability of each species.

Higher temporal and spatial resolution of environmental data should be increasingly available with the advance in remote-sensing tools. Especially, increasing the LULC spatial resolution. This can help to capture habitat quality information such as the availability of specific nesting and feeding resources, which might greatly improve habitat suitability modelling for arthropod species. This level of spatial resolution when estimating and predicting LULC from aerial photographs and satellite images is not yet available for the CSA. Therefore, coarser LULC data were used as proxies to determine species' suitable habitat for this work. Future research should explore the feasibility of SDMs at higher thematical, temporal and spatial resolutions and their capacity to better predict species occurrence. Crucially, increasing sampling efforts and sharing existing recorded species data are needed to improve the availability of species occurrence data and the accuracy of SDMs. In Europe, data are particularly scarce in southern countries and sampling in these areas would drastically improve modelling performances. Besides, increasing the share of and access to species record data (from monitoring schemes or individual scientific studies) between researchers can also considerably increase data availability and quality. Another way to increase data availability is the use of standardised citizen science monitoring. Citizen-science records offer a low-cost approach to collecting species occurrence data covering a wide extent with a high temporal and spatial resolution, otherwise hardly feasible (Feldman et al., 2021).

Despite considerable research on ES and although it is well understood that ES supply strongly relies on biodiversity (Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2012; Harrison et al., 2014), there is still limited empirical research on the explicit causal and quantified relationships between the different aspects of biodiversity, ecosystem condition and ES (Mace et al., 2012; Harrison et al., 2014). There is definitely a need for more research to explain the mechanisms underpinning the relationships between the different biodiversity elements and the different ES (Duncan et al., 2015; Hossain et al., 2018). For pollination and natural pest control ES potentials, for instance, the relationships between ESPs occurrence, richness, abundance and how it influences crop production is still not well understood (IPBES, 2016) as only a few empirical studies have demonstrated that enhancing pollination or natural pest control ES potentials positively affect crop production and agronomic benefits (Kleijn et al., 2019). Therefore, in Chapters 4 and 5, only ES potentials were assessed, whereas the ES flows (contribution to crop production) were not determined. There are many different methods to assess the impacts of ESPs on crop production, ranging from simple to more complex methods (see IPBES, 2016 for an overview). Comparing open-fields and pollinator-excluded sub-samples can allow for an accurate assessment of the benefits of pollination and natural pest control. To date, this methodology is not standardised and analysing the gain due to ESPs is measured considering a wide range of parameters, including flower visitation, pollen deposition, crop yield, crop quality, plant damage and/or profitability (IPBES, 2016). Besides, this method does not account for the potential gain in sustainability and resilience (or stability) that comes from a high diversity of ESPs. In addition, only few studies have considered opportunity costs and the loss of cropped area and harvest implied by the establishment of AES (Kleijn et al., 2019). A better understanding of how ESP communities and the establishment of different AES affect the economic benefit of farmers and yield stability are therefore still needed to convince and support these actors to shift from conventional to more nature-friendly practices (Kleijn et al., 2019).

The developed ES potential models are mainly based on SDMs, i.e., correlative models that do not explain the mechanisms behind species distribution. In SDMs, species are typically assumed to be at equilibrium with their environment and dispersal capacity, species plasticity and source-sink populations are not taken into account (Guisan and Thuiller, 2005). By contrast, mechanistic models (or process-based models) aim at explaining distribution or occurrence patterns based on a theoretical understanding of the biology of the different species (Cuddington et al., 2013). Mechanistic approaches may therefore be able to describe non-equilibrium dynamics such as dispersal, migration and demographic processes (Gallien et al., 2012) and better assess extinction risks than SDMs. Physiology and demographic constraints are however generally implicitly integrated into statistical models, as they are sensitive to environmental conditions. Several ecological, species-specific processes can still increase the realism of ESP and ES models when incorporated. For instance, including information on how environmental variables affect survival, population growth, fitness and reproductive capacity and how it determines habitat suitability can be a way to improve models' performance and transferability (Kearney and Porter, 2009; Cabral and Schurr, 2010). Such models require considerable data and knowledge for model calibration and evaluation, which are currently not available for many species. Besides, the feasibility for multiple species assessment is questionable. Further research on species' ecological processes will nevertheless help to determine the level of detail needed to accurately model species-specific responses to environmental variables (Jeltsch et al., 2008).

A wide range of ES modelling and mapping tools have been developed over the last years but their performances are generally not assessed, mainly because of the scarcity of empirical data, but also because many ES are inherently difficult to measure (Bennett et al., 2015; Ochoa and Urbina-Cardona, 2017). As few studies have validated ES model results against independent datasets, the uncertainties associated with most ES models remain largely unknown (Bryant et al., 2018). Another approach consists of assessing model performance using different methods and evaluating if there is a consensus in the results (Araújo and New, 2007; Marmion et al., 2009). Overall, more research is required on ES model validation and towards the standardisation of model performance assessment within the ES research community. This could increase confidence in ES research and findings and help to increase the inclusion of ES assessments in policy and decision-making processes (Wong et al., 2015). However, as sampling of independent high-quality data is resource-intensive, there will always be financial and practical limits to model validation using independent datasets.

6.5 Final conclusions

This thesis shows how different modelling methods can assist in the assessment of multiple ES. The use of indicators, models and maps can guide land use decisions, particularly when empirical data and knowledge on ecological processes are limited. Models are however only simplified representations of complex processes and only consider specific properties of ecological systems. The results should be interpreted considering the assumptions behind the models and knowing the associated uncertainties. Mapping using proxies and simplified relationships between ecosystem condition and the delivery of ES is a rough simplification of reality. Similarly, ecological niche models are only a representation of the habitat suitability of species, given the considered environmental variables and prior assumptions. The different ES mapping and assessment methods are not exclusive and coupling different approaches may be the way forward to take advantage of different approaches and limit uncertainties. For this thesis, different model types of varying complexity and level of detail including field observations, expert-based approaches and habitat suitability modelling approaches were applied. The mapping outputs were then presented for a case study area in northern Germany. Together, the results of the different approaches can help managers to design more effective conservation strategies. Spatial information on ES can also assist economical decisions underlying agricultural practices. For instance, higher pollination and natural pest control ES potential can increase crop yields, save resources and have a positive impact on nature management and biodiversity conservation.

The concept of ES has great potential to influence land use planning and decisions because it links – via ES - biodiversity and ecosystem processes to human well-being. As a major thread for ES and because it relies on a broad range of ES, agricultural landscapes can greatly benefit from applying the ES concept. This thesis highlights the importance of numerous arthropod species in providing essential

ES and the importance of considering species' life cycles and ecological niches to be able to predict where they occur. The results of this thesis contribute to the knowledge of arthropod species distributions in agricultural fields. The modelling results highlight the complexity of designing conservation measures for different species and species communities. One of the main findings of the thesis is that a comprehensive assessment implies a multi-scale assessment, as the delivery of ES is determined by multi-scale variables and processes. Ecosystems and their biophysical properties are also affected by various variables at different scales: Typically, bioclimatic variables at global scale and land use management at local scale. Moreover, ecosystems may deliver ES outside of their boundaries. Understanding the spatial context and distribution patterns of ES informs of where and how land use management measures can be improved to maximise the delivery of (specific desired) ES. This thesis also highlighted numerous knowledge gaps and needed future research to increase the reliability of ESP and ES models. However, we should not wait to take actions until all knowledge gaps have been answered. Both abundance and diversity of arthropod species are currently declining at alarming rates due to agricultural intensification, habitat loss, pollution and climate change. If the arthropod decline are not rapidly halted, they will have serious repercussions for ecosystem functions and human well-being.

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Acknowledgments

Firstly, I would like to thank my supervisor Benjamin Burkhard for the opportunity to do this PhD, for welcoming me to his team in Hannover and for the support throughout this journey. I am grateful for the freedom I was given in my research, the scientific support and enthusiasm you always showed about my work.

I would like to thank my co-authors Felix Müller, Boris Schröder, Emily Poppenborg, Tim Diekötter, Jens Groß and Philip Roche for their encouragement and valuable contributions.

I am grateful to the Graduate Academies from the universities of Kiel and Hannover, particularly to Sabine Milde, Izabela Dyczek and Meike Huntebrinker, for their kindness and valuable advice.

I thank all my colleagues and PhD fellows from the universities of Kiel and Hannover for all the nice coffee breaks, other social events and their friendships. Special thanks to Sylvie for her help and her enthusiasm. I also wish to thank Angie for the language check throughout this thesis, as well as Heiko and Frank for the technical support.

Lastly, I would like to express my gratitude to my family: to my grandparents and my parents, who always believed in me and to Christopher, for his help, his patience and for being such a good cheerleader. The magnificent illustrations introducing each chapter of this thesis are from my dad.

List of publications and presentations

Perennes, M., Diekötter, T., Hoffmann, H., Martin, E., Schröder, B., Burkhard, B. (2023). Modelling natural pest control ecosystem services potential provided by arthropods in agricultural landscapes, Agriculture, Ecosystems and Environment, 342, DOI: https://doi.org/10.1016/j.agee.2022.108250

Perennes, M., Diekötter, T., Gross, J., Burkhard, B. (2021). A hierarchical framework for mapping pollination service potential at the local scale using multi-scale drivers, Ecological Modelling, 444, DOI: https://doi.org/10.1016/j.ecolmodel.2021.109484

Perennes, M., Campagne, C.S., Müller, F., Roche, P., Burkhard, B. (2020): Refining the Tiered Approach for Mapping and Assessing Ecosystem Services at the Local Scale: A Case Study in a Rural Landscape in Northern Germany, Land 9 (10): 348, DOI: https://doi.org/10.3390/land9100348

Müller, F., Bicking, S., Ahrendt, K., Bac, D.K., Blindow., I., Fürst, C., Haase, P., Kruse, M., Kruse, T., Ma, L., **Perennes, M.**, Ruljevic, I., Schernewski, G., Schimming, C-G., Schneiders, A., Schubert, H., Schumacher, J., Tappeiner, U., Wangai, P., Windhorst, W., Zeleny, J. (2020). Assessing ecosystem service potentials to evaluate terrestrial, coastal and marine ecosystem types in Northern Germany – An expert-based matrix approach. Ecological Indicators, 112, DOI: 10.1016/j.ecolind.2020.106116

Perennes, M., Campagne, C.S., Mueller, F., Roche, P., Burkhard, B. (2019) Refining the tiered approach for mapping and assessing ecosystem services at the local scale: a case study in a rural landscape in northern Germany. 10th World Conference of the Ecosystem Services Partnership (ESP10). Oral presentation.

Perennes, M. (2019) Mapping pollination services from wild bees at the landscape scale. 14th ALTER-Net Summer School. Poster presentation.

Lindner, J.P., **Perennes, M.**, Bos, U., Koellner, T. Quantification of land use impacts on biodiversity with local ecosystem indicators: A case study in southwestern Germany. In Proceedings of the LCA Food 2018, Bangkok, Thailand, 16–20 October 2018; Mungkung, R., Gheewala, S.H., Eds.; Kasetsart University: Bangkok, Thailand, 2018; pp. 106–108. Oral presentation.

Bos, U., Horn, R., Maier, S., Lindner, J.P., **Perennes, M**. Evaluation of regionalized land use and biodiversity aspects in LCA for biobased products. 5th Meeting Lignocellulose, Research Programme Bioeconomy BW, Heidelberg. Oral presentation.

Curriculum Vitae

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WORK EXPERIENCE

2021 - current	**Research assistant**, Swiss ornithological institute, Sempach *BioDivERsa project: “Global Biomass flows of Aerial Migrants” (GloBAM)* • Modelling annual spatio-temporal distribution of bird migrants and prediction of the impacts of global change on migration
2017 - 2021	**PhD student**, Institute of Physical Geography and Landscape Ecology, Hannover University & Department of Landscape Ecology, Kiel University *BioDivERsa project: “Integrative Management of Green Infrastructures Multifunctionality, Ecosystem Integrity and Ecosystem Services” (IMAGINE)* • Assessing and mapping ecosystem services at the local scale • Modelling ecosystem services in agroecosystems from arthropods using Species Distribution Models (SDM, jSDM, HSDM)
10.2016 - 05.2017	**Master’s thesis and research assistant,** Fraunhofer Institute, Stuttgart • Using local ecosystem indicators to determine land-use impacts on biodiversity in Life Cycle Assessment: A case study in Baden-Württemberg
2011-2014	**Environmental Impact Assessment Specialist**, French Ministry of Ecology, Paris • Providing recommendations and guidance to public and private stakeholders on Environmental Impact Assessments of regional and urban planning projects
03.2011 - 08.2011	**Research internship and master’s thesis**, Veolia Environment, Stockholm • Research on the development potential of plastic waste management
03.2010 - 08.2010	**Internship**, Water Resources Graduate Program, Oregon State University • Temperature data collection and modelling to assess stream ecological restoration success
05.2009 - 07.2009	**Internship**, Local department for environment and spatial planning, Orleans • Streamflow data measurement for flood forecasting and management

EDUCATION

21-31.08.2019	ALTER-Net Summer School "Biodiversity and ecosystem services: science and its impact on policy and society", Peyresq (France)
2017 - 2019	**BSc in Applied Economics**, Paris Sud University
2015 - 2017	**MSc in Geoecology and Landscape Ecology**, Bayreuth University (Germany)

	• Supported by a scholarship from the German Academic Exchange Service (DAAD)
2008 - 2011	**MSc in Environmental Engineering and Planning**, Ecole Nationale des Travaux Publics de l'Etat (ENTPE), Lyon
2010 - 2011	Study Abroad, Industrial Engineering Department, Royal Institute of Technology (KTH), Stockholm
2006 - 2008	**BSc in Biology** and intensive program preparing for the national competitive exam for entry to the engineering schools "Grandes Ecoles", (Classes préparatoires BCPST), Rennes (France)
2006	High School diploma equivalent to A Levels, scientific option with honours (Baccalauréat Scientifique), Guingamp (France)

LANGUAGES AND SOFTWARE SKILLS

French: native speaker
English: fluent
German: fluent
Spanish: very good command
Swedish: basic communication skills

Microsoft Office, LaTeX
R, Matlab
ArcGIS, QGIS
FRAGSTATS (Spatial Pattern Analysis Program)
InVEST (Mapping and valuing ecosystem services)
SWAT (Soil and Water Assessment Tool)
SimaPro, GaBi (Life Cycle Assessment)

INTEREST AND ACTIVITIES

Volunteering: Bird ringing volunteer (petite Camargue Alsacienne), French language and literacy teaching for migrants (Paris), Lifeguard (Bretagne)
Hobbys: Birdwatching, triathlon, reading, hiking