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**Simulating biodiversity responses to
land use mosaics in agricultural landscapes:**
An overview of the possibilities and potential

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Simulating biodiversity responses to land use mosaics in agricultural landscapes: an overview of the possibilities and potential

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"In 2050, we live well, within the planet's ecological limits. Our prosperity and healthy environment stem from an innovative, circular economy where nothing is wasted and where natural resources are managed sustainably, and biodiversity is protected, valued and restored in ways that enhance our society's resilience. Our low-carbon growth has long been decoupled from resource use, setting the pace for a safe and sustainable global society."

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ZUSAMMENFASSUNG

Seit Mitte des 20. Jahrhunderts haben Industrialisierung und Globalisierung einen tiefgreifenden Wandel der Landnutzung in Europa eingeleitet. Fortschreitende Technisierung und Intensivierung der Landwirtschaft, Flächenkonkurrenz, aber auch globale Klimaänderungen verändern die Zusammensetzung und Beschaffenheit der Agrarlandschaften. Zugleich wandelt sich damit der Lebensraum aller Tier- und Pflanzenarten, die in ihren Habitatansprüchen eng an das System Agrarlandschaft gekoppelt sind. Zahlreiche Studien der letzten Jahrzehnte zeigen einen allgemeinen Rückgang der Biodiversität in Agrarlandschaften sowie die Gefährdung vieler Arten. Die Gemeinsame Agrarpolitik (GAP) der Europäischen Union, welche die Rahmenbedingungen für Landwirtschaft in Europa setzt, versucht diesem Trend entgegen zu wirken, indem sie Direktzahlungen für nachhaltige Umweltleistungen („Greening“) an Landwirte vergibt. Dazu gehören Anbaudiversifizierung, Erhaltung von Dauergrünland und die Ausweisung von ökologischen Vorrangflächen. Da diese Maßnahmen erst mit der letzten GAP-Reform von 2013 verbindlich eingeführt worden sind, gibt es bisher nur wenige Studien, die deren Nutzen für die Artengemeinschaften der Agrarlandschaft evaluieren.

In meiner Arbeit untersuche ich verschiedene Greening-Maßnahmen, die als ökologische Vorrangflächen angerechnet werden können, hinsichtlich ihres Nutzens für Feldhasen (*Lepus europaeus*). Als Werkzeug zur Beantwortung meiner Forschungsfragen wende ich zwei räumliche Computersimulationsmodelle an und vergleiche sie, um Möglichkeiten und Potentiale solcher Modelle zur Folgenabschätzung von Landnutzungsänderungen auf die Biodiversität zu identifizieren. Ein besonderes Augenmerk lege ich dabei auf die den Modellen zugrundeliegenden Landschaften und auf die Frage, inwieweit ihr Design und ihre Komplexität den Anwendungsbereich der verwendeten Simulationsmodelle bestimmen. Zudem gebe ich einen Überblick über verschiedene Tools, mit denen Modelllandschaften erzeugt werden können, zeige ihre Vor- und Nachteile auf und leite daraus Anforderungen an generische und vielseitig einsetzbare Tools ab.

Im zweiten Kapitel wende ich ein etabliertes und komplexes räumliches Simulationsmodell (ALMaSS) an, um die Effekte verschiedener Greening-Maßnahmen auf Feldhasen zu untersuchen. Entsprechend der EU-Regularien erhöhe ich ihren Anteil auf jeweils 5 % der Agrarfläche in drei dänischen 10 x 10 km großen Modelllandschaften und verfolge die Entwicklung der Feldhasen-Population über 30 Jahre. Die Bereitstellung von permanenten Brachflächen, die über das ganze Jahr hinweg Schutz und Futterpflanzen bieten, erweist sich als

die günstigste der untersuchten Greening-Maßnahmen, auch wenn die Population damit immer noch am unteren Limit für stabile Feldhasen-Populationen liegt. Auch die Erweiterung von krautigen Feldrändern und extensiv genutztem Grünland führt zu signifikanten Steigerungen der Populationsdichte. ALMaSS arbeitet mit hochaufgelösten Landschaften, die auf realen Karten basieren und Landschaftsstrukturen bis zu einer Auflösung von 1m² abbilden können. Weiterhin integriert es verschiedene Submodelle, die das Modellverhalten der einzelnen Individuen in Rückkopplung mit realistischem Pflanzenwachstum, Wetterbedingungen und Bewirtschaftungsmaßnahmen simulieren. Damit ist ALMaSS komplex genug, um detaillierte Analysen von Umwelteinflüssen durchzuführen und spezifische Fragestellungen für konkrete Landschaften und verschiedene Tierarten zu beantworten. Die Verwendung von neuen Landschaften mit ihren spezifischen Bewirtschaftungsformen ist jedoch aufgrund der Detailschärfe des Modells und den umfangreichen Datenanforderungen sehr zeitaufwendig.

Aufgrund der Erfahrungen mit ALMaSS erstelle ich im dritten Kapitel eine Übersicht über sogenannte Agrarlandschafts-Generatoren (ALG), die Variationen von Landnutzungsmosaiken, also künstliche Landschaften, als Input für räumliche Simulationsmodelle generieren können. Es zeigt sich, dass bisher nur wenige ALG entwickelt wurden und diese kaum breitere Anwendung gefunden haben. Die identifizierten Tools erzeugen mehrheitlich einfache Landschaftsmosaik aus gleichmäßig geformten Feldern, welche mit nur wenigen Nutzungstypen (z.B. bestimmte Feldfrüchte) belegt werden können. Die Verwendung weniger Landschaftsmaße begrenzt die Einsatzmöglichkeiten auf eher allgemeine oder theoretische Anwendungen. Auf Grundlage der Ergebnisse und des identifizierten Bedarfs entwickeln wir Anforderungen an generische ALG, die großflächig für verschiedene Szenarien, Regionen und Modelltypen eingesetzt werden können. Ein flexibles modulares Design und eine offene Modellarchitektur erachten wir dabei als obligatorisch und stellen einen Prototyp vor.

Einen der bereits existierenden ALG verwende ich im vierten Kapitel, um 4 x 4 km große Input-Karten für ein räumliches Simulationsmodell zu erzeugen, welches ich in NetLogo entwickelt habe. Mit diesem, im Vergleich zu ALMaSS einfachen Modell, untersuche ich speziell den Einfluss von Greening-Maßnahmen auf Feldhasen, die Alternativen zu den in Deutschland großflächig angebauten Energiepflanzen Mais und Raps darstellen. Weiterhin untersuche ich die Effekte einer Erweiterung von Brachflächen und der Erhöhung der Anbaudiversität. Die alternativen Energiepflanzen Durchwachsene Silphie und Klee gras sowie die Erhöhung der Anbaudiversität in der Landschaft erzielen die positivsten Effekte auf die Feldhasenpopulation. Des Weiteren zeigt sich, dass nicht nur die Komposition der Landschaft einen entscheidenden Einfluss hat, sondern auch eine geringere mittlere Feldgröße vorteilhaft ist. Trotz des hohen Abstraktionsgrads des Modells lassen sich Trends der Populationsentwicklung quantifizieren und der Einfluss von Greening-Maßnahmen vergleichen. Jedoch können aufgrund der

Vereinfachungen und Modellannahmen eher generelle Rückschlüsse gezogen werden als spezifische Analysen für konkrete Landschaften durchgeführt werden. Das Modell ist im Vergleich zu ALMaSS flexibler und leichter anpassbar sowie durch die Verwendung des ALG für viele andere Fragestellungen und Landschaften leicht nutzbar.

Insgesamt zeigt diese Arbeit verschiedene Möglichkeiten auf, den Einfluss von Landnutzungsänderungen auf Tierarten der Agrarlandschaft mit räumlichen Simulationsmodellen zu bewerten. Darüber hinaus stellen die durchgeführten Simulationsexperimente wertvolle Folgenabschätzungen von Politikmaßnahmen auf Feldhasen dar, die Grundlage für nachhaltige Bewirtschaftungsstrategien sein können. Die beiden Anwendungsbeispiele, die vorgestellten Tools zur Generierung von Landschaften sowie der Ausblick auf zukünftige Entwicklungen zeigen das große Potential des Einsatzes von computergestützten Bewertungsinstrumenten auf drängende Fragen unserer Zeit.

ABSTRACT

Since the middle of the 20th century, industrialisation and globalisation have initiated a profound land use change in Europe. Increasing mechanisation and intensification of agriculture, competition for land, but also global climate change are modifying the structure and composition of agricultural landscapes. At the same time, the habitat of animal and plant species adapted to the agricultural landscape system is changing. Numerous studies in recent decades have shown a general decline in biodiversity in agricultural landscapes and the endangerment of many species. The Common Agricultural Policy (CAP) of the European Union, which sets the framework conditions for agriculture in Europe, attempts to counter this trend by granting direct payments for sustainable environmental services ('greening') to farmers. These provisions include crop diversification, the maintenance of permanent grassland and the establishment of ecological focus areas. Because these measures were introduced with the last CAP reform of 2013, there are only a few studies that have evaluated their benefits for the agricultural species communities.

In my thesis, I investigate various greening measures that are eligible as ecological focus areas with regard to their benefit for the brown hare (*Lepus europaeus*). As tools to answer my research questions, I apply two spatial computer simulation models and compare them to identify the possibilities and potential of such models for impact assessment of land use change on biodiversity. I particularly focus on the landscapes underlying the models and on the extent to which their design and complexity determine the scope of the simulation models. In addition, I give an overview of various tools that can be used to generate model landscapes, show their advantages and disadvantages, and derive requirements for generic and versatile tools.

In the second chapter, I apply an established and complex spatial simulation model (ALMaSS) to investigate the effects of different greening measures on brown hares. According to the EU regulations, I increase their proportion to 5 % of the agricultural area in three Danish 10 x 10 km model landscapes and investigate the hare population development over 30 years. Permanent set-asides that provide protection and forage throughout the year prove to be the most favourable of the investigated greening measures, even though the population is still at the lower limit for stable hare populations. The expansion of herbaceous field margins and extensive grassland also leads to significant increases in population density. ALMaSS works with high-resolution landscapes that are based on real maps and can map landscape structures up to a resolution of 1 m². Furthermore, it integrates different submodels that simulate the

behaviour of individuals in feedback with realistic plant growth, weather conditions and management measures. This integration makes ALMaSS sufficiently complex to carry out detailed analyses of environmental impacts and to answer questions regarding specific landscapes and different animal species. However, the application of new landscapes with their specific management activities is particularly time-consuming due to the sharpness of detail and the large amount of data required.

Based on my experiences with ALMaSS, I provide in the third chapter an overview of so-called Agricultural Landscape Generators (ALG), which can generate variations of land use mosaics (i.e. artificial landscapes), as input for spatial simulation models. It turns out that so far, only a few ALGs have been developed and that they have not found wider application. The identified tools generate mostly simple landscape mosaics of uniformly shaped fields, which can be covered by a few land use types (e.g. certain crops). The consideration of few landscape metrics limits the application possibilities to more general or theoretical purposes. Based on the results and the identified needs, we develop requirements for generic ALGs that can be used widely for different scenarios, regions and model types. We consider a flexible modular design and an open model architecture as obligatory and present a prototype.

In the fourth chapter, I apply one of the existing ALGs to create 4 x 4 km input maps for a spatial simulation model, which I developed in NetLogo. Using this model, which is significantly simpler than ALMaSS, I am investigating the effects of greening measures, which are alternatives to the large-scale cultivation of maize and rape in Germany, on brown hares. I also examine the effects of increasing set-asides and general crop diversity. The alternative energy crops silphie and grass-clover ley, as well as the increase of crop diversity in the landscape, achieve the most positive effects on the hare population development. Furthermore, it appears that not only the composition of the landscape has a decisive effect, but also that a smaller average field size is beneficial. Despite the high degree of abstraction of the model, trends in population development can be quantified and the effects of greening measures can be compared. However, due to the simplifications and model assumptions, more general conclusions can be drawn rather than providing specific analyses for concrete landscapes. Compared to ALMaSS, the model is more flexible and easier to adapt, and can be used for many other questions and landscapes by using the ALG.

This thesis presents different possibilities to evaluate the effects of land use changes on animal species using spatial simulation models. In addition, the simulation experiments carried out are valuable impact assessments of policy measures on brown hares, analyses which can be useful for sustainable management strategies. The two application examples, the presented tools for

landscape generation and the outlook on future developments demonstrate the potential of computer-based assessment tools for urgent questions of our time.

CONTENTS

| | | |
|-------|--|----|
| 1 | INTRODUCTION | 1 |
| 1.1 | Research background and need | 1 |
| 1.1.1 | Land use change in agricultural landscapes | 2 |
| 1.1.2 | Implications for agricultural biodiversity..... | 8 |
| 1.1.3 | The European brown hare | 9 |
| 1.2 | Research approach und methods | 11 |
| 1.2.1 | Spatial Simulation Models | 11 |
| 1.2.2 | Agent-based Models..... | 13 |
| 1.3 | Objectives of this thesis and chapter overview..... | 14 |
| 2 | A MODELLING APPROACH TO EVALUATING THE EFFECTIVENESS OF ECOLOGICAL FOCUS AREAS: THE CASE OF THE EUROPEAN BROWN HARE | 17 |
| 2.1 | Abstract..... | 18 |
| 2.2 | Introduction | 18 |
| 2.3 | Methods | 21 |
| 2.3.1 | Landscape simulation system..... | 21 |
| 2.3.2 | Hare model | 25 |
| 2.3.3 | Greening scenarios | 26 |
| 2.3.4 | Data analysis | 28 |
| 2.4 | Results | 29 |
| 2.5 | Discussion..... | 33 |
| 2.6 | Conclusions | 37 |
| 2.7 | Acknowledgements | 38 |
| 3 | AGRICULTURAL LANDSCAPE GENERATORS FOR SIMULATION MODELS: A REVIEW OF EXISTING SOLUTIONS AND AN OUTLINE OF FUTURE DIRECTIONS | 39 |
| 3.1 | Abstract..... | 40 |
| 3.2 | Introduction | 40 |
| 3.3 | Methods | 43 |
| 3.4 | Results | 45 |
| 3.4.1 | Existing ALGs..... | 45 |
| 3.4.2 | Aims | 47 |
| 3.4.3 | Configuration | 49 |
| 3.4.4 | Composition | 60 |
| 3.4.5 | Validation..... | 63 |
| 3.4.6 | Evaluation of policy measures | 63 |
| 3.4.7 | Availability of the ALGs..... | 64 |

| | | |
|-------|--|-----|
| 3.4.8 | Other tools for generating neutral landscapes | 64 |
| 3.5 | Outline of a future generic ALG..... | 66 |
| 3.6 | Discussion..... | 69 |
| 3.7 | Conclusion | 74 |
| 3.8 | Acknowledgements..... | 75 |
| 4 | MITIGATING BIOENERGY-DRIVEN BIODIVERSITY DECLINE: A MODELLING APPROACH WITH THE EUROPEAN BROWN HARE | 77 |
| 4.1 | Abstract..... | 78 |
| 4.2 | Introduction..... | 78 |
| 4.3 | Methods | 81 |
| 4.3.1 | Landscape generation | 82 |
| 4.3.2 | Reference landscapes..... | 82 |
| 4.3.3 | Hare model | 83 |
| 4.3.4 | Hare parameterization | 86 |
| 4.3.5 | Scenarios | 89 |
| 4.3.6 | Data analysis..... | 91 |
| 4.4 | Results..... | 91 |
| 4.5 | Discussion..... | 94 |
| 4.6 | Conclusion | 98 |
| 4.7 | Acknowledgements..... | 99 |
| 5 | CONCLUSION AND OUTLOOK..... | 101 |
| 5.1 | Summary of main results | 101 |
| 5.1.1 | A complex simulation model for the assessment of policy measures | 101 |
| 5.1.2 | Agricultural landscape generators for spatial simulation models..... | 105 |
| 5.1.3 | A simplified simulation model for the assessment of policy measures | 107 |
| 5.2 | Conclusions for the protection of the brown hare..... | 110 |
| 5.3 | Reflections on methodological approaches | 112 |
| 5.3.1 | Spatial simulation models as assessment tools..... | 112 |
| 5.3.2 | Generalisation of landscapes | 113 |
| 5.3.3 | Future perspectives of the simulation of agricultural landscape | 114 |
| 5.4 | Synthesis and outlook | 115 |
| | APPENDICES..... | 117 |
| A | Appendix of Chapter 2..... | 117 |
| B | Appendix of Chapter 3..... | 127 |
| B1 | List of ALG publications..... | 127 |
| B2 | VDP Example..... | 128 |
| C | Appendix of Chapter 4..... | 131 |
| C1 | Hare model: ODD protocol | 131 |
| C2 | Hare-specific preferences | 143 |
| C3 | Results of sensitivity analysis..... | 145 |

| | | |
|-----------------------|-----------------------|-----|
| C4 | Hare model code | 147 |
| FIGURES..... | | 163 |
| TABLES..... | | 167 |
| ABBREVIATIONS..... | | 171 |
| BIBLIOGRAPHY | | 173 |
| ACKNOWLEDGEMENTS..... | | 191 |

1 INTRODUCTION

1.1 RESEARCH BACKGROUND AND NEED

Agricultural landscapes are landscape types characterised by agriculture and are the habitat of numerous animal and plant species adapted to it. In terms of the European Union (EU28), agricultural landscapes account for approximately 40 % of the total land area (Eurostat, 2018), composed of 60 % arable land (which includes land for cereals and other arable land) and 34 % permanent grassland and meadows. Farmers thus play a key role in tackling climate change and protecting the environment, landscapes and biodiversity. To provide farmers with suitable political and economic incentives in this regard, reliable information and predictions on the state and trends of biodiversity that depends on land use in agricultural landscapes are needed.

This thesis examines the possibilities and potential to quantify biodiversity responses to land use mosaics in agricultural landscapes using computer simulation models. Therefore, methodological tools with which trends and states of biodiversity development in agricultural landscapes can be made visible and quantified are partly applied, are partly developed and are compared, and an overview of further useful methodological tools is provided, as well. Specifically, I will focus on EU policy measures as control instruments to improve biodiversity in agricultural landscapes. I will implement a range of suitable greening and mitigation measures into two different spatially explicit simulation models to test their suitability to assess policy measures, and I will use the European brown hare (*Lepus europaeus*) as an indicator species. In this context, I will also provide a review of so-called Agricultural Landscape Generators (ALGs), as they are of increasing importance in regard to evaluating management options and regulations, in particular those adopted by the European Commission.

The following sections provide background information on the drivers of land use change in Europe, the influence of European agricultural policy and the impact of land use change on biodiversity in agricultural landscapes. Then, I will present the research tools, in particular the modelling approaches used, formulate the research questions and give an overview of the chapters of this thesis. Since the research areas for my simulation experiments are located in Germany and Denmark, and I have investigated European policy measures, I will especially refer to Europe and in particular to these two countries.

1.1.1 *Land use change in agricultural landscapes*

Agricultural landscapes are an essential source of supply for human survival. They not only provide the production of food but also provide other essential raw materials, such as biomass for energy production. For centuries, agriculture was organised locally and was small-scale, provided mainly local supplies and was tied to local conditions. This has gradually changed since the middle of the 20th century, as industrialisation and globalisation have initiated a profound change in land use. This change is characterised by four main processes: competition for land, intensification and extensification, bioenergy production and the influence of agricultural policy.

Competition for land

To supply billions of people with sufficient food and energy, agricultural land has become the focus of many interest groups from society, politics and industry, resulting in increasing pressure on land (Steinhausser *et al.*, 2015). A useful indicator to make this development visible is the price of agricultural land, which increased by more than 140 % between 2007 and 2016 in Germany (Destatis, 2018). The reason is that agricultural land competes with other forms of land use, such as settlements and transport routes, forestry and nature conservation (Figure 1.1). There is not enough land available or that can be converted to meet the needs of all user groups, leading to land use conflicts that are likely to worsen in the future (Sturmer *et al.*, 2013, Steinhausser *et al.*, 2015).

A large interview study by Steinhausser *et al.* (2015) shows that conflicts in Germany arise primarily from the growing demand for land for settlements and transport routes. In the years 2013 to 2016, the settlement and transport area increased daily by 61.5 ha (Destatis, 2018). This sector requires not only dedicated land but also additional land for compensatory measures, which are mandatory under the Federal Nature Conservation Act (BnatSchG).

Another growing sector and thus competitor for agriculture is forestry. Between 2000 and 2010, contrary to the global trend, the proportion of forested areas in the EU increased by 2 % due to natural expansion and afforestation (Destatis, 2018). Almost all member states show this trend. In regions where agriculture has been abandoned, most of the land is forested, so the proportion of agricultural land in Europe as a whole has declined in recent decades.

The energy transition towards a sustainable energy supply using renewable energies has pushed the energy industry as a new competitor for agricultural land, especially in Germany. By 2050, the goal is to increase the proportion of renewable energies in electricity production to at least

80 % in Germany (EEG 2017), which causes land use conflicts between food, nature conservation and bioenergy production (e.g., WBGU, 2008, Tomei & Helliwell, 2016).

Since the intensification of land use in recent decades has caused considerable damage to many ecosystems and biodiversity (e.g., Donald *et al.*, 2001, Stoate *et al.*, 2009, Geiger *et al.*, 2010), policymakers are endeavouring to create protected areas, which in turn act as further competitors for land. Due to these many actors and pressures from different areas, the direct effects on agricultural land are difficult to understand and can only be analysed locally in comparison with the original situation (van Vliet *et al.*, 2015).

In Denmark, the same problem is emerging, and land is becoming a precious natural resource. Scientists at Aalborg University estimate that Denmark's land area would need to be 40 % larger to meet all land needs (Arler *et al.*, 2015). Currently Denmark is the country in the EU with the largest relative proportion of arable land at 61 % (Eurostat, 2018).

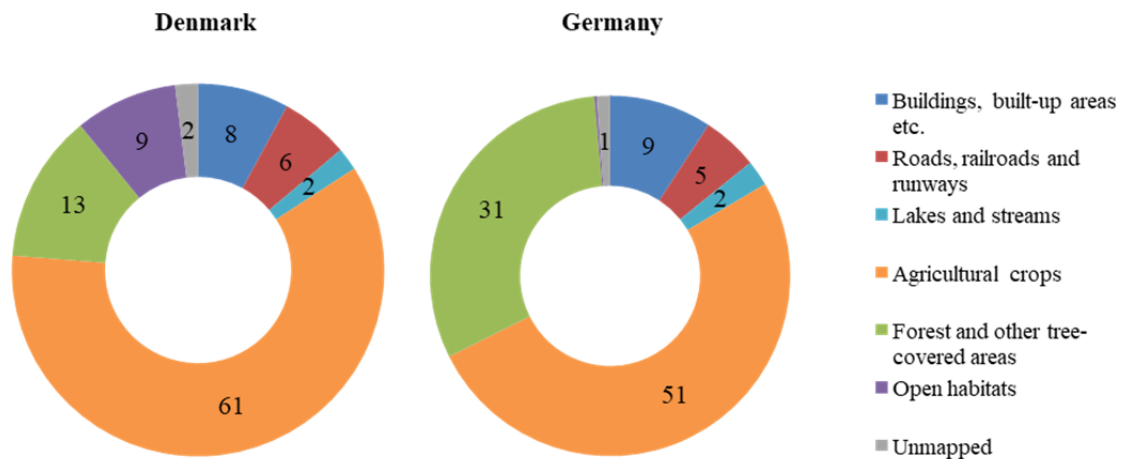


Figure 1.1: Land cover of Denmark and Germany. The data are provided by Eurostat (2018) and Destatis (2018).

Intensification and extensification

The industrialisation of agriculture, which took place in Europe between 1960 and 1980, was accompanied by a considerable intensification (e.g., van Vliet *et al.*, 2015, van der Sluis *et al.*, 2016). The improvement in efficiency and productivity on agricultural land, as well as technological developments, led to large increases in yields (Trnka *et al.*, 2016). Today, Europe is one of the most intensively managed agricultural regions on earth. Nevertheless, there are also many areas in Europe that have been abandoned due to economic constraints or rural depopulation (Navarro & Pereira, 2015). These developments show that land use change in Europe is characterised by both phenomena at the same time: intensification and extensification of agriculture (e.g., Feranec *et al.*, 2010, van Vliet *et al.*, 2015, Plieninger *et al.*, 2016).

Intensification means more intensive farming methods, mechanisation, specialisation, enlargement of fields and farms, reduction in crop rotations and the use of fertilisers and pesticides. Furthermore, it is usually accompanied by an increase in agricultural land through the conversion of marginal sites and the loss of (semi-)natural landscape elements and areas (Pedroli *et al.*, 2013). In the course of this process, for example, grassland is often converted into arable land. Extensification in turn stands for the opposite process, e.g., reducing the intensity of cultivation and abandoning arable land. However, intensification on the one hand and abandonment of land on the other led to the loss of traditional agricultural landscapes.

I have focused on intensively used agricultural landscapes in my model landscapes in Denmark and Germany. Germany is facing ongoing structural change in agriculture towards intensification. Larger agricultural areas are being managed by fewer holdings. Between 2013 and 2016, the number of agricultural holdings has decreased by approximately 3.4 % (Destatis, 2018). On the other hand, the average size of agricultural holdings increased from 44 ha in 2005 to 59 ha in 2013. A change towards larger farm structures can also be observed in almost all other EU countries. In Denmark, there is a slight trend towards extensification. The proportion of intensively used land has declined slightly in recent years, while the proportion of extensively used grassland and fallow land increased slightly by 1.1 % between 2011 and 2016 (Statistics Denmark, 2018). This development can be explained by the introduction of mandatory measures, such as Ecological Focus Areas (EFAs).

Bioenergy production

For over 20 years, the European Union has been trying to reduce its dependence on fossil fuels by promoting renewable energies. In this way, the EU wants to become a sustainable, low-carbon and environmentally friendly economic power, a leader in the production of renewable energy, and aims to limit climate change. By 2020, 20 % of the EU's total energy needs are to be generated from renewable energies (EU Directive 2009/28/EC). All member states have committed themselves to this goal by implementing national action plans for renewable energies.

To achieve these ambitious goals, biomass has become an important part of the energy mix. Biomass – organic material of non-fossil origin, including organic waste – can be converted into bioenergy by combustion, either directly or through derived products. Plants for bioenergy production (e.g., maize, wheat, sugar beet, rape, sunflowers) and fast-growing woody plants are cultivated on agricultural land or in short-rotation coppices. This, however, puts the production of biomass on agricultural land in competition with agricultural food production (e.g., Karp &

Richter, 2011, Pedroli *et al.*, 2013). In 2011, 13 % of agricultural land in Europe was used for the cultivation of energy crops, and production continues to rise (Eurostat, 2018).

The increased cultivation of biomass has changed land use in Europe (Miyake *et al.*, 2012) and has led to the conversion of non-agricultural landscapes – either directly or indirectly – into agricultural landscapes (Fritsche *et al.*, 2010, Gawel & Ludwig, 2011). Indirect land use change (iLUC) means displacement effects triggered by additional demand. Thus, the previous production (e.g., of food) is displaced to other areas. This, in turn, leads elsewhere to the development of new arable land, which can result in the loss of valuable ecosystems, such as forests, species-rich grasslands and moors, or landscape elements that have positive effects on biodiversity. Increasing imports of food and feed from abroad can also be a consequence (Steinhausser *et al.*, 2015).

The promotion of renewable energies also changes the composition of agricultural holdings. Energy producers earn more money than conventional farmers thanks to fixed feed-in payments for electricity, enabling them to pay higher rents and land prices (Steinhausser *et al.*, 2015). This in turn creates price pressure in the agricultural land market and leads to price increases for agricultural commodities. In the end, this can lead to the displacement of small farmers and extensive forms of land use.

In addition to spatial changes, energy crop cultivation is also characterised by new crop types and crop rotations, which lead to a change in the agricultural land use pattern and affect ecosystems. In many regions, for example, there is a trend towards increased cultivation of maize and rapeseed and thus a narrowing of crop rotations to a few crop types and a reduction of crop diversity.

Germany is by far the largest producer of bioenergy in the EU, especially biogas (Eurostat, 2018). The area under energy crop cultivation has increased from approximately 349,400 ha in 2000 to 2.1 million ha in 2014 (Figure 1.2, Steinhausser *et al.*, 2015). The energy crops silage maize (18.2 %) and winter rape (11.2 %) accounted for the largest proportion of agricultural land in 2016 (Destatis, 2018).

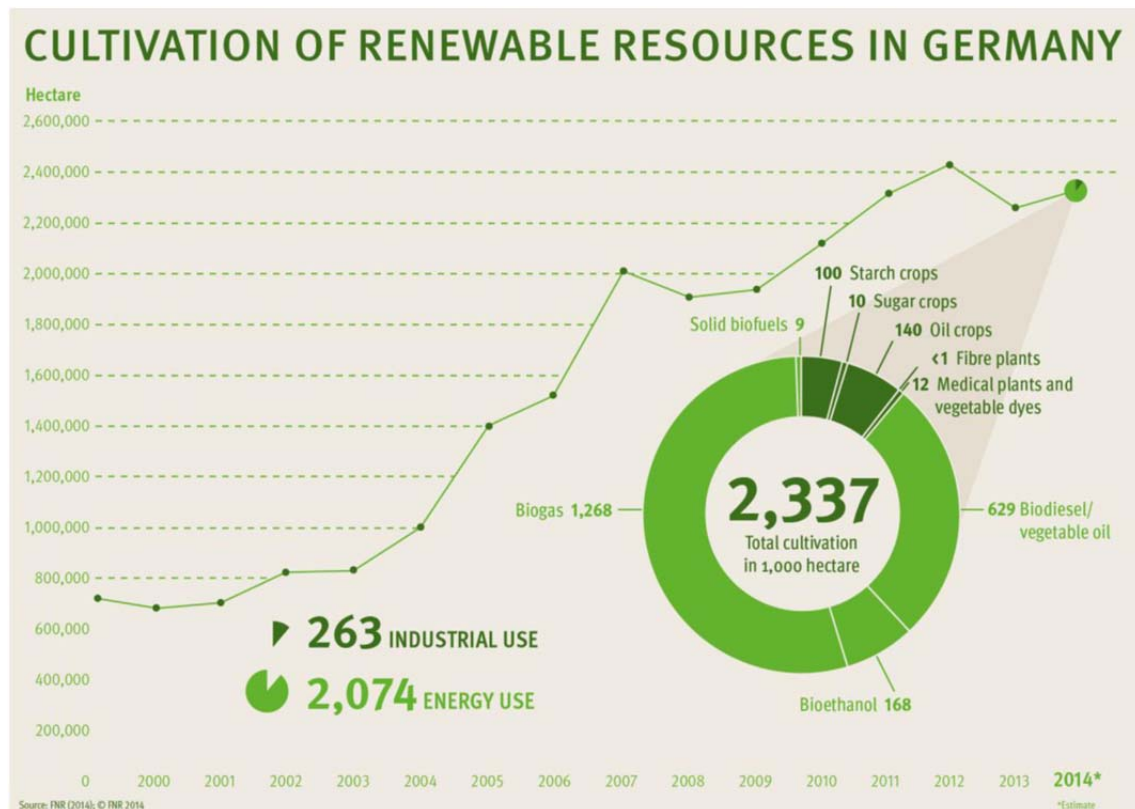


Figure 1.2: Cultivation of renewable resources in Germany (from Steinhauser *et al.*, 2015).

Danish renewable energy production has also grown rapidly in the last 25-30 years and has increased almost sevenfold since 1980 (Statistics Denmark, 2018). However, the cultivation of energy crops for the production of biomass plays a minor role, as biomass is mainly used in the form of straw, fuel wood, wood waste, etc.

Agricultural policy

The type and speed of land use change is directly influenced by national and EU policies, such as the Common Agricultural Policy (CAP) (Lefebvre *et al.*, 2012). CAP has been one of the most important fields of European policy since the beginning of the unification of Europe. Therefore, it has been repeatedly adjusted in line with the change in living conditions in Europe (Hill, 2012). While the CAP was initially responsible for support for agricultural prices, the 1992 agricultural reform (MacSharry-Reform) brought about a paradigm shift towards market orientation (Garzon, 2006). It turned away from market and price supports and focused on direct support for agricultural holdings. Since then, farmers have received direct payments linked to conditions such as food safety, animal welfare and environmental protection. In addition, accompanying measures such as extensification or afforestation made environmental concerns an integral part of the CAP for the first time (Matthews, 2013).

The reforms of agricultural policy continued with Agenda 2000: support prices were again reduced and direct payments increased in return. Another environmental aspect was added, as the member states were able to link direct payments to compliance with environmental regulations. In 2003, the EU began to decouple direct payments from production. Environmental protection and animal welfare were further enhanced by making direct payments fully subject to certain conditions (so-called cross-compliance) (Schmid *et al.*, 2007).

In 2013, another major reform of the CAP was adopted. The course of market orientation in agriculture was continued, and the CAP was geared even more strongly to the remuneration of social services. For example, fairer and more environmentally friendly direct payments have been introduced, the position of farmers within the food production chain has been strengthened, and the CAP as a whole has been set up more efficiently and transparently.

As part of the 2013 reform, the so-called greening obliges farmers to provide additional environmental services to enhance the protection of common goods such as biodiversity and clean water (European Commission Regulation (EU) No 1307/2013). Since implementation in 2015, the receipt of part of the direct payments has been directly linked to greening measures, except for organic farms and small producers. The greening requirements include three mandatory measures: (1) crop diversification, in which farms up to 30 ha must cultivate at least two crops, while farms over 30 ha must cultivate at least three crops; (2) ecological focus areas, in which farms with 15 ha or more of arable land must dedicate at least 5 % to ecologically beneficial elements, and this applies to landscape elements on or near the arable land, including ecologically valuable buffer strips, short-rotation coppices and afforested areas; and (3) maintaining permanent grassland. However, the evaluation of the greening measures in the last years resulted in much criticism, and many environmental associations regard these measures as having failed (e.g., Matthews, 2013, Pe'er *et al.*, 2014, Pe'er *et al.*, 2017).

Therefore, on 1 June 2018, the European Commission presented a legislative package with proposals for the CAP after 2020¹, which includes the following aspects: The environmental and climate performance of agriculture should be supported even more comprehensively. In particular, the receipt of direct payments should be more closely linked to compliance with environmental and climate regulations (so-called conditionality). The EU Commission is thus proposing a new green architecture for the CAP; the previous greening concept is to be abolished, but direct payments will be linked to environmental services much more comprehensively than before. Furthermore, agriculture in the European Union should be geared more closely to society's expectations regarding food and health.

¹ https://ec.europa.eu/info/food-farming-fisheries/key-policies/common-agricultural-policy/future-cap_en

1.1.2 *Implications for agricultural biodiversity*

Over the past centuries, European cultural landscapes have created a characteristic and diverse fauna and flora, which have a significant influence on the processes and functions of ecosystems. However, the land use change and the ongoing intensification of agriculture in recent decades has led to a drastic decline in agricultural biodiversity and endangered many species (e.g., Donald *et al.*, 2001, Stoate *et al.*, 2001, Stoate *et al.*, 2009). Scientifically verified analyses are available in particular for birds, individual insect groups and plants.

Compared to that in 1990, the average agricultural bird population in Europe has fallen to 68.5 % (Figure 1.3, Donald *et al.*, 2001, Leopoldina *et al.*, 2018). The lapwing (*Vanellus vanellus*), for example, has declined in Europe by 50 % since the 1980s (Souhay & Schaub, 2016). The field hamster (*Cricetus cricetus*), which used to be very common in Germany such that hunting it was allowed until 1990, is now highly threatened or locally extinct (La Haye *et al.*, 2014). Forty-one percent of the wild bee species, one of the most important pollinator groups in Germany, are endangered (Leopoldina *et al.*, 2018). A meta-analysis of the arable flora in Europe has shown that the average number of arable weed species living between crops such as cereals and vegetables has decreased by 20 % (Richner *et al.*, 2015). The examples mentioned are representative of many other species that usually disappear quietly and unnoticed.

The decline in biodiversity is also caused by side effects of land use change, such as the growing mechanisation of farming with increased use of machinery, ever larger field sizes, simplified and narrower crop rotations, the use of performance-enhancing and yield-securing inputs (e.g., fertilisers and pesticides) and the loss of landscape structures, leading to a reduction in landscape diversity (Stoate *et al.*, 2001). Ecologically valuable fallow land, field margins and fringe structures have fallen victim to the merging of fields. In particular, the conversion of species-rich grassland into agricultural land is considered to be harmful for nature conservation. The loss of semi-natural habitats has led to the impoverishment of typical agricultural biocenosis, leading to a disruption of food chains and a decline in many species adapted to the habitat and unable to escape, e.g., to protected areas (Krauss *et al.*, 2010).

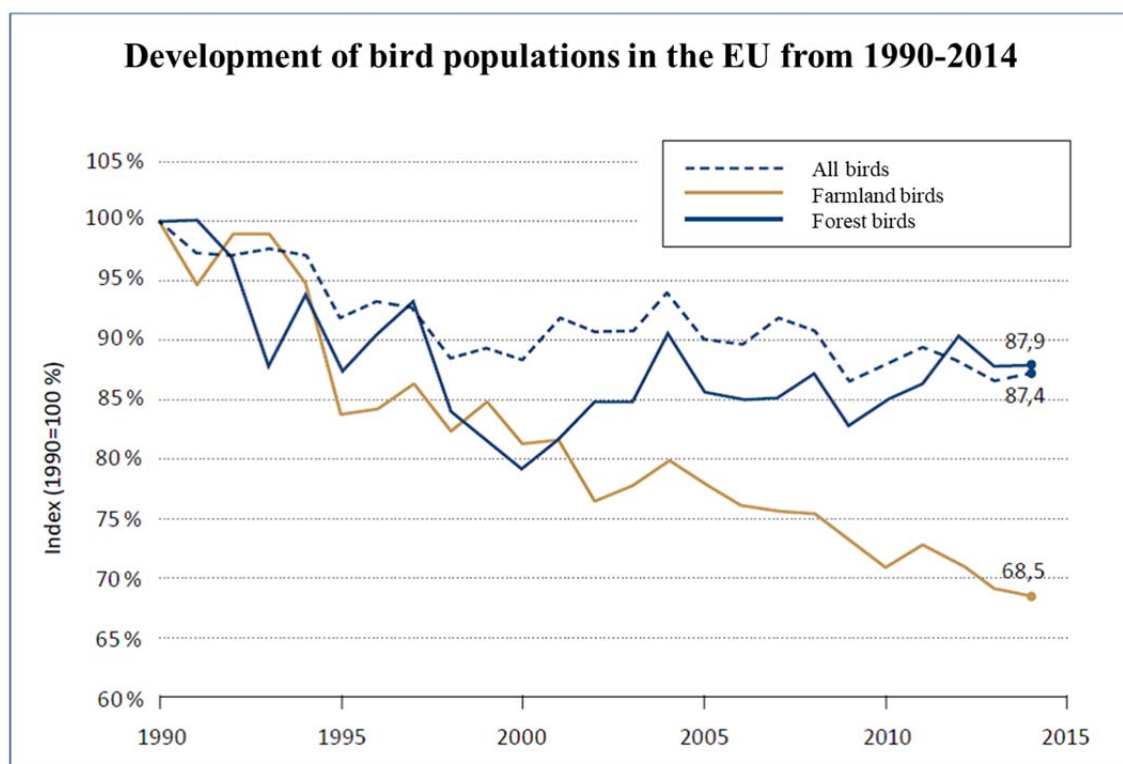


Figure 1.3: Changes in the abundance of 167 bird species in 26 European countries between 1990 and 2014, presented as an index. In addition, the index was calculated for 39 farmland bird species and 34 forest bird species (from Leopoldina *et al.*, 2018).

With the current EU Biodiversity Strategy (2010-2020)², the EU wants to stop this development and implement the globally agreed commitments to the conservation of biological diversity. The aim is to halt the loss of biodiversity and the degradation of ecosystem services and to restore them in so far as is feasible. Unfortunately, the current Environmental indicator report (European Environment Agency, 2018) shows no improvement but a deteriorating trend in this field. The indicators for small birds and grassland butterflies continue to show a declining trend in populations of these species. Furthermore, the status of 60 % of species and 77 % of habitats is classified as "unfavourable". The study concludes that all previous measures are not sufficient to protect biodiversity in the agricultural landscape or even to increase it again.

1.1.3 The European brown hare

The brown hare (*Lepus europaeus* PALLAS, 1778, Figure 1.4) is an excellent species by which to examine agricultural changes in a larger section of the landscape and across fields, as it has an average home range of more than 20 ha depending on the landscape type (Schai-Braun &

² http://ec.europa.eu/environment/nature/biodiversity/strategy/index_en.htm

Hackländer, 2014). The brown hare is common in Europe and Western Asia and has been introduced to a number of other countries around the world. In general, it is considered to be moderately common in its natural habitat, but since the 1960s, the Central European hare population has been declining due to the intensification of agriculture (Edwards *et al.*, 2000, Smith *et al.*, 2005, Zellweger-Fischer *et al.*, 2011).

The IUCN Red List of Threatened Species³ classifies the protection status of the European hare as of ‘least concern’ but with a decreasing population trend (Smith & Johnston, 2008). At low population densities, hares are susceptible to local extinction. The BfN Red List of threatened species Germany⁴ classifies the brown hare as ‘endangered’ nationwide - with a negative development trend.



Figure 1.4: The European brown hare (*Lepus europaeus*). Photo by Shirui Cheng on Unsplash.

It is undisputed that the current land use change is altering the food supply of the brown hare strongly (Reichlin *et al.*, 2006). The reasons are the increasing frequency of restricted crop rotations, the drastic decline in the cultivation of perennial crops such as alfalfa and clover, the decrease in weed abundance and the strong dominance of certain crop species (e.g., maize). From a nature conservation point of view, the increased ploughing up of grassland and the use of former fallow land for the cultivation of energy crops is particularly problematic, as these

³ <https://www.iucnredlist.org/>

⁴ <https://www.bfn.de/en/activities/red-list.html>

areas have a high proportion of herbaceous plants and grasses as a food source (Strauss *et al.*, 2008, Gevers *et al.*, 2011).

If there is a lack of suitable forage plants, hares eat plants with a high proportion of raw fibres (e.g., maize, rape), which have a lower energy value and do not meet the needs of lactating females and their offspring (Hackländer *et al.*, 2002). In structure-rich agricultural areas, significantly less rapeseed and wheat can be found in the stomachs of hares than in monotonous arable farming areas (Frylestam, 1986). The habitat function of arable crops is highly dependent on their relative location in the landscape compared to other biotope types (e.g., fringe structures, other field crops), their proportion in the landscape and on management activities. Lewandowski & Nowakowski (1993) were able to show a significantly positive correlation between the habitat selection of hares and the diversity of the selected habitat described by the Shannon index.

In addition to changes in food supply, the continuous increase in spatial barriers associated with larger field sizes and decreasing landscape structural diversity, as well as a possible predation pressure, could be main reasons for the decline in recent decades (Rühe *et al.*, 2001, Ruhe & Hohmann, 2004). However, the factors are weighted differently in the literature, since the population-ecological relationships and the influences of the individual factors in the complex agricultural ecosystem landscape are only insufficiently known (Smith *et al.*, 2005). Without this knowledge, targeted solutions and improvements in living conditions cannot be achieved. To understand the ecological significance of agricultural effects on hares and the causes of their widespread decline, habitat use in space and time must be examined more closely (Rühe & Hohmann, 2004, Strauss *et al.*, 2008). Modelling approaches are valuable tools for this, as they can visualise and quantify population developments under changing environmental conditions.

1.2 RESEARCH APPROACH UND METHODS

1.2.1 *Spatial Simulation Models*

Because landscape changes are multifactorial and take place at different spatial and temporal scales, the consequences are difficult to quantify. Models play an important role in land use science when investigating the complex interactions arising within the land use system. While field experiments are time-consuming and always illuminate a specific landscape section characterised by local conditions, generalised and transferable results can be achieved with the help of models. For example, by identifying general, archetypal patterns of land use change (Rounsevell *et al.*, 2012) that have similar land use intensities, environmental conditions and

socioeconomic factors. Even if field experiments are not possible or data are missing, models offer the possibility to investigate the system behaviour by means of artificial experiments, quasi as an artificial laboratory. Multifactorial systems and their interactions can be mapped and analysed, and suitable management recommendations can be tested and evaluated. In this way, impact assessments of policy measures (e.g., Davis *et al.*, 2011, van Delden *et al.*, 2011, Schulp *et al.*, 2016) or climate change (e.g., Abildtrup *et al.*, 2006, Schaldach *et al.*, 2012, Aurbacher *et al.*, 2013) as the main drivers of land use change can be carried out with models.

Models can be categorised in different ways: by subject area, by modelling techniques or methods used, or by the scope of application (Agarwal *et al.*, 2002). There are conceptual models, physical models, mathematical models or simulation models (O'Sullivan & Perry, 2013). For a simulation model, a computer is programmed to iteratively recalculate the modelled system state over time, according to the relationships describing the system.

Because land use obviously has a strong spatial component, I developed or used spatially explicit simulation models for this work. A spatially explicit model includes elements representing regions of geographical space and/or individual entities, for example animals or trees, located in space (O'Sullivan & Perry, 2013). Each region or entity has its own set of state variables interacting with each other. These interactions can be based on mathematical relationships but also empirically derived relationships or semi-quantitative “rules” (O'Sullivan & Perry, 2013). The basic idea is that the underlying mechanisms are similar to those that exist in the real world. A standard type of spatially explicit simulation models is Cellular Automata (CA), which are simple mathematical models to investigate self-organisation in statistical mechanics (Wolfram, 1983).

The representation of landscape in spatial simulation models depends on the research question to be investigated, but some basic differences can be distinguished: The model landscape is (1) realistic or artificially created, (2) contains discrete (object-based) or continuous (cell-based) units and is (3) static or dynamic. I have used both realistic and artificial landscapes and would therefore like to briefly describe both variants.

Realistic landscapes are often imported from Geographic Information Systems (GIS) and are used in order to address questions specific to a particular geographical area or to compare model results with empirical data from a particular region. There are numerous geographical models that can be used to simulate the development of spatial patterns of land use types, e.g., the CLUE model framework (Veldkamp & Fresco, 1996) and the SALU model (Stephenne & Lambin, 2001). A disadvantage of using realistic landscapes is that they usually represent snapshots that make it difficult to understand the influence of temporal processes such as farm management (Verburg *et al.*, 2011).

Artificial landscapes are used if landscape data of sufficient quality are not available or if general and transferable conclusions are to be made. They can be further distinguished between very simple and abstract landscapes and structurally realistic landscapes. The distribution of landscape features can be adopted from the distributions observed in real landscapes, so that the findings gained from the model are relevant, for example, for the analysis of ecological processes or policy measures.

Structurally realistic but simplified artificial representations of agricultural landscapes can be created with computer programs such as Agricultural Landscape Generators (ALGs). ALGs systematically and automatically generate variations of artificial agricultural land cover mosaics in the spatial resolution of individual fields for a given set of parameters. Both the landscape configuration (spatial distribution of land cover) and the landscape composition (type and proportion of land cover) are variable.

1.2.2 *Agent-based Models*

Since land use is characterised by the spatial and temporal interaction of biophysical factors, such as soil, climate, topography, etc., and human factors, such as cultivation, settlement, etc. (Veldkamp & Fresco, 1996), there are numerous model approaches that represent human-environment interactions, either using transition rules in system-based modelling approaches or using agents as the smallest decision unit (Turner *et al.*, 2007). The agents mostly represent humans (e.g., farmers) but can also represent individuals of animal species that interact with each other and with the environment (Grimm *et al.*, 2005).

In human decision models, a changed land use pattern arises as a result of human-environment interactions by connecting humans with pixels or patches. An advantage of agent-based models (ABMs, also referred to as individual-based models) is the integration of adaptation, learning and evolution (Matthews *et al.*, 2007). At the same time, complex systems can quickly become difficult to parameterise and validate and often lack a theoretical basis (Groeneveld *et al.*, 2017).

In agent-based models, agents interact directly with their environment, the landscape, whereby the way in which the model is implemented has a great influence on the behaviour and movement patterns of the actors (McLane *et al.*, 2011). Individuals react to changing environmental conditions, allowing the estimation of population dynamics as well as reliable predictions of how populations will respond to certain measures. The agents can move within their environment and be designed to adapt their state and behaviour in response to stimuli from other agents and their environment. A great strength of these models is that both individual habitat use and interactions within the population and with the environment can be represented.

Expert knowledge about the behaviour and movement patterns of animal species is combined with explicit and dynamic environmental factors (McLane *et al.*, 2011). Thus, the influence of environmental impacts, management and policy measures can be investigated with the help of land use scenarios in the complex system. The same applies to mitigation measures to reduce the consequences of harmful environmental impacts and agriculture.

For many years, ABMs have been used to investigate a wide range of questions related to the management of environmental resources, such as water, forest and agroecosystems (McLane *et al.*, 2011). Furthermore, ABMs in ecology have been used for more than 40 years to study species relationships and population dynamics and to understand how animals perceive, learn and adapt to their environment (DeAngelis & Grimm, 2014). The two simulation models I use for my studies are agent-based and simulate brown hares as individuals in the landscape, acting independently of each other.

1.3 OBJECTIVES OF THIS THESIS AND CHAPTER OVERVIEW

Agricultural landscapes are subject to constant change, which has a considerable influence on the adapted animal and plant species. The protection and promotion of agricultural biodiversity requires targeted and well-founded research.

For this purpose, computer simulation models are valuable tools to analyse complex ecological and socio-ecological systems and their responses to processes of change. However, the particular challenge is to reduce their complexity to the necessary minimum and to parameterise them optimally, even in difficult data situations. So far, the scientific community has taken two paths. One path has developed computationally intensive models with high spatial and temporal resolutions that are very complex and difficult to use, parameterise and understand. They are adapted to specific regions, ecosystems or species communities and therefore are difficult to transfer to other environmental systems or regions. The other path has resorted to more simplified simulation models that are important (and often indispensable) for understanding spatial system dynamics. Each path has its pros and cons, and it is often unclear which modelling path should be chosen for which problem.

I, therefore, compare one model of each pathway with regard to its application options using a sensitive indicator species of the European cultural landscape – the brown hare – as an example. Two different models, a complex existing spatial simulation system and a simpler spatial simulation model developed in this work, were used to investigate the influence of policy and conservation measures on the hare population dynamics and survival in agricultural landscapes.

Finally, the results were compared. In addition, I present methods and possibilities for broadening the application horizon of spatial simulation models.

In the first study (Chapter 2), an established complex simulation model, the Animal, Landscape and Man Simulation System (ALMaSS), was used to investigate the effects of Ecological Focus Areas (EFAs) on hares. The main objectives of the first study are:

- (1) To investigate the population responses to an increased proportion of several EFA types.
- (2) To estimate whether these enlarged EFA sites are sufficient for hares to achieve viable population densities.
- (3) To evaluate the qualitative differences of different EFA types regarding hare population dynamics.

The effects of the following EFA types on hare population dynamics were investigated: the cultivation of legumes such as (1) peas and (2) beans, (3) permanent and (4) rotational set-asides, (5) permanent extensive grasslands, and (6) herbaceous and (7) woody field margins. The cover of each type was increased separately up to 5 % in three Danish landscapes that are characterised by low hare densities. It turned out that all greening scenarios had significant positive effects on hare populations. However, only one EFA type, the permanent set-aside, led to viable densities in all three landscapes. The study shows that complex spatial simulation models are valuable tools for performing these evaluations.

ALGs that are able to automatically generate an agricultural landscape offer new possibilities for including land use mosaics in simulation models. To get an overview of the current state of research on this topic, I reviewed existing approaches in terms of their objectives, design and scope in the second study (Chapter 3). The main objectives of that study are:

- (1) To provide an overview of existing tools and methods to generate different configurations and compositions of agricultural landscapes.
- (2) To find the main features and criteria of generic software tools that could generate agricultural landscapes with more comprehensive and variable configuration and composition.

The approaches found are either based on generic mathematical algorithms (pattern-based) or on representations of ecological or land use processes (process-based). Most ALGs integrate only a few landscape metrics, which limits the design of the landscape pattern and thus the range of applications. The existing ALGs contain useful approaches that can be used for specific purposes, but ideally, generic modular ALGs are developed that can be used for a wide range of

scenarios, regions and model types. To point the way, the review study compiles the features of such generic ALGs and proposes a possible software architecture.

In the third study (Chapter 4), a simplified spatial simulation model was developed and used to investigate the impact of various mitigation measures on hare population development. The objectives of the third study are:

- (1) To investigate the effects of different mitigation measures in bioenergy-driven landscapes on long-term hare population development.
- (2) To test the significance and scope of the application of a simple habitat-based simulation model working with generated landscapes.

The spatially explicit simulation model was developed in NetLogo to study the effects of different landscape configurations and compositions. As an input, two 4 x 4 km large model landscapes were used, which were generated by an ALG based on real field sizes and crop proportions. In six mitigation scenarios, the effects of a 10 % increase of the following measures were investigated: (1) mixed silphie, (2) miscanthus, (3) grass-clover ley, (4) alfalfa, (5) set-aside and (6) general crop diversity. The results show that both landscape configuration and composition have a significant effect on the hare population development, whereby it responds particularly strongly to compositional changes. The increase of crop diversity, e.g., through the cultivation of alternative energy crops such as mixed silphie and grass-clover ley, proves to be highly beneficial for the brown hare. The study demonstrates that using a simplified simulation model in combination with generated agricultural landscapes makes it possible to show and quantify trends in hare population development under changed habitat conditions.

This work enriches the knowledge base in the dynamic field of ecological modelling with an overview of the possibilities and potential of spatial simulation models and gives a perspective for future developments. Furthermore, the model-based assessments for the brown hare presented here provide new findings on population development under changed habitat conditions and help to develop sustainable management strategies and policy options.

2 A MODELLING APPROACH TO EVALUATING THE EFFECTIVENESS OF ECOLOGICAL FOCUS AREAS: THE CASE OF THE EUROPEAN BROWN HARE

This chapter is based on the publication Langhammer *et al.* (2017):

Langhammer, M., Grimm, V., Pütz, S. and Topping, C. J. (2017): A modelling approach to evaluating the effectiveness of Ecological Focus Areas: The case of the European brown hare. *Land Use Policy* 61: 63-79.

2.1 ABSTRACT

With the current implementation of the Common Agricultural Policy (CAP) for 2014-2020, the European Commission wants to move towards “greener” farming practices in the European Union. Therefore, the EU funds both obligatory measures, such as Ecological Focus Areas (EFAs) through the Green Direct Payment program, and voluntary agri-environment measures. However, empirically evaluating the effectiveness of these measures is challenging. We therefore demonstrate here that mechanistic simulation models are a valuable tool for performing these evaluations. As an example, we use the Animal, Landscape and Man Simulation System (ALMaSS), an established simulation system that has been used to simulate a wide range of farmland species relevant to biodiversity. We analysed the benefits of seven greening scenarios for the European brown hare (*Lepus europaeus*), which has been in widespread decline throughout Europe since the 1960s. We examined the effects of the following EFA types on hare population dynamics: the cultivation of legumes such as (1) peas and (2) beans, (3) permanent and (4) rotational set-asides, (5) permanent extensive grasslands, and (6) herbaceous and (7) woody field margins. The cover of each type was increased separately up to 5% of the area in three Danish landscapes, which are characterised by low hare densities. The effects on female and yearling abundance were observed over a period of 30 years. All greening scenarios had significant positive effects on hare populations. The relative change in female abundance ranged from a factor of 0.4 in the peas scenario to 3.6 in the permanent set-aside scenario. However, only one EFA type, permanent set-asides, led to densities of more than 10 females per km² in all three landscapes, which we assumed to be the threshold for population viability. Herbaceous field margins were the second best EFA type, leading to population viability in two landscapes. Our results indicate that overall, 5% coverage with Ecological Focus Area is insufficient to improve the living conditions of the brown hare to a necessary degree. Permanent set-asides seem to be the most valuable type of EFA, but this needs to be confirmed for a wider range of species and landscapes. Using mechanistic simulation models for a suite of representative species, types of agricultural landscapes, and eco-regions could help in achieving the aim of the European Commission to promote biodiversity in the European community via greener farming practices.

2.2 INTRODUCTION

The intensification of agriculture in recent decades is accelerating the loss of habitats and putting many species commonly found in agricultural areas at risk. With the current reform of the Common Agricultural Policy (CAP) for 2014-2020, the European Commission wants to

achieve, inter alia, a change towards a more environmentally friendly, sustainable and “greener” agricultural policy in the European Union. Therefore, a new policy instrument, the Green Direct Payment program (European Commission, 2013), was introduced from 2015 onwards, which links direct payments to farmers to requirements for obligatory environment-friendly farming practices, the so-called “greening” of farming (European Commission Regulation (EU) No 1307/2013). “Greening” practices include (1) crop diversification, (2) the maintaining of permanent grassland and (3) Ecological Focus Areas (EFAs). EFAs are areas of ecological interest or measures considered to have environmental benefits. From 2015 on, agricultural holdings with more than 15 ha must establish 5% of their land as an EFA (European Commission Regulation (EU) No 1307/2013). In addition to these obligatory measures, the CAP promotes various voluntary agri-environment measures (Council Regulation (EC) No 1698/2005, European Commission, 2005).

However, critical voices have been raised recently, accusing the new CAP prescriptions of being so diluted that they are unlikely to benefit biodiversity (Pe'er *et al.*, 2014). Thus, it is critical to evaluate actual CAP measures from a biodiversity conservation perspective. Empirical evaluations are challenging, if not infeasible, as they would require large scale and long term monitoring of abundance and distribution for a wide range of species, landscapes, and eco-regions and for the implementation of different EFA types. We therefore demonstrate here that well-tested mechanistic simulation systems are suitable for assessing the effectiveness of EFAs.

In particular, agent-based models (ABM) are ideally suited to this task as they simulate how the structure and dynamics of complex systems emerge from first principles such as adaptive behaviour and energy budgets (Grimm *et al.*, 2005, Grimm & Berger, 2016). They combine physiological and behavioural processes at the individual level with demographic processes at the population level (Railsback & Grimm, 2012). Comprehensive agent-based simulation models can take landscape features, including farming practices into account, and can represent the social-ecological processes necessary to understand management and policy implications relevant to agricultural systems (Malawska *et al.*, 2014, Malawska & Topping, 2016). Importantly, they can represent existing expert knowledge and are rich enough in their structure and mechanisms to be evaluated and validated simultaneously at different levels of organisation and different scales (Grimm *et al.*, 2005, Augusiak *et al.*, 2014).

As a promising and well-established example of a simulation system, we used the spatially explicit agent-based Animal, Landscape and Man Simulation System (ALMaSS) (Topping *et al.*, 2003). ALMaSS represents real landscapes and farming practices in great detail and at a high spatial and temporal resolution, and has been used to predict population dynamics and the

consequences of different landscape structures and pesticide applications for a wide range of species. ALMaSS has been in use and under development since 1998 and includes a hare model (Topping *et al.*, 2010). The hare model is well tested (Topping *et al.*, 2010) and fully documented using an extended version of the ODD protocol for describing agent-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010), which combines software for documenting program code with the rationale of ODD (ALMaSS Model Documentation, 2014). The resulting ODDox documentation is a hypertext which is openly available on the internet⁵. A range of population control parameters was evaluated using “pattern-oriented modelling” (Wiegand *et al.*, 2004, Grimm *et al.*, 2005). Model testing followed “the modelling cycle” (Railsback & Grimm, 2012), which is an iterative process whereby models are tested against carefully selected performance criteria (Topping *et al.*, 2010, Augusiak *et al.*, 2014). Moreover, the generation of the Danish landscapes and implementation into ALMaSS is described in detail in Topping *et al.* (2016). Therefore, as the model has already been documented and tested comprehensively, we here will use it as a given “virtual laboratory” and restrict tests and model analyses to the features we added in the definition of the agricultural landscapes.

To demonstrate the potential of ALMaSS and similar modelling systems in general for evaluating CAP measures, we used the case of the European brown hare (*Lepus europaeus* PALLAS, 1778). The brown hare has been in widespread decline throughout Europe since the 1960s (Flux & Angermann, 1990, Homolka & Zima, 1999, Edwards *et al.*, 2000, Smith *et al.*, 2005, Smith & Johnston, 2008). Although present across a wide geographic range, the brown hare is listed under Appendix III of the Bern Convention in Europe, and several countries have placed the species on their Red List as “near threatened” or “threatened” (Reichlin *et al.*, 2006). Located in the European cultural landscape, the hare is a typical example of many other open farmland species in Europe (e.g., European hamster, Eurasian skylark and Grey partridge) that are affected by agricultural intensification and its side effects (Donald *et al.*, 2001, Stoate *et al.*, 2001). Having an average home range of more than 20 ha depending on the landscape type (Schai-Braun & Hackländer, 2014), the brown hare is an excellent species to examine agricultural changes in a larger section of landscape and across fields.

Numerous studies show that monocausal explanations of hare population dynamics are not possible (Marboutin *et al.*, 2003, Schmidt *et al.*, 2004, Smith *et al.*, 2005). Thus, assessments and evaluations of hare population trends are difficult to perform due to the interactions that occur between multiple stressors and the spatial and temporal variability in field data (Smith *et al.*, 2005, Topping *et al.*, 2010). Furthermore there is still a lack of long-term and large-scale population data, despite extensive observation efforts in recent decades (Strauss *et al.*, 2008). To understand the ecological significance of agricultural effects on hare populations, habitat use

⁵ http://www2.dmu.dk/ALMaSS/ODDox/ALMaSS_ODDox/V1_02/index.html

must be examined precisely in space and time (Rühe & Hohmann, 2004, Smith *et al.*, 2004, Strauss *et al.*, 2008). In the present study, we use ALMaSS for this task.

In this study, we assessed the benefits of several EFA types for the brown hare. Specifically, we addressed the following research questions: (1) How do hare populations respond to an increased proportion of several EFA types in the landscape? (2) Are these enlarged EFA sites sufficient for hares to achieve viable population densities? (3) Are there qualitative differences between the effects of different EFA types regarding hare population dynamics? As the population density of hares fluctuates enormously at a local scale and depends on many external factors, previously published reports provide only very few reliable numbers. Homolka & Zima (1999) estimated that typical densities of stable hare populations in Europe range from 20 to 70 individuals per km². Based on this estimation we set our long-term viability criterion for this study at 10 females per km².

To answer our research questions, EFAs that are assumed to be relevant to the brown hare were selected according to the EU Regulation No 1307/2013 (Article 45, 46) and Delegated Regulation (EU) No 639/2014 (Article 45). We implemented seven greening scenarios in which the cover of the following EFA types was increased to 5% of the whole agricultural area: cultivation of nitrogen-fixing crops such as (1) peas and (2) beans, (3) permanent and (4) rotational set-asides, (5) permanent extensive grasslands, and (6) herbaceous and (7) woody field margins. We expected all greening scenarios to lead to higher hare abundances but also expected noticeable differences between their effects. For example, one might assume that areas such as set-asides or grasslands would be more beneficial as they provide larger contiguous habitats for hares than do narrow field margins. Likewise, permanent measures, such as long-term set-asides, might be more effective than temporary measures, such as rotational set-asides, as they provide year round food sources and cover. However, quantitatively verifying and accurately predicting these effects without a detailed mechanistic model seem to be impossible.

2.3 METHODS

2.3.1 *Landscape simulation system*

ALMaSS was developed as a predictive analytics tool to answer policy questions regarding the effect of land use change on different key animal species (Topping *et al.*, 2003). Therefore, the model combines agent-based animal models with a detailed and dynamic landscape simulation, which is explicit in space and time and based on a detailed land use map. Integrated weather information, farm management practices and vegetation growth simulations directly influence

the structure and dynamics of the simulated landscape. Every vegetation unit is based on its own growth model, and the specific management of agricultural land is simulated in detail, thus facilitating a wide range of different scenarios (Topping *et al.*, 2003). The landscape model creates the environmental conditions for the hare model in ALMaSS. References to a full model description and comprehensive tests of the hare model in ALMaSS are provided in the introduction.

The landscape simulation model is grid-based and represents detailed landscape structures at a resolution of 1 m² (Topping *et al.*, 2003). Every grid cell has a reference number to a polygon, which is classified into one of 64 polygon types featuring specific attributes and behaviours. The polygon types are differentiated into non-vegetated areas, such as roads or streams, and vegetated areas, such as arable fields or field boundaries. The vegetation growth curves and farm management simulations for each polygon depend directly on weather data, which include daily records for mean temperature, mean wind speed, total daily precipitation and geographically determined daylight times. Vegetation growth for each crop model contains three curves to predict total leaf-area index (LAI), live (green) LAI and vegetation height (Topping & Olesen, 2005, Topping *et al.*, 2016). Vegetation cover is calculated using Beer's law, and biomass is calculated from the cover, LAI values, insolation, and crop management practices.

A general overview of the processes by which ALMaSS incorporates farm management information is provided by Topping *et al.* (2016), Appendix 2. All farms are managed by the *FarmManager*, which defines farm units, farm types and individual crop husbandry plans for all arable fields. Field polygons in the real world are simulated as farm units in the model. Each farm type (e.g., conventional arable farm) includes a specific crop rotation scheme, which determines the replacement of crops in a field on an area basis. The crop rotation scheme consists of 100 crop entries with multiple entries of each crop type in accordance with typical agricultural farming practices (Table 2.1). At the start of the simulation, a random crop in the rotation is taken as the starting point for each arable field and the next crop in the list is assumed to be grown in the same field in the following year. After four years, all fields of one farm type would have raised each of the 100 crops in the rotation list once. If a specific crop, e.g., spring barley, occurs 37 times out of 100 in the rotation (Table 2.1) it will on average occur on 37% of all fields covered by that rotation at any point in time. Unique crop husbandry plans for each crop are created from a set of farm events, such as harvesting, that directly influence the model animals in each field each day. Examples of the implementation can be found in the ALMaSS ODDox (ALMaSS Model Documentation, 2014).

Table 2.1: The crop rotation scheme of a conventional arable farm. Eight crop types with different numbers of entries are included in the rotation list. Spring barley, for example, occurs 37 times out of 100, representing 37 % of the farm's crop type.

| Crop type in ALMaSS | Number of entries |
|---------------------------|-------------------|
| <i>SpringBarley</i> | 37 |
| <i>WinterWheat</i> | 35 |
| <i>WinterRape</i> | 11 |
| <i>WinterBarley</i> | 7 |
| <i>WinterRye</i> | 4 |
| <i>Oats</i> | 3 |
| <i>CloverGrassGrazedI</i> | 2 |
| <i>SeedGrassI</i> | 1 |
| Sum | 100 |

The landscape simulation in ALMaSS is based on weather and farm management data from Denmark. We assume that the climatic conditions and the agricultural management practices in Denmark are similar to those in Northwestern Europe, and therefore the results of the model should be relevant for other countries of the same agro-climatic zone too. We selected three landscape maps from different regions in Denmark (Mors, Naestved and Odder, each 10 km x 10 km) as a basis for the greening scenarios (Figure 2.1, Appendix: Figure A1-A2). The detailed generation of these landscapes is described in Topping *et al.* (2016). The landscapes represent agricultural areas with a range of landscape configurations that display different amounts of landscape structures and land cover types (Table 2.2, Appendix: Table A1-A3).

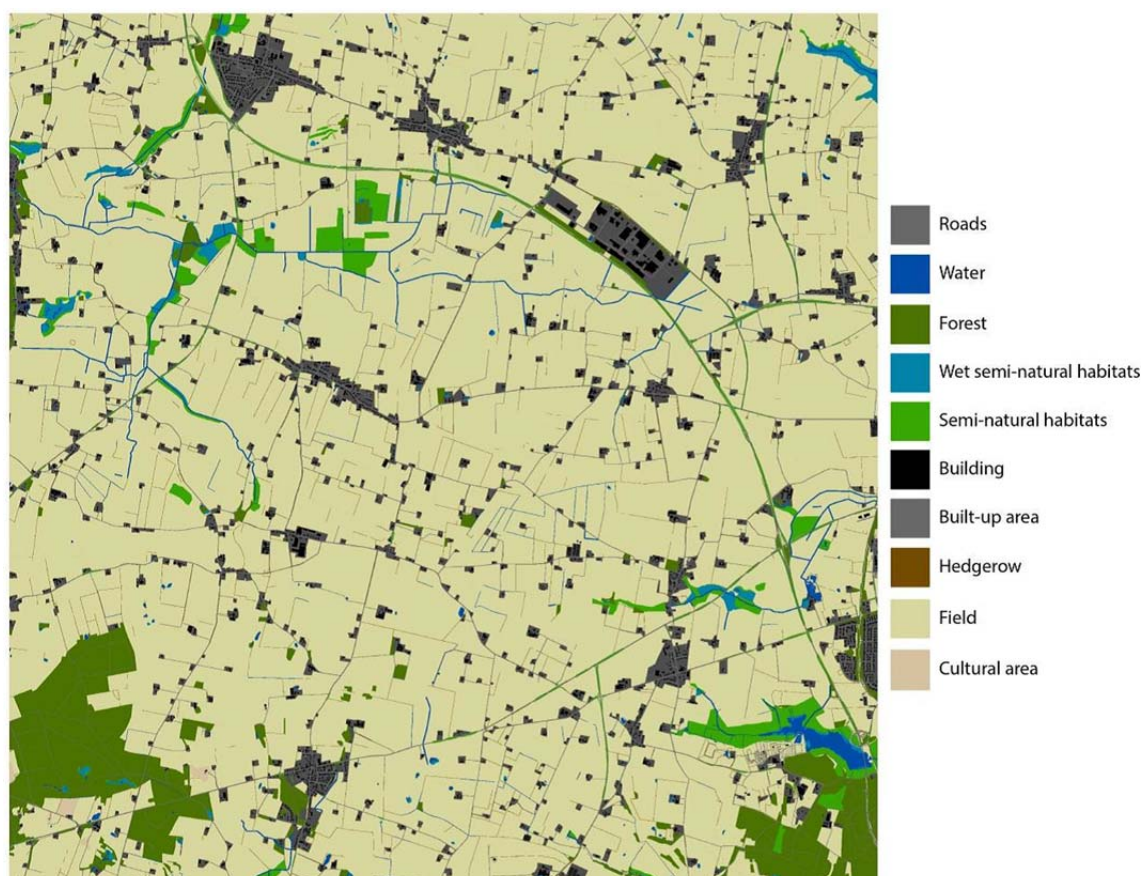


Figure 2.1: Visual overview of Mors, 10 x 10 km, mapping the basic elements of the landscape visible at this scale.

Table 2.2: Percent cover of basic landscape elements in the three model landscapes.

| Landscape element | Mors | Naestved | Odder |
|-------------------|------|----------|-------|
| Field | 75.2 | 77.6 | 67.6 |
| Forest | 5.0 | 5.4 | 12.2 |
| Wasteland | 2.0 | 2.2 | 2.4 |
| Road | 1.1 | 0.9 | 1.0 |
| Building | 1.4 | 0.9 | 0.7 |

Table 2.3: The most common farm types in the three model landscapes by area.

| Mors | | Naestved | | Odder | |
|--------------|--------|-------------------|--------|--------------|--------|
| Type | % area | Type | % area | Type | % area |
| Conv. pig | 56 | Conv. arable | 61 | Conv. pig | 42 |
| Conv. cattle | 18 | Conv. mixed stock | 16 | Conv. cattle | 14 |
| Conv. arable | 18 | Conv. pig | 8 | Conv. arable | 36 |
| Conv. hobby | 5 | Conv. cattle | 7 | Conv. hobby | 4 |

Conv. = Conventional

The landscapes in Mors and Naestved are characterised by large areas of fields and a low proportion of grasslands and forests, even though Mors consists of smaller fields and landscape structures. Odder exhibits greater forest and grassland areas and less field area. Regarding farm types, Mors is dominated by conventional pig farms, Naestved by conventional arable farms and Odder has a mix of both (Table 2.3). Pig farms are classified as farms with more than 20 animal units, of which pigs comprise 75% or more, or where the proportion of land used for grazing pigs is above 15%. Arable farms are characterised by large areas with few or no animals and little or no grazing (Topping *et al.*, 2016).

2.3.2 *Hare model*

ALMaSS integrates a detailed agent-based model of the European brown hare, which is a behaviour-based model built upon a state/transition principle (Topping *et al.*, 2003). This means a hare is in a specific state where it exhibits specific behaviour; a transition to another state, and thus behaviour, takes place when predetermined conditions are fulfilled, e.g., according to certain probabilities and internal or external events (Figure 2.2). The model was based on available literature data and multiple patterns observed in Denmark (Topping *et al.*, 2010). All individuals belong to one of five specific life-stages: males, females, juveniles (36-265 days), mobile young (12-35 days) and infants (1-11 days), each showing an associated range of potential behavioural patterns.

A simulated population manager tracks every animal object and runs the particular behaviour, e.g., foraging, in 1-minute time-steps. As a result, the hares respond quickly to changes in environmental conditions and landscape configurations. They are able to extract food resources over a wide area when not occupied with nurturing offspring. The key behaviours are movement (dispersal/foraging), growth, lactation and starvation, all of which are described in the ALMaSS Hare ODDox (ALMaSS Model Documentation, 2014). Energy is the primary driving variable, and if a hare exceeds a fixed number of consecutive days at a negative energy balance, it dies. Forage quality is based on a combination of vegetation type, vegetation age and vegetation structure. Farming activities actively influence the model animals via changes in habitat structure and direct disturbances. Hunting takes place in autumn, and other external influences are related to life-stage specific probabilities (e.g., predation) or management activities.

For the simulations, the starting number of the hares was set at 10 individuals per km². After 50 years all landscapes showed baseline densities of less than 10 females per km², which is characteristic for species-poor regions, as e.g., intensively used agricultural landscapes.

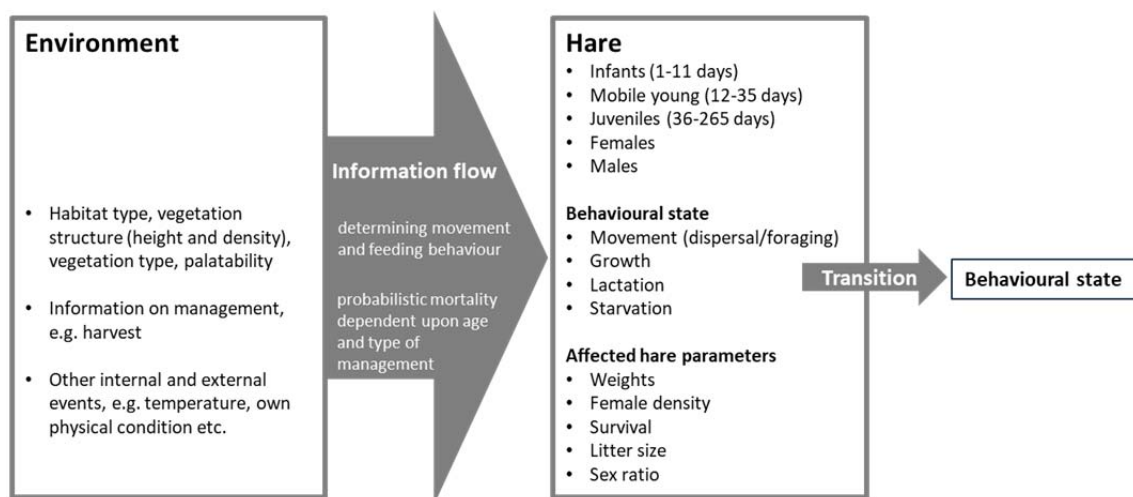


Figure 2.2: Effect of environmental conditions on hare simulation settings. Hares are categorised into five life stages that showing specific behavioural states.

2.3.3 Greening scenarios

We developed seven greening scenarios to analyse the influence of different EFA types, which may be enhanced by the current EU CAP reform, on the European brown hare. We selected measures that can be assumed to have direct effects on habitat and survival of the hares: the cultivation of legumes, such as peas and beans, permanent and rotational set-asides, permanent extensive grasslands, and herbaceous and woody field margins. Permanent grasslands cannot directly be classified as an EFA, but maintaining permanent grasslands is one of the three greening options. For each scenario, the area of the one EFA type being considered was increased at the start of the simulation to approximately 5% of the whole agricultural area of the landscape (Table 2.4). We decided to implement EFAs on landscape level, because farms that are legally obliged to fulfil the EFA requirement cover more than 94% of the agricultural area in each model landscape. The EFAs were randomly distributed in the model landscape (Figure 2.3).

Three of the scenarios directly influence the crop composition of the farm management model: the planting of peas and beans and establishing rotational set-asides. Therefore, we conducted new crop rotations for each farm type, replacing winter wheat with peas or beans or converting it to a rotational set-aside (Appendix: Table A4-A6). The replacement decisions were made with regard to agricultural restrictions on crop rotations. For example, beans stay in the field over winter, and therefore, they must precede a crop in the rotation that does not have any autumn activities, e.g., spring barley.

All other scenarios affect the landscape configuration. Permanent set-aside sites and extensive grasslands are fixed landscape polygons outside the field area. We increased their amount up to 5% by reducing field area (Appendix: Table A7). In a second set of simulations we increased the percentage of these two EFA types in one landscape (Mors) to 7%, 10% and 15%, to obtain an idea of the sensitivity of the hare population development beyond the 5% scenario.

Field margins are fixed edge structures that are also outside the field area. For these scenarios, we used landscape maps where all edge structures were widened to approximately 5 metres. These extensions use an additional polygon type in ALMaSS, named “chameleon”, which can be changed from one habitat type to another at run-time. Thus the same map can be used for comparing different field margin management practices, applying elements of theoretical landscape models (Pe'er *et al.*, 2013). We calculated the correct percentages of these structures for the field margin scenarios and assigned the remaining amount to one farm (Appendix: Table A8).

Table 2.4: Percentages of EFA types in the three model landscapes. The baseline is the original unchanged landscape, where almost all of the measures are already included to some degree. The scenario percentages show small deviations from 5 % because the implementation could not be precisely achieved in the model in some cases. Where model code terms are, for historical reasons, different from scenario terms used here, these are specified.

| Scenario Type | Scenario | | Mors | Naestved | Odder |
|----------------|--|----------|------|----------|-------|
| Rotation | Peas | Baseline | 0.05 | 0.05 | 0.10 |
| | | Scenario | 4.85 | 4.80 | 4.75 |
| | Beans (<i>BroadBeans</i>) | Baseline | 0.00 | 0.00 | 0.00 |
| | | Scenario | 4.85 | 4.80 | 4.75 |
| | Rotational set-asides (<i>Setaside</i>) | Baseline | 0.00 | 0.00 | 0.00 |
| | | Scenario | 4.85 | 4.80 | 4.75 |
| Field | Permanent set-asides (<i>PermanentSetaside</i>) | Baseline | 0.27 | 0.38 | 0.57 |
| | | Scenario | 5.01 | 5.00 | 5.00 |
| | Permanent grasslands (<i>PermPastureTussocky</i>) | Baseline | 0.13 | 0.00 | 0.03 |
| | | Scenario | 5.00 | 4.99 | 5.00 |
| Edge structure | Herbaceous field margins (<i>FieldBoundary</i>) | Baseline | 0.54 | 0.49 | 0.43 |
| | | Scenario | 5.00 | 5.00 | 5.02 |
| | Woody field margins (<i>Hedges</i>) | Baseline | 0.69 | 0.60 | 0.32 |
| | | Scenario | 5.01 | 5.00 | 5.06 |

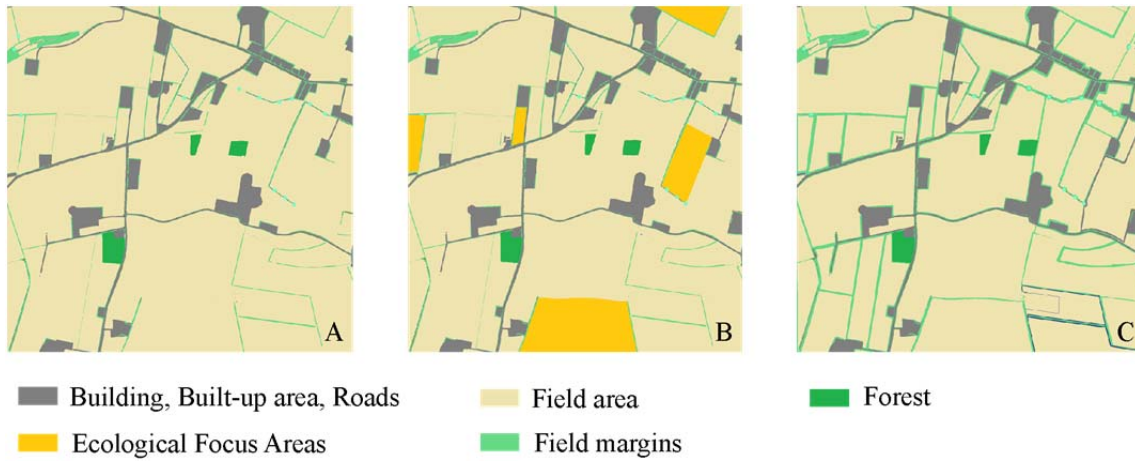


Figure 2.3: Exemplary presentation of the scenario changes in Mors. The landscape section (1 x 1 km) shows the baseline conditions (A), the distribution of field related EFA types (B) and the widened field margins (C).

2.3.4 Data analysis

Ten replicates of each scenario were run in each of the three model landscapes. Initial conditions for each replicate differed in the initial distribution of hares across the landscape and the initial allocation of crops in the fields. The total number of simulations was 240. To obtain results that did not depend on the randomly chosen initial distribution of individuals and crops, 50 years were simulated before data were recorded. Then, output data were recorded for each year from a simulation of the subsequent 30 years.

To display population responses in detail, we recorded and analysed three different outputs: female abundance, yearling abundance and AOR (Abundance-Occupancy Relationship)-index. Regarding female abundance, the number of females at day 270 of each year in the landscape was counted. We focused on females because males do not limit the population size. Yearling abundance was calculated by counting the average number of infants, young and juveniles alive at day 270 of each year. Boxplots display the effects of the scenarios on female abundance for each landscape, including the yearly output data for ten replicates.

The AOR-index is an indicator that facilitates the interpretation of agent-based model outputs by simultaneously quantifying the relative changes in abundance and occupancy in response to a scenario (Hoye *et al.*, 2012). Occupancy is quantified based on the proportion of grid cells with at least one individual, and abundance based on the mean number of individuals in the occupied cells (Hoye *et al.*, 2012).

Wilcoxon rank sum tests were used to test the significance of the differences between the values at baseline and for the scenarios for each landscape. We used a number of replicates (10) that corresponds to the replicate numbers used in many empirical studies. Therefore, we did not

artificially increase the significance levels by increasing the number of simulations. Moreover, mean female abundance showed only little change with an increasing number of replicates (Appendix: Figure A3). All statistical evaluations were performed with R 3.2.2 (R Development Core Team, 2015).

2.4 RESULTS

Baseline hare densities varied between 1.1 and 4.1 female hares per km² (Table 2.5). Odder showed the highest female abundance, whereas the females in Mors nearly went extinct (Figure 2.4). The number of yearlings ranged between 2.6 and 10.5 individuals per km² (Table 2.5, Figure 2.4). Direct comparisons with field counts under comparable conditions are not possible, but the numbers match current observations of Danish hare populations (Miljøministeriet and Naturstyrelsen, 2013). The literature does not provide estimates of overall hare population sizes for Denmark as densities vary between different regions depending on land use, topography and the presence of predators.

Table 2.5: Baseline hare densities predicted for each landscape.

| Landscape | Mors | Naestved | Odder |
|---------------------------------|------|----------|-------|
| Total females/km ² | 1.06 | 2.09 | 4.11 |
| Total yearlings/km ² | 2.58 | 5.35 | 10.45 |

All greening scenarios had significant positive effects ($P < 0.01$) on the hare populations (Table 2.6, Figure 2.5, Appendix: A9-A10). The effect on female and yearling abundances was not significantly different for each scenario type. Regarding legumes, beans had a significantly greater effect on hare population densities than did peas ($P < 0.001$). Likewise, permanent set-aside sites resulted in greater effects than rotational set-asides ($P < 0.001$). Overall, permanent set-aside sites and herbaceous field margins produced the largest population responses of all scenarios, i.e., female abundance increased by factors of 3.6 and 3.5, respectively. In contrast, extensive grasslands had a minor effect ($P < 0.001$). Woody field margins had a far smaller effect than that of herbaceous field margins (factor of 1.7 and 3.5, respectively; $P < 0.001$).

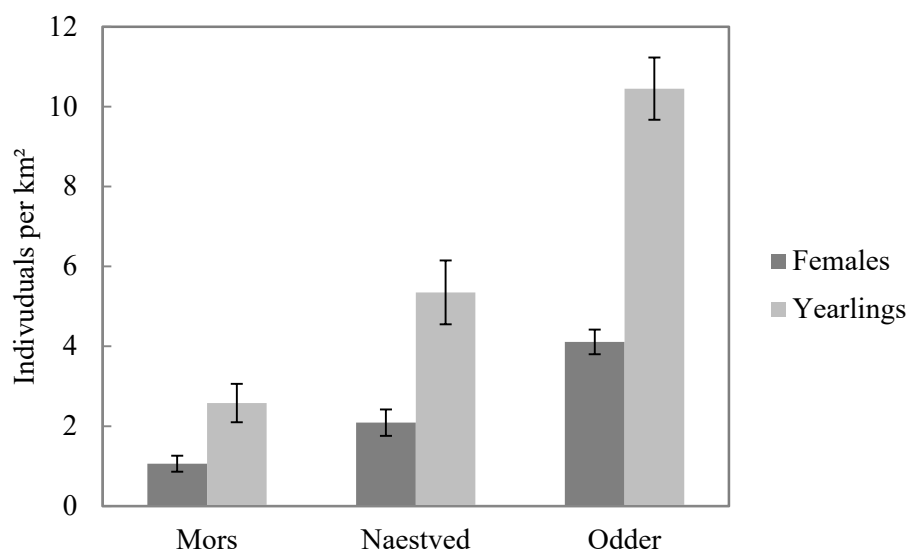


Figure 2.4: Female abundance and number of yearlings in the three model landscapes under the baseline scenario, observed on day 270 in each of 30 simulated years. The bars indicate the 95 % confidence interval calculated for the ten replicates.

Table 2.6: Factors by which female and yearling abundances increased relative to the baseline scenarios. Factors are averaged across the three landscapes considered.

| Scenario | | Females per km ² | Abs. change | Rel. change | Yearlings per km ² | Abs. change | Rel. change |
|------------------|------------|--------------------------------|----------------|----------------|----------------------------------|----------------|----------------|
| Baseline | | 2.4 | | | 6.1 | | |
| Legumes | Peas | 3.3 | 0.9 | 0.4 | 8.3 | 2.2 | 0.4 |
| | Beans | 7.6 | 5.2 | 2.2 | 19.2 | 13.1 | 2.1 |
| Set-asides | Rotational | 7.9 | 5.5 | 2.3 | 20.7 | 14.6 | 2.4 |
| | Permanent | 11.0 | 8.6 | 3.6 | 30.2 | 24.1 | 4.0 |
| Grasslands | Extensive | 9.4 | 7.0 | 2.9 | 25.4 | 19.3 | 3.2 |
| Field margins | Herbaceous | 10.8 | 8.4 | 3.5 | 25.2 | 19.1 | 3.1 |
| | Woody | 6.4 | 4.0 | 1.7 | 14.7 | 8.6 | 1.4 |

The average increase in female abundance relative to the baseline was greatest in Naestved (ø 6 females) and lowest in Mors (ø 5 females) (Appendix: Table A9-A10). Only one EFA type, permanent set-asides, achieved an increase in female density that exceeded 10 females per km² in all three landscapes (ø 11 females, Figure 2.6). Extensive grasslands and herbaceous field margins reached or exceeded this threshold in Naestved (10 and 11 females, respectively) and Odder (10 and 13 females, respectively). Using 5% herbaceous field margins in Odder achieved the highest female density of all scenarios.

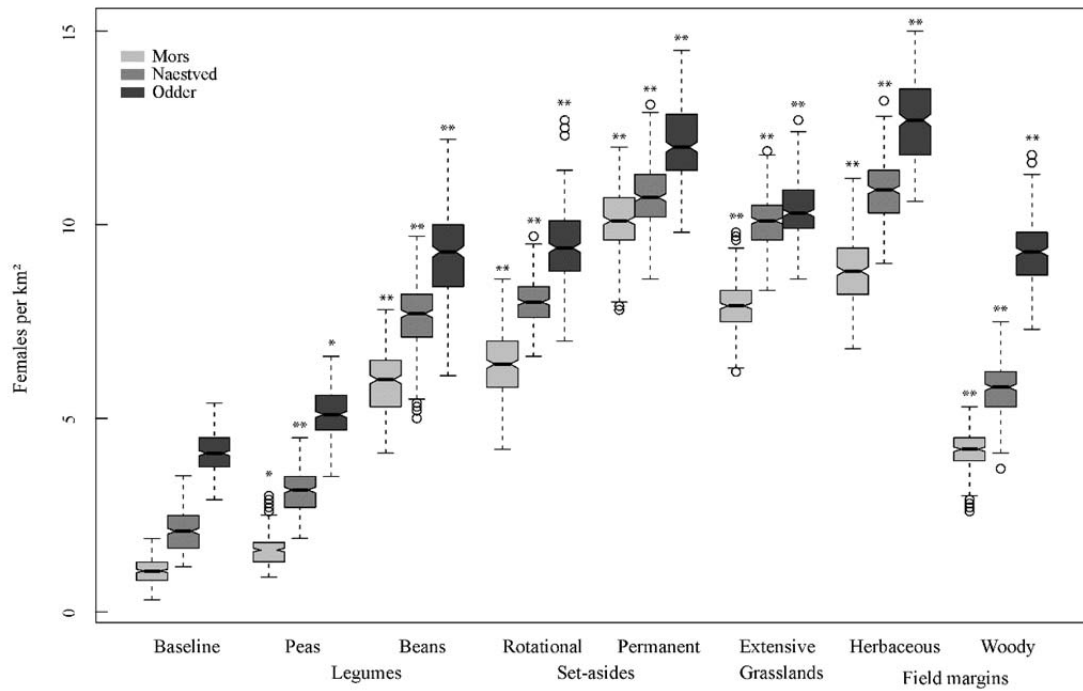


Figure 2.5: Effect of the evaluated scenarios on female abundance in each landscape. Stars specify the level of significance, i.e., $*P \leq 0.01$, $**P \leq 0.001$, for each scenario relative to the baseline.

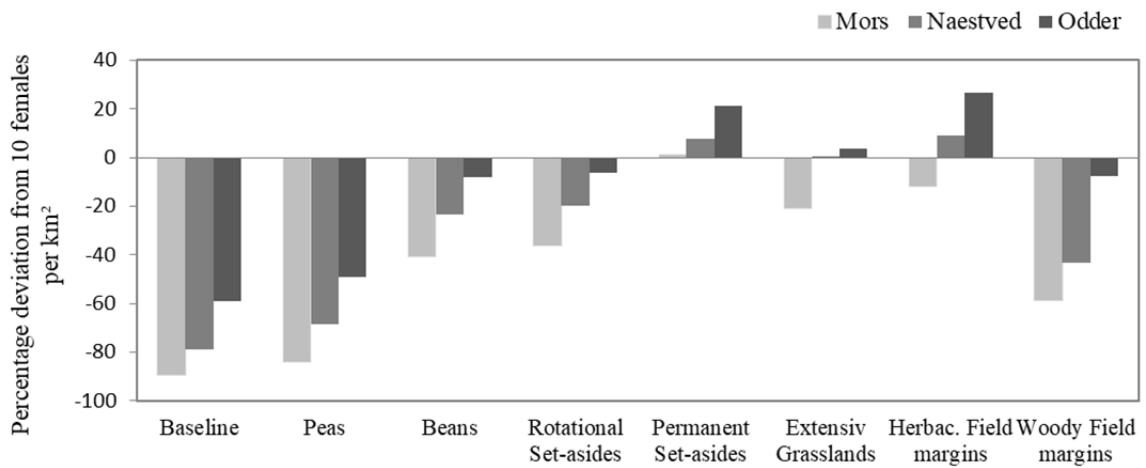


Figure 2.6: Percentage deviation from the long-term viability criterion of 10 females per km².

The AOR plots show that all scenarios affected the hare population in similar ways but to varying degrees (Figure 2.8). They are all located in the first quadrant, which means population size, habitat quality and the proportion of favourable habitat was improved. Increases in abundance but not in occupancy indicate that the quality of the habitat is clearly different

between the scenarios. Again, the biggest effect was observed with permanent set-asides and the lowest with peas. A comparison of the landscapes shows that the effects of EFA types, especially permanent set-asides, are increased in Mors and reduced in Odder.

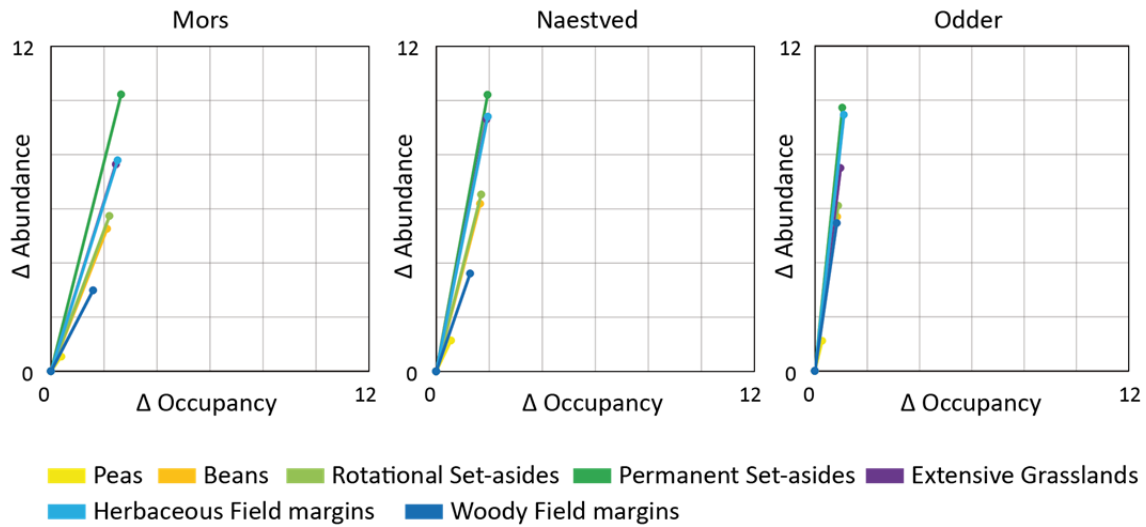


Figure 2.7: The AOR (abundance-occupancy relationship)-index plotted for the evaluated scenarios in all three landscapes relative to the baseline.

The exemplary percentage increase of the EFA types permanent set-asides and extensive grasslands in Mors leads to an approximation of the female abundance (Figure 2.8, Appendix: A11). While the effect of these two measures raises with increasing percentage, it seems to asymptotically approach a female density of 15 hares per km².

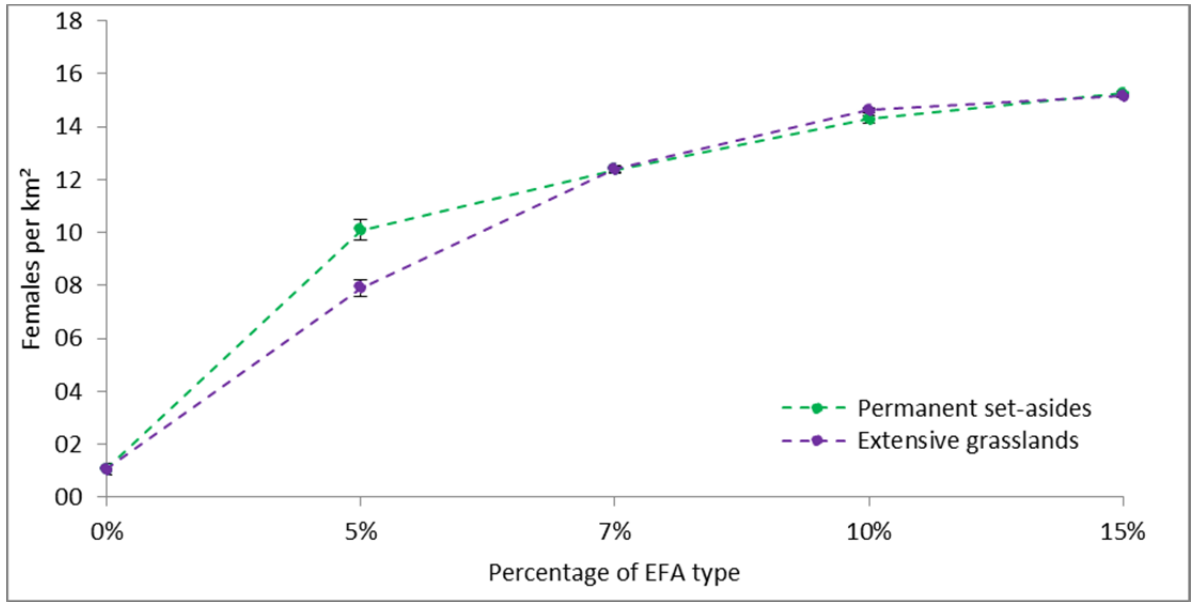


Figure 2.8: Effect of a percentage increase of two EFA types on female abundance in Mors. The bars indicate the 95 % confidence interval calculated for the ten replicates.

2.5 DISCUSSION

Current global environmental issues require the development of new approaches in environmental research. This study shows that it is possible to evaluate policy measures with simulation models. For the first time, the effects of mitigation measures on hares were analysed solely using a computer model. ALMaSS is rich enough in structure to map environmental effects in detail and to reproduce interactions between landscapes, management practices, weather data and the traits of individuals. Thus, it opens up endless possibilities for addressing environmental questions.

The greatest strength of ALMaSS is its ability to depict landscape structures at a resolution of 1 m² and the details of farm management practices in 1-day steps, while considering behavioural changes at an even finer resolution. Previous studies have shown how sensitive hares are in reacting to farming and landscape changes (Topping, 2011, Topping *et al.*, 2016). Landscape structure has a proven impact on habitat quality and thus on the living conditions of species (Dauber *et al.*, 2003); however, landscape composition is a greater determinant than landscape configuration (Bennett *et al.*, 2006). The Danish model landscapes used in this study vary in their proportion and distribution of landscape elements and edge structures, field sizes, spatial diversity and degree of fragmentation.

However, the Danish landscapes were used here as a demonstration only. Other landscapes are easy to incorporate into ALMaSS, and a diverse pool of European landscapes is necessary to

allow for a wider assessment of these issues in the EU. A set of tested models for a range of key animal species are already present, which cover invertebrates, birds and mammals (e.g. Bilde & Topping, 2004, Topping *et al.*, 2010, Topping *et al.*, 2012).

Previously published research shows that quantitative estimates of the effects of mitigation measures on population development are rare and usually relate to plants, birds or insects (Kleijn *et al.*, 2001, Vickery *et al.*, 2004, Kleijn *et al.*, 2006, Concepcion *et al.*, 2008). While there are currently no reliable evaluations of the CAP reform's greening measures, studies on the overall effects of agri-environment schemes (AESs) can be found as this instrument was established in most European countries in the early 1990s. These studies describe some examples of limited positive effects of AESs on biodiversity (Kleijn *et al.*, 2006, Whittingham, 2007, Concepcion *et al.*, 2008). Regarding the brown hare, there are only a few studies analysing the effects of specific agri-environmental measures on population trends in several European countries (Genghini & Capizzi, 2005, Zellweger-Fischer *et al.*, 2011, Petrovan *et al.*, 2013, Meichtry-Stier *et al.*, 2014). Our results show that all of the analysed EFA types had moderate, positive effects on the development of hare populations. However, only one EFA type, permanent set-asides, led to a viable hare density of 11 females per km², averaged for the three landscapes. Herbaceous field margins and extensive grasslands barely reached this point in two landscapes. Based on this, our results indicate that the 5% limit for Ecological Focus Areas is insufficient to improve the living conditions of the European hare to a necessary degree.

How consistent are the observed effects of EFAs on hare populations with what we know about hare behaviour? Checking for such consistency is important, even for the most realistic and well-tested models. We should never blindly trust model outputs and should make sure we understand why and how these outputs emerged (Augusiak *et al.*, 2014).

It is undisputed that the land use changes of the last decades have changed the food supply of hares enormously. The main causes are restricted crop rotations, the drastic decline in the cultivation of perennial crops such as lucerne and clover, the lack of catch crops, the strong dominance of a small number of crops (e.g., maize), and the intensification of crop husbandry and the use of agrochemicals (herbicides) (Smith *et al.*, 2005, Pépin & Angibault, 2007, Zellweger-Fischer *et al.*, 2011). Our results show that a small increase in crop diversification via the cultivation of legumes, such as peas and beans, which are forage plants for hares, positively influences hare population development. Beans have a much higher effect because the crop is sown late, provides resources over the winter, is easy for hares to access and is usually ploughed in the spring. Therefore, it is a good food source for wildlife in the summer and especially in the winter.

Set-asides are often considered to be biodiversity hotspots and important retreat areas for many species (e.g. Van Buskirk & Willi, 2004). Although they were an established CAP agri-political instrument, the European Commission abolished the set-aside requirement in 2008, removing most of the set-asides from EU landscapes. As a consequence, the living conditions of many species common to agricultural areas worsened, especially if no compensating areas were provided and if the land was used for the cultivation of monocultures such as energy crops (Gevers *et al.*, 2011). Our results show that a 5% increase in permanent set-asides strongly favours hare population development. Hares prefer set-aside sites over field area with arable crops throughout most of the year (Smith *et al.*, 2004) because this habitat meets several important requirements. First, it is a foraging habitat with a high proportion of herbaceous plants and grasses. Second, the height of the vegetation provides protection for young hares against predators. In ALMaSS, permanent set-asides are assumed to be patchy; therefore, forage is accessible. Thus, the improvement in forage and protection for successful breeding resulted in permanent set-asides having the strongest positive influence of all the analysed EFA types. In contrast, although similarly positive in its effects, the resources provided by rotational set-asides are only present during part of the year, and there is the potential for increased mortality of the young during ploughing; hence, the benefits of this type of EFA were lower.

Permanent, extensive grasslands had a slightly lower effect on hare population development than was observed for permanent set-asides. Previous research shows that hare densities are often low in grassland sites and decrease with stocking density (Barnes *et al.*, 1983, Smith *et al.*, 2005, Zellweger-Fischer *et al.*, 2011). Grazing pressure is included in ALMaSS and can generate a 25% reduction in forage availability as it shifts from low to high levels. Thus, hares will leave permanent grasslands if their energy balance is low. Combined with the lower vegetation height caused by grazing, the suitability in the model of grasslands for foraging is limited at high grazing densities. However, some grazing is beneficial in that it prevents grass from becoming too tall and dense both in ALMaSS model and in the real world (Karmiris & Nastis, 2007).

Herbaceous field margins showed a similar strong influence on female abundance to that of the permanent set-asides. Hares select field margins during active and inactive periods of the day and more frequently remain closer to field boundaries than within large fields (Petrovan *et al.*, 2013). These landscape structures offer both species-rich vegetation, including essential forage plants, such as wild herbs and grasses (higher food value in the model), and protected resting sites for young hares. In contrast, woody field margins, such as hedges or tree lines had a significantly lower impact on hare abundances, which was caused by the higher amount of inedible woody plants (lower food value in the model) and their unsuitability as breeding areas.

In line with the results of other studies, our results show that the EFA types that are most favourable for hare population development are those that enable year-round forage and protection at the farm level (Tapper & Barnes, 1986, Smith *et al.*, 2004, Macdonald *et al.*, 2007, Pépin & Angibault, 2007). Nevertheless, 5% Ecological Focus Area coverage is probably not enough to improve the living conditions of the brown hare to ensure long-term population viability. To support this conclusion, the general validity of the results must be verified with further studies.

The AOR plots display comparable population responses for each scenario. However, permanent grasslands in Mors had a remarkably higher impact compared to those of the other EFA types. This suggests that the benefit of this measure is higher in intensively farmed landscapes. In contrast, the effects of permanent grasslands and herbaceous field margins in Odder were nearly equal. Nevertheless, one should be aware of the context dependency in relation to landscape and farming, which limits the generalisation of these results (Topping, 2011, Topping *et al.*, 2016).

The ecological quality and quantity of greening measures, as well as an appropriate management plan, is critical for their environmental outcomes. In the case of hares, those EFA types that promote landscape heterogeneity at the farm-level scale and provide year-round shelter and food sources are the most suitable, especially in intensively managed landscapes. As these features are also important for other open farmland species, the particular importance of permanent set-asides should be reconsidered and valued through the reintroduction of a set-aside requirement.

One limitation of our study is that we increased each EFA type to approximately 5% to make the single measures comparable. In practice, these 5% areas consist of various measures, which do not need to be explicitly hare-friendly. Thus, the scenarios used in our simulations would not normally be implemented in reality; however, they provide important insights into the impacts of EFA measures.

Another limitation is that the model is based on Danish landscapes and Danish farm management practices. The agriculture of each country depends on national policy provisions and regional characteristics. In this case, Danish agriculture is characterised by a high proportion of small farms (< 50 ha), often with small fields, a high proportion of animal husbandry (especially pigs) and intensive fertilization. To increase the validity of the results, we have examined landscapes (Mors, Naestved and Odder), which differ in farm types and field sizes. Regarding farm types, Mors is dominated by pig farms (56%), Naestved by arable farms with crop production (61%) and Odder has a mix of both (42% pig farms, 36% arable farms). Thus, we have tested both landscapes that are featured with a high amount of livestock

production and landscapes that are featured with a high amount of crop production. We are aware that the transferability of the specific results of our study may be limited due to Danish farming conditions, but we predict that the trends demonstrated will be similar in other EU countries with similar agricultural systems. Further studies will be needed to reveal regional variations across the EU regarding the implementation and impact of greening measures.

If it turns out that 5% of EFA is not enough to attain a sustainable benefit for a large spectrum of open farmland species, the question arises of which obligatory percentage is enough. Our results show that an increase of permanent set-asides and extensive grasslands from 5% to 7% enhances the female abundance by 22% and 57%. At 15% it is 51% and 92%, respectively. From about 10% on, the measures do not seem to favour hare population development very much more, indicating that other factors controlling population density, such as predation or intra-specific competition, limit the carrying capacity of the landscapes. Other studies suggest an increase of areas covered by high-quality AES options and semi-natural habitats to at least 14% (Meichtry-Stier *et al.*, 2014), or even just 10% (Oppermann *et al.*, 2012) may be required to sustainably protect agricultural biodiversity.

The EU regulations say that EFAs only have to be implemented on farms with more than 15 ha and that certain landscape features can be credited. Hence, greening measures only have to be applied to approximately 50% of EU farmlands and many farms are excluded from this implementation (Pe'er *et al.*, 2014). Our results indicate that these restrictions might severely limit the effectiveness of greening measures. Simulation systems such as ALMaSS could be used to quantitatively assess these restrictions.

2.6 CONCLUSIONS

We demonstrated that EFAs and other elements of the CAP reform can be quantitatively assessed with well-tested, mechanistic simulation models. Our results indicate that overall, 5% coverage with Ecological Focus Area is insufficient to improve the living conditions of the brown hare to a necessary degree. In order to allow general statements about the effectiveness of EFAs, investigations for other open farmland species are needed. If it turns out that EFAs fail to attain a sustainable benefit for a large spectrum of open farmland species, the European Commission should consider increasing the obligatory percentage of EFAs in the course of the EU evaluation of the CAP reform in 2017. To substantiate this assumption with facts, we recommend a scientifically thorough evaluation of the greening regulations regarding their environmental benefit. Kleijn & Sutherland (2003) suggest that periodic ecological evaluations be mandatory for any agri-environmental scheme in the future. As in pesticide risk assessments,

where a range of test species is used to assess potential adverse effects at different scales and for different taxa, an assessment scheme based on tools such as ALMaSS could cover a range of species, eco-regions, and farmland practices, as well as projected changes in climate and land use. This would not only allow for the assessment of specific measures but also for the optimization of measures in a given region.

2.7 ACKNOWLEDGEMENTS

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3 AGRICULTURAL LANDSCAPE GENERATORS FOR SIMULATION MODELS: A REVIEW OF EXISTING SOLUTIONS AND AN OUTLINE OF FUTURE DIRECTIONS

This chapter is based on the publication Langhammer *et al.* (2019):

Langhammer, M., Thober, J., Lange, M., Frank, K., Grimm, V. (2019): Agricultural landscape generators for simulation models: a review of existing solutions and an outline of future directions. *Ecological Modelling* 393: 135-151.

3.8 ABSTRACT

There is an increasing need for an assessment of the impacts of land use and cover change (LUCC). In this context, simulation models are valuable tools for investigating the impacts of stakeholder actions or policy decisions. Agricultural landscape generators (ALGs), which systematically and automatically generate realistic but simplified representations of land cover in agricultural landscapes, can provide the input for LUCC models. We reviewed existing ALGs in terms of their objectives, design and scope. We found eight ALGs that met our definition. They were based either on generic mathematical algorithms (pattern-based) or on representations of ecological or land use processes (process-based). Most ALGs integrate only a few landscape metrics, which limits the design of the landscape pattern and thus the range of applications. For example, only a few specific farming systems have been implemented. We conclude that existing ALGs contain useful approaches that can be used for specific purposes, but ideally generic modular ALGs are developed that can be used for a wide range of scenarios, regions and model types. We have compiled features of such generic ALGs and propose a possible software architecture. Considerable joint efforts are required to develop such generic ALGs, but the benefits in terms of a better understanding and development of more efficient agricultural policies would be high.

3.9 INTRODUCTION

In response to climate change, a growing human population, and globalisation, land use and land cover are changing at unprecedented rates. Understanding and predicting these changes and their consequences for biodiversity and ecosystem services are among the grand challenges of ecological and environmental research. For intensively used agricultural landscapes, for example, in Europe, key questions include how spatio-temporal patterns in land cover are affected by national and EU policies or by the global market and how, in turn, they are affecting ecosystem services and biodiversity. Empirical approaches to meeting these challenges are limited because of the scale dependency and the multitude of factors involved. Simulation models on land use and land cover change (LUCC) are therefore widely and increasingly developed to back- and forecast landscape changes (Lambin *et al.*, 2000, Agarwal *et al.*, 2002, Parker *et al.*, 2003, Heistermann *et al.*, 2006). Such simulation models, if they are sufficiently realistic, allow us to generate scenarios and to rigorously explore, by using mathematics and computer logics, the consequences of stakeholder actions or political decisions (e.g., Johst *et al.*, 2015).

However, when using spatially explicit simulation models for this purpose, there is a dilemma when it comes to representing land cover in agricultural landscapes. On the one hand, such land cover maps can be taken from maps from geographical information systems (GIS). While such input implies high realism and significance for regional case studies (e.g., Wätzold *et al.*, 2016), general insights and transferability to other regions or questions are limited. A single map does not allow us to systematically vary the features of a landscape. Even if we contrast different real landscapes, we only obtain snapshots of possible relationships, which are likely to be nonlinear. Moreover, the creation of such detailed maps is time-consuming, as it often requires manual data processing, parameterisation and calibration.

On the other hand, an unlimited number of virtual landscapes can be generated using algorithms that systematically and automatically vary landscape metrics such as percentage cover, fragmentation, or spatial autocorrelation (Gardner *et al.*, 1987, Gardner, 1999, Saura & Martínez-Millán, 2000, Hiebeler, 2007, Cambui *et al.*, 2014). Using these virtual landscapes as input, models can provide insights into the consequences of changing landscape features and help to formulate, test and validate hypotheses (Gardner & Urban, 2007). However, such landscapes are usually difficult to relate to real landscapes such that it remains unclear what we have learned about the real world.

The alternative to these abstract landscapes is landscape generators, which generate virtual, but structurally realistic, maps of land cover by trying to combine both realism and the option to vary landscape features. The generators create variations of artificial agricultural land cover mosaics at the spatial resolution of individual fields for a given set of parameters. To be classified as a “generator”, we here require that they allow for varying features of the generated landscapes in a systematic and automated way.

Changes in agricultural landscapes and their ecological consequences occur at small scales (Houet *et al.*, 2010), e.g., the variation of the field mosaic and the implementation of crop rotations or policy measures at the farm level. There is thus a need for high-resolution spatial simulation models and corresponding tools that are capable of generating artificial land cover maps at high resolution under a predefined parameter set. Still, limited research has been done in the field and few such landscape generators have been developed so far. These generators define agricultural landscapes as a mosaic of land use patches (fields) and landscape elements (e.g., hedges). Landscape features that are typically varied are composition (type and proportion of land cover) and landscape configuration (spatial arrangement of the land covers). The distributions of these features can be taken from distributions observed in real landscapes, such that insights gained from the model are relevant for, e.g., analysing ecological processes or

exploring the consequences of EU policy instruments such as the “greening” of farming (e.g., Langhammer *et al.*, 2017) or agri-environment schemes (e.g., Sturm *et al.*, 2018).

So far, no common term has been established for this type of landscape generator. Therefore, we here suggest referring to them as “agricultural landscape generators” (ALGs) and use it in the following as a generic term. ALGs are computer programs that generate structurally realistic but simplified artificial representations of agricultural landscapes, i.e. maps of land cover. Both the landscape configuration (field mosaic) and the landscape composition (land cover) are variable. We nevertheless refer to them as generators to emphasise that they are not used for simulations by themselves and do not display temporal and spatial dynamics. The output of ALGs is a map that can be used as input for LUCC models or other model types. ALGs can still represent change over time by producing a series of consecutive maps. ALGs are either implemented as stand-alone programs or as sub models within LUCC models.

The approaches to generating landscapes can be distinguished into two main categories: pattern-based and process-based. Pattern-based generators, also known as neutral landscape models, are based on generic algorithms and produce virtual landscapes regardless of the underlying ecological or social processes (Gardner *et al.*, 1987, With & King, 1997). They work with one or more characteristics of composition and configuration of a landscape. Regarding complexity, they range from pure neutral models to more-realistic models in terms of landscape structure (Johnson *et al.*, 1999, Gaucherel *et al.*, 2014). The resulting landscapes are mostly pixel matrices, with each pixel representing a spatial unit assigned to a certain land cover class. So far, neutral landscape models have been used primarily in the research field of forest and landscape ecology, but rarely for agricultural landscapes. The coupling of neutral landscapes with population models allows species’ perceptions of landscape configuration, e.g., habitat fragmentation and landscape connectivity, to be addressed (With, 1997).

Process-based generators, also known as mechanistic models, produce landscape patterns as a result of ecological or socio-economic processes that are explicitly integrated into the model (Jackson *et al.*, 2000, Cuddington *et al.*, 2013). The result of these generators is also a static map to be used as input for dynamic simulation models. “Process-based” in this context means that the mechanisms leading to a certain landscape pattern can be explicitly addressed. An example is *Dinamica* (Filho *et al.*, 2002). Such generators are based on a theoretical understanding or hypotheses of the relevant processes that cause landscape patterns, and they are helpful in determining how real agricultural landscapes and their dynamics emerge. The resulting landscapes allow more explicitly stated hypotheses and can be used as the basis for addressing specific questions, e.g., pattern-process interaction (Schröder & Seppelt, 2006), land

use change prediction, the fate of specific species or of biodiversity in general, and effects on ecosystem functioning and resilience.

In this review, we examine existing ALGs that are able to automatically generate an agricultural landscape with given features. Our two main motivations are as follows: (1) There is an increasing need to evaluate the driving forces behind and the extent and consequences of land use and land cover change. Recent EU policies, for example, aim at increasing biodiversity by requiring environmentally friendly farming practices; the so-called “greening” of farming (European Commission Regulation (EU) No 1307/2013). Whether or not such policies will in fact increase biodiversity is an open question (Pe'er et al., 2014). The usefulness of such policies requires two things: a realistic simulation model and realistic landscape, where both different eco-regions and policies can be represented. In the case of honeybees, the model BEEHAVE (Becher et al., 2014) is such a model, and so far only the software tool NePoFarm (Horn, 2017) exists, that takes the structure of a given landscape, important from GIS, implements different crop diversity and rotation scenarios, and then explores how different greening measures, such as flower strips, affect the resilience and persistence of honeybee colonies. With a kind of generic ALG, one could also vary the structure of the landscape, for example regions with mostly small or large fields, or landscapes with and without semi-natural habitat or hedges. The same landscapes could then also be used for exploring the performance of bumblebees (Becher et al., 2018), wild bees (Everaars et al., 2018), or completely different taxa, where other landscape features might be important. (2) Our second interest is in finding the main features and criteria of generic software tools that could generate agricultural landscapes with more comprehensive and variable configuration and composition by using a modular design. The landscapes generated by such generic ALG could be used as input for any specific LUCC model addressing specific questions. This would generate coherence and synergies across individual studies that currently do not exist.

3.10 METHODS

Because there is no consistent term for agricultural landscape generators so far, in our literature search, we used the following search terms: “ecological model*” AND crop* AND landscape*, “landscape model*” AND crop*, “landscape model*” AND neutral, “landscape generat*” AND crop*, “landscape generat*” AND neutral, “landscape simulat*” AND crop*, and finally, “landscape simulat*” AND neutral. Using these terms in Web of Science (Clarivate Analytics) led to 186 publications that cover a broad range of approaches, aspects of agricultural landscape simulations, and fields of application.

The most important selection criterion for including an ALG approach in our review was the user-defined automatic generation of agricultural land cover patterns, which can serve as an input for dynamic simulation models. We excluded landscape generators that do not encompass any characteristics of agricultural landscapes or did not include the land use type agriculture. We also did not include geographical information system (GIS) models, remote sensing land use and land cover change (LUCC) models and agent-based land use models (ABMs) (Lambin *et al.*, 2000, Agarwal *et al.*, 2002, Schulze *et al.*, 2017), although they too allow landscape maps to be altered. Firstly, these models usually work with real landscapes and data, and secondly, landscape changes in composition and configuration are mostly based on the outcome of decision models and not on automated procedures, which were mandatory according to our definition of a landscape generator.

We examined the following features of the ALGs: the specific aims, the method of landscape generation in terms of configuration and composition, the validation, the application regarding policy measures, and the software availability. Regarding landscape composition, we analysed which method for crop generation and allocation of crops to the fields has been applied. The more complex an ALG is, the more compositional details can be varied, such as crop types, fringe structures, and other land use types. We explored which of them have been implemented so far in the context of specific case studies. We also compiled a brief overview of existing additional software tools that allow crop rotation to be implemented for a given landscape configuration.

Moreover, because it is important for allowing the exploration of ecological questions in agricultural landscapes, we examined whether natural and semi-natural habitats were included. The same applies to the coupling with ecological population models to allow the analysis of landscape effects on species. Because enormous potential of agricultural landscape simulations lies in the evaluation of management and policy measures, we investigated whether and how such scenario analyses were carried out. Finally, programming language, software application, documentation, and availability of the models were determined.

Based on these findings, we finally derived and outlined the requirements for generic ALGs. In particular, we wanted to identify which landscape features are essential or optional for user-friendly agricultural landscape generation and which conclusions can be drawn for the model and software architecture.

3.11 RESULTS

3.11.1 Existing ALGs

The list of publications containing solutions for generating such agricultural landscapes was short (Figure 3.1). We identified ten relevant peer-reviewed articles published between 2006 and 2017. These ten publications relate to a total of seven ALG approaches, as several landscape generators were described or applied in more than one publication. We added four more relevant publications describing one of the selected ALG approaches more precisely. To display even more possibilities, we added the non-ISI-listed Scottish Natural Heritage Commissioned Report No. 692 (Begg & Dye, 2015) describing another ALG approach. Altogether, we found eight ALG approaches.

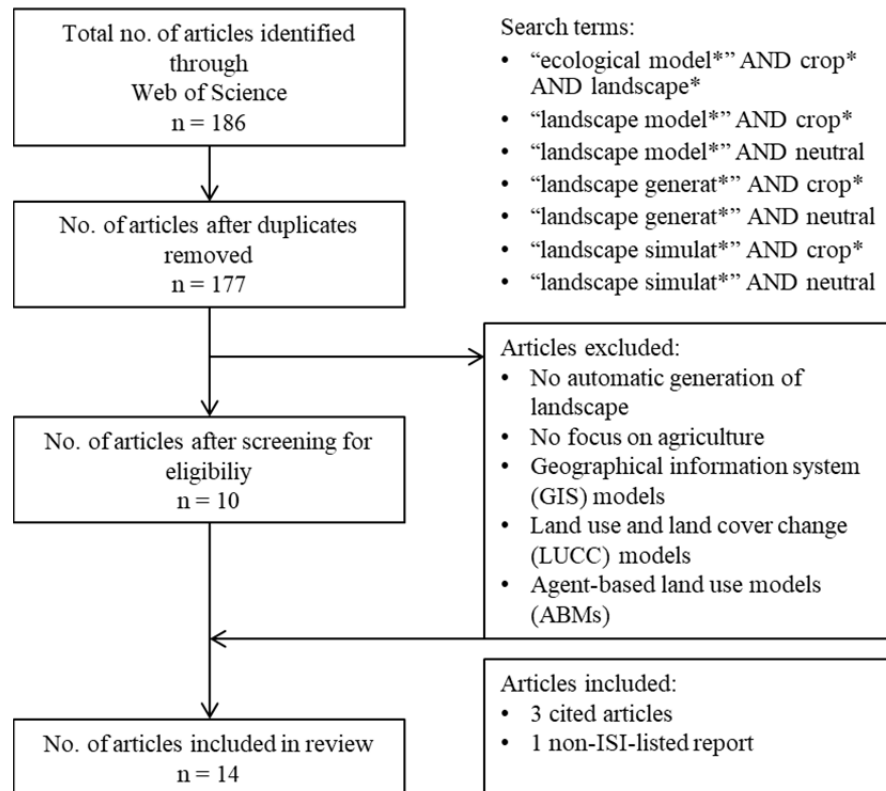


Figure 3.1: Flowchart of literature search and selection process.

An overview of the reviewed ALG approaches is given in Table 3.1 and Figure 3.2. The approaches differ widely in their method of landscape generation and agricultural details; therefore it was difficult to give an integrated and structured overview and to derive general concepts. To emphasise and better compare the range of existing approaches for each feature,

we present our results feature by feature, not model by model. Nevertheless, Table 3.2 provides an overview of the reviewed ALGs. The ALGs presented here have mainly been published within the last 10 years (Appendix: Table B1). This makes it a young field of research with few approaches so far, and most of them are described and/or applied in a small number of publications only. For each ALG we show one example output map to get an impression of the application possibilities, even if there may be many more output options available.

Table 3.1: General information on existing agricultural landscape generators (ALGs), i.e., models or programs that have the option to automatically and systematically generate virtual agricultural landscapes with given features in terms of configuration and composition.

| Publication | Name | Nr. of publications* | Time span | Language | Validation |
|---------------------------------|---------------------------------|----------------------|-----------|----------|------------|
| Begg & Dye (2015) | AgBioscape | 1 | 2015 | C# | n.i. |
| Engel <i>et al.</i> (2012) | Landscape generator | 2 | 2012-2014 | C++ | n.i. |
| Gaucherel <i>et al.</i> (2006) | DYPAL | 8 | 2006-2017 | C++ | yes |
| Inkoom <i>et al.</i> (2017) | SG4GISCAME | 2 | 2017 | n.i. | yes |
| Le Ber <i>et al.</i> (2009) | GENEXP-LANDSiTES | 4 | 2008-2013 | Java | yes |
| Papaix <i>et al.</i> (2014) | <i>Ddal</i> Landscape simulator | 1 | 2014 | n.i. | n.i. |
| Pe'er <i>et al.</i> (2013) | <i>G-RaFFe</i> | 3 | 2011-2018 | n.i. | yes |
| van Strien <i>et al.</i> (2016) | Landscape Generator (LG) | 4 | 2011-2016 | Java | yes |

* Listed in Table 4.

n.i. No information available.

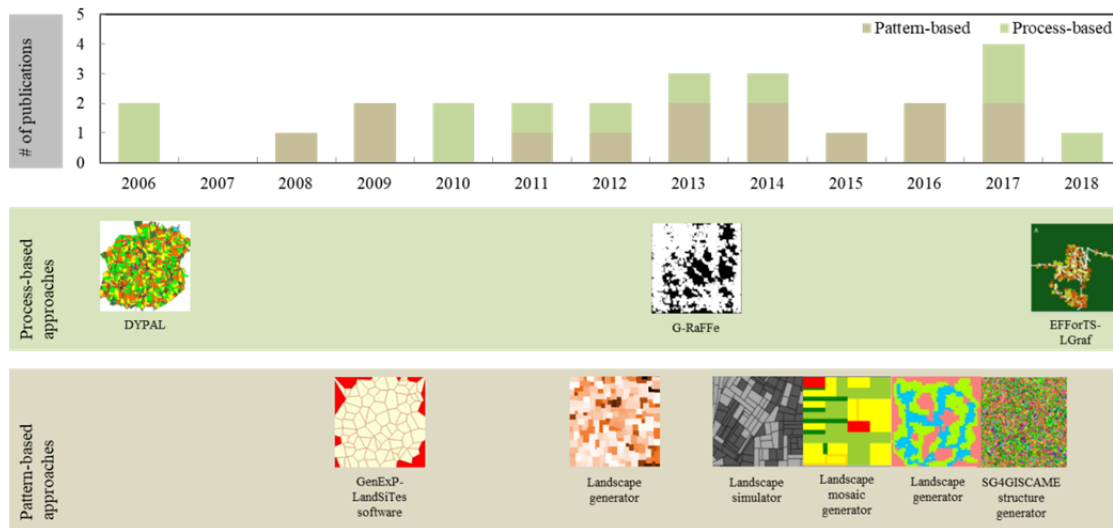


Figure 3.2: Evolution of the reviewed ALG approaches sorted by date of the first publication. DYPAL (Gaucherel *et al.*, 2006), G-RaFFe (Pe'er *et al.*, 2013), EFForTS-Lgraf (Dislich *et al.*, 2018), GenExP-LandSiTes software (Le Ber *et al.*, 2009, Le Ber & Mari, 2013), Landscape generator (Engel *et al.*, 2012, Everaars *et al.*, 2014), Landscape simulator (Papaix *et al.*, 2014), Landscape mosaic generator (Begg & Dye, 2015), Landscape generator (van Strien *et al.*, 2016), SG4GISCAME structure generator (Inkoom *et al.*, 2017).

Purpose of the ALG

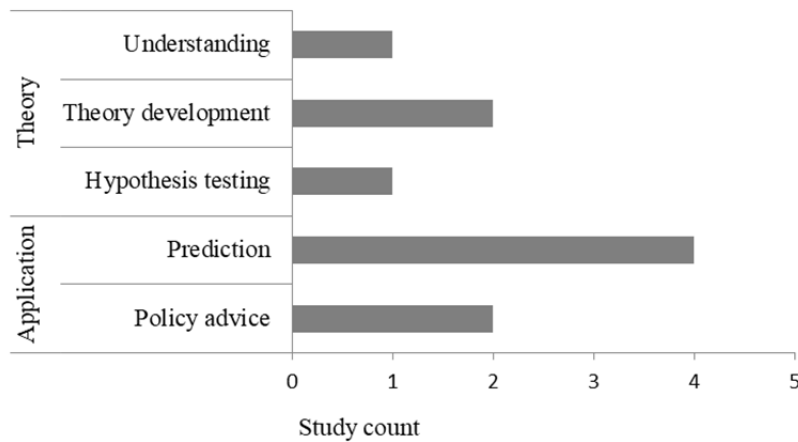


Figure 3.3: Overview of purposes of the reviewed ALGs. Numbers do not have to add up to the total number of reviewed papers, because multiple entries (e.g., multiple model purposes) are possible.

3.11.2 Aims

“Aim” here refers to the purpose of an ALG. There are various motivations for developing and applying computer-generated agricultural landscapes. However, there are two general objectives, which are not exclusive but lead to different foci and, hence, different designs of an ALG (Figure 3.3).

A first general objective in ALGs is to gather theoretical understanding and foster theory development. For example the software platform *DYPAL* (*Dynamic PATCHy Landscape*) by Gaucherel *et al.* (2006), was designed to analyse processes that drive changes in landscape patterns and ecological functioning, e.g., field aggregation and land use allocation. This not only allows investigating the relationships between landscape-shaping processes and the resultant landscape pattern but also how agricultural landscapes affect ecological processes. The generated landscapes of *G-RaFFe* (Pe'er *et al.*, 2013), which mimics the processes in which roads penetrate into natural habitats, serve as templates for theoretical analyses and the testing of hypotheses. In the same context, neutral models of agricultural landscapes, for example the vector-based model *GenExP-LandSiTes* (Le Ber *et al.*, 2009), are used for studying agro-ecological processes within a certain variability of landscape patterns.

A second objective of ALGs is the application of computer-generated agricultural landscapes for spatial simulation models in order to predict the ecological consequences of landscape dynamics or to give policy advice. The landscape generator by Slager & de Vries (2013) and its updated version (van Strien *et al.*, 2016), for example, was developed to investigate the influence of landscape patterns on spatial ecological processes. The landscapes generated are used to analyse the effects of changes in the landscape configuration and composition on biodiversity and conservation issues at the landscape scale. Therefore, they are usually coupled with models of specific species to investigate habitat suitability and population dynamics (Table 3.2). The aim of the AgBioscape modelling framework (Begg & Dye, 2015) is to explore options of managing arable landscapes and their ability to enhance functional biodiversity and devise conservation recommendations. The landscape generator of Engel *et al.* (2012) and its updated version (Everaars *et al.*, 2014), were developed to simulate changes in land use mosaics caused by bioenergy scenarios such as the thinning and spatial agglomeration of crops and to analyse their effects on the abundance of different farmland bird species. The modelling framework *Ddal* (disease dynamics in agricultural landscapes) aims at exploring the effects of landscape configuration and composition on the development of an epidemic (Papaix *et al.*, 2014). The structure generator SG4GISCAME (Inkoom *et al.*, 2017) aims at giving inputs for spatial ecosystem service assessment in data-scarce areas.

The range of aims shows that the purpose of the approaches presented here is different. Thus, some ALGs are a simulation model by themselves that can be used as a stand-alone tool to investigate certain questions or processes, e.g. on the drivers producing a landscape pattern. The result, however, is a computer-generated landscape pattern that can be used further for analysing respective consequences.

3.11.3 Configuration

“Configuration” refers to the size, shape, and spatial arrangement of structural elements of agricultural landscapes such as fields, semi-natural habitats, or hedgerows. ALGs generate landscape configurations that are either pattern-based (i.e., provide heuristic design rules and algorithms for reproducing typical structural characteristics of agricultural landscapes without addressing the pattern-forming driving forces) or are process-based by explicitly including underlying ecological or land use processes. Overall, there are more pattern-based approaches (6) than process-based approaches (2). In the remainder of this section, we first give a general overview of the different features of the ALGs and then present each ALG in detail (Table 3.2).

Pattern-based approaches

The landscape mosaic generator of the AgBioScape model platform generates a pattern of rectangular fields and narrow fringe structures such as hedges, whereby the size, shape and clustering of the fields can be controlled (Figure 3.4). The generator from Engel *et al.* (2012), Everaars *et al.* (2014) also generates rectangular fields of variable size, which are distributed irregularly and randomly in the landscape (Figure 3.5). Other landscape structures cannot be displayed. The landscape generator described by van Strien *et al.* (2016) is more complex than the two previous approaches, as the user can set target values of landscape metrics that quantify landscape configurations, e.g., the maximum perimeter or shape of the bounding box of a patch (Figure 3.6). Therewith, the linear shape of hedgerows can be depicted, and the configuration in general becomes more realistic.

In contrast to these grid-based approaches, there are also pattern-based models that work on the basis of vectors. Raster (grid-based) and vector landscapes differ fundamentally in terms of their spatial composition. Raster landscapes with one grid cell being the smallest unit are particularly suitable for gradual landscape dynamics and continuous processes. In vectorial landscapes, patches, typically polygons of varying sizes, are described by the exact coordinates of their bounding vertices. Since landscapes, especially agricultural landscapes, are strongly characterised by patches and corridors (Forman & Godron, 1981, Turner, 1989), the vector-based approach is very well suited for this type of landscape. Nevertheless, it is much less used because the geometry and algorithms are more complex.

The vectorial approaches of Le Ber *et al.* (2009), Inkoom *et al.* (2017) and Papaix *et al.* (2014) are based on tessellation methods that are used to manage sets of polygons. Tessellation starts from a point pattern and determines polygons based on distances to the closest neighbour points without overlapping or holes. The spatial distribution is determined by the distribution of the

tessellation seeds (point pattern). If a landscape mosaic is based on the seed distribution of a real landscape, the spatial pattern will be similar to the real landscape (Le Ber *et al.*, 2009). By controlling the size, shape and clustering of the polygons, a landscape mosaic develops and different land uses can be assigned to each patch or field.

Landscape mosaic generator (Begg & Dye, 2015)

The AgBioscape modelling framework (Begg & Dye, 2015) integrates a landscape mosaic generator and a population module to simulate interactions between a range of species and cropping systems, management and landscape characteristics. The landscapes consist of fields and the boundaries between them (Figure 3.4). Fringe structures such as grass margins and hedgerows can be depicted. By specifying the height, width, and total number of fields, the size, shape and clustering of the fields can be controlled. The generator continually subdivides a two-dimensional space to produce a mosaic of rectangular fields. The algorithms for generating the landscape structure contain stochastic elements, leading to a spatial variation of landscape patterns.

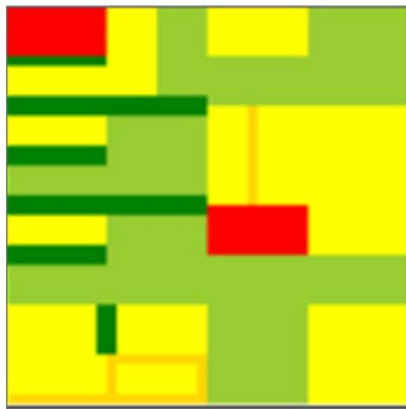


Figure 3.4: Example of a 4 km² landscape generated by the software platform AgBioscape (Begg & Dye, 2015) with wheat crops (yellow), grass ley (light green), woodland (red), grass margins (orange), and hedgerow (dark green).

Landscape generator (Engel et al., 2012, Everaars et al., 2014)

A given mean field size is used by this generator to create landscapes that consist of an irregular and randomly distributed mosaic of agricultural fields with varying shapes, sizes and edge lengths (Figure 3.5). The landscapes are 9 km² in size and are divided into grid cells with a 4 m grain size (750 by 750 grid cells). In a first step, fields of a predefined size are placed randomly on the main grid until the whole space is occupied. Afterwards, a correction algorithm replaces all fields that are too small by merging them with neighbouring fields. Field margins and in-field strips can be implemented.

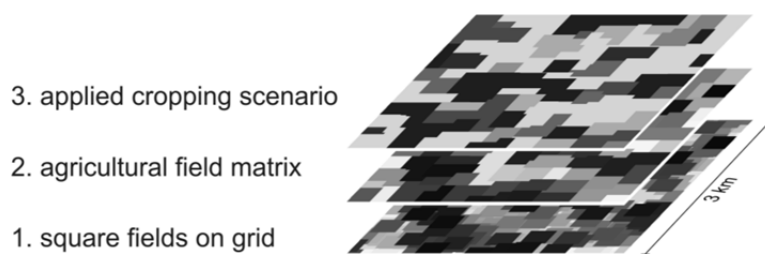


Figure 3.5: Visualization of different calculation steps in the model of Everaars *et al.* (2014). A given mean field size is used by a landscape generator to produce a natural-looking mosaic of agricultural fields (Layers 1 and 2; grey values chosen arbitrarily). A given cropping scenario determines which crops are present in the landscape and at what proportions (Layer 3; each crop represented by a shade of grey).

Landscape generator (van Strien et al., 2016)

This generator integrates different landscape metrics, quantifying the landscape configuration and composition. The distribution and clustering of land use classes as well as the proportion of adjacent landscape components can be determined (e.g., hedgerows around fields). The required input of the generator is configuration files with target values for the landscape metrics and an initial input raster in the ASCII format that can either be a random percolation map or an existing landscape. In random percolation maps, each raster cell is randomly assigned to a predefined land use class with a certain probability (Gardner *et al.*, 1987). It can be created with several GIS and programming languages (e.g., R, Python). The following landscape metrics can be varied on the class level or patch level: number of patches for a certain land use class, area of a certain patch, maximum perimeter, contact with another land use class, shape of the bounding box of a patch, total area within a bounding box occupied by a certain patch and the rectangular

criterion. The generator uses an optimisation algorithm to “find” landscapes of which the composition and configuration correspond to the target values of the landscape metrics. It does so by iteratively swapping raster cells and determining whether the new landscape is an improvement with regard to the target values. The algorithm contains stochastic components, so the generation of two identical landscapes with the same input settings is not possible. In return, it is feasible to generate landscape series in which single landscape metrics are varied (Figure 3.6).

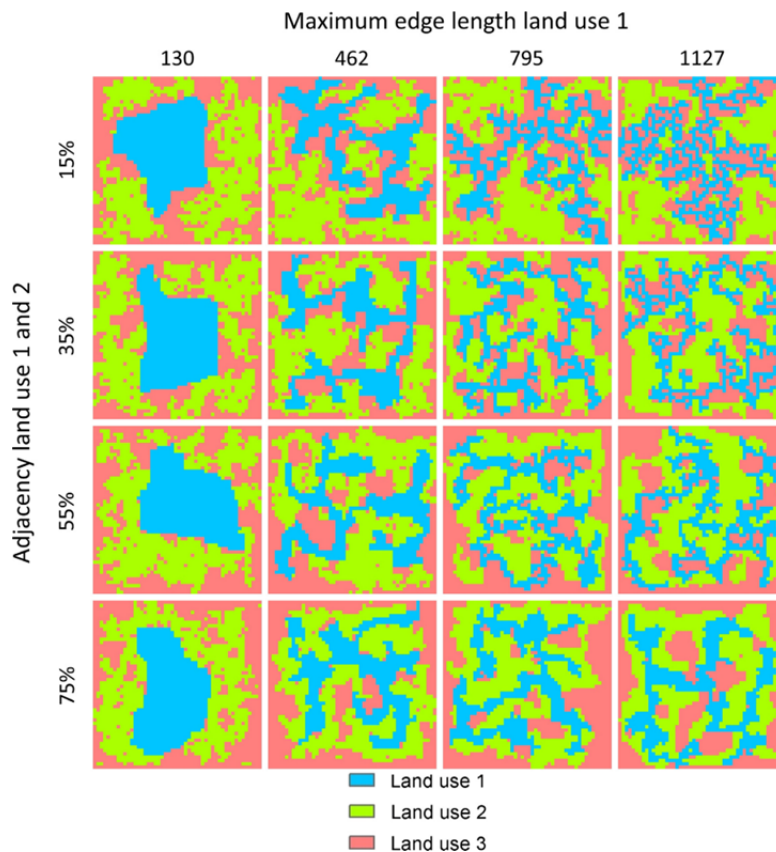


Figure 3.6: Landscape series generated by the landscape generator of van Strien *et al.* (2016). Landscapes in this series have three land use categories, various maximum edge lengths of land use 1 and different proportions of the adjacency between land uses 1 and 2. Note that for agricultural landscapes, “land use” would actually refer to “land cover”.

GenExP-LandSiTes software (Le Ber et al., 2009, Le Ber & Mari, 2013)

This software simulates neutral agricultural landscapes to explore the variability of landscape characteristics and the variation in the geometry of fields (Figure 3.7). An irregular patchy landscape mosaic without fringe structures develops. The field patterns are obtained by using two different tessellation methods, the Voronoi tessellation and a rectangular tessellation, which make it possible to control the size, number and the shape of fields. The user can choose the kind of seed distribution (original, simulated or random), the tessellation type (Voronoi or rectangular) and the cropping pattern distribution (random or stochastic). The model provides a library to calculate basic landscape descriptors (field area, perimeter, number of vertices, centroid and shape). File export is possible in raster or vector format and with shape files.

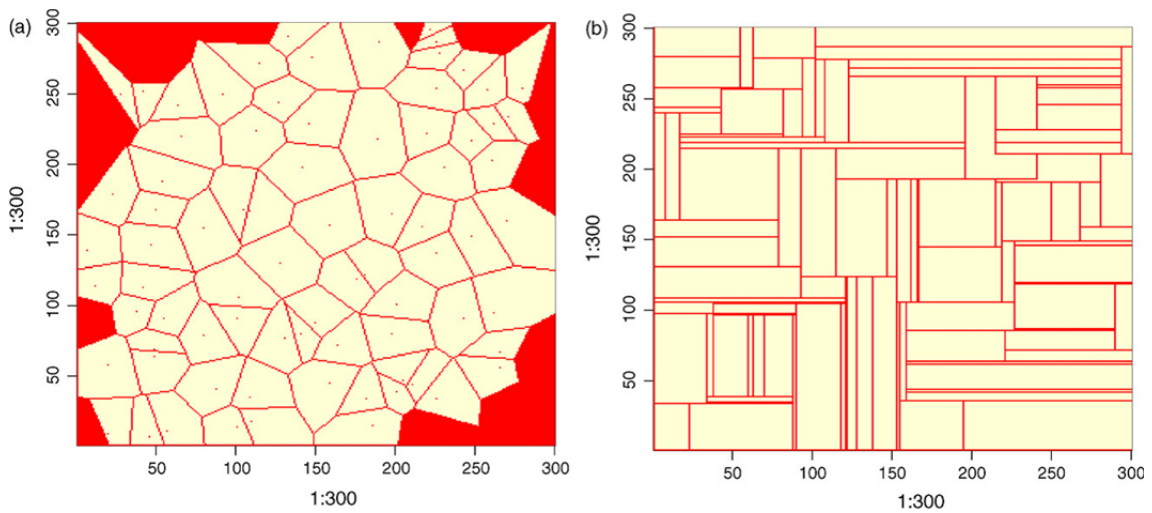


Figure 3.7: Two different tessellations based on sets of seeds generated by the GenExP-LandSiTes software (Le Ber et al., 2009): the Voronoi tessellation (a) and the rectangular tessellation with only T-vertices (b). Infinite Voronoi cells were eliminated.

SG4GISCAME structure generator (Inkoom et al., 2017)

The SG4GISCAME structure generator, which is a module within the GISCAME software, uses Voronoi tessellation and different algorithms to produce realistic landscape patterns (Figure 3.8). First, the landscape is separated into a number of triangles from a regular midpoint (triangulation). The edge, shape and size of the polygons can be altered through initial split and tolerance levels and spatial resolution. As a second step, the irregular triangles are merged to form more-realistic polygons on the basis of a user-designed or random process (merging).

Finally, users can alter or refine the output geometry of the landscapes using either a manual distribution option or a cellular automaton algorithm (refinement). The resulting vector data are transformed into raster data, and the output is an ASCII text file. A set of landscape pattern metrics is implemented to assess variations in landscape configuration and composition: patch cohesion, average patch shape, contagion, area weighted mean shape index, and landscape patch index.

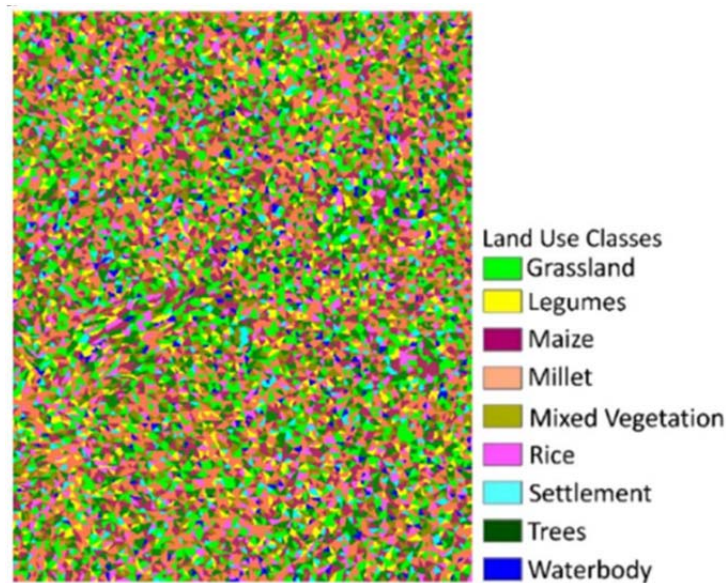


Figure 3.8: Application of a cellular automaton algorithm on a simulated landscape with 25 m resolution in SG4GISCAME (Inkoom *et al.*, 2017).

*Landscape simulator (Papaix *et al.*, 2014)*

The simple landscape simulator within the *Ddal* framework generates a landscape mosaic based on the T-tessellation simulation algorithm developed by Kiêu *et al.* (2013) (Figure 3.9). The input parameters number of fields, field surface average, field surface variability, and the square-like form of fields can be determined. As a result, it is possible to influence the degree of fragmentation of the landscape and to prevent triangular fields. The simulator is coupled with a pathogen population dynamics model.

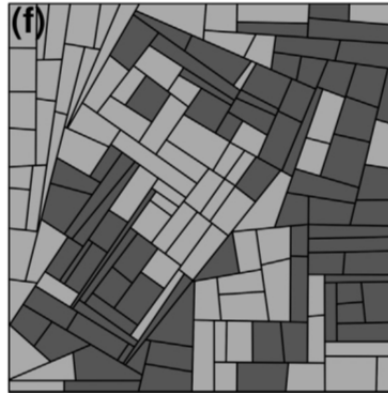


Figure 3.9: Example of simulated landscape structures generated by the *Ddal* landscape simulator (Papaix *et al.*, 2014) with two host types (light (50 %) and dark (50 %) grey) dispatched among a 155-field landscape.

Process-based approaches

The following two approaches work with explicit spatial locations determining the process being modelled. By using the modelling platform *DYPAL*, many different processes can be investigated at the landscape level, e.g., the spatial aggregation and distribution of fields and hedges, land use allocation, and land use rotations. The landscape processes are applied to landscape units by using one or more algorithms. Even though most of the previous applications of *DYPAL* are based on real landscape patterns, Gaucherel *et al.* (2006) have implemented neutral models (Patchy Landscape Neutral Models) in the software platform. In contrast to the complex modelling platform *DYPAL*, the *G-RaFFe* model (Pe'er *et al.*, 2013) generates landscapes based on a single process: forest fragmentation by roads and the generation of agricultural fields.

DYPAL (Gaucherel et al., 2006)

DYPAL, formerly known as *LI* (Gaucherel *et al.*, 2006), is a modelling platform for generic landscape modelling on various scales and landscape types (field, farm, and region). Landscape processes such as hedgerow planting and removal, when applied to landscape units, lead to evolution in the composition and configuration of the landscape. The ALG can simulate the patch dynamics of fields as well as dynamic fringe structures such as hedgerows (Figure 3.10). The patches are defined as polygons, but a pixel definition of the polygons was kept to be able to simulate continuous processes. The required input parameters depend on the process being modelled. The platform was designed around a kernel that provides an organisational data structure and a generic landscape structure. Several libraries provide specific algorithms permitting the handling of sets of points, linear networks or a mosaic of adjacent polygons. The user can freely choose the data structures, the driving decisions and processes, the simulation

steps, the level of detail of the description, and the chosen scales. Several further developments of the software platform and a number of applications have been made so far. Gaucherel *et al.* (2010) and Gaucherel *et al.* (2012) implemented additional mathematical models (formal grammar equations) into the platform to mechanistically simulate landscape dynamics. Bonhomme *et al.* (2017) implemented further configurationally changes of patches that enable all possible operations and combine them into a coherent mathematical framework.

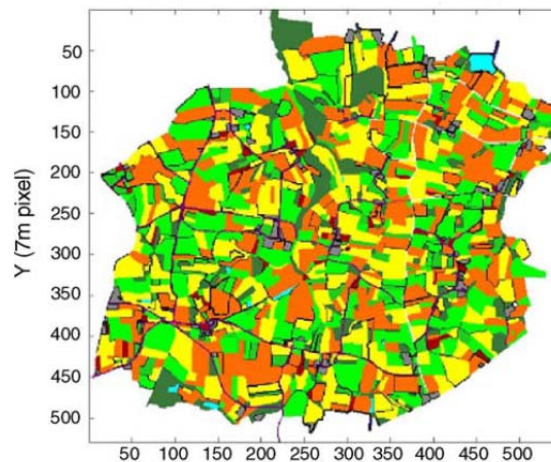


Figure 3.10: Example of an agricultural landscape mosaic generated by the modeling platform DYPAL (Gaucherel *et al.*, 2006).

G-RaFFe (Pe'er *et al.*, 2013)

The simple process-based simulator *G-RaFFe* is able to generate the spatial patterns of agricultural fields embedded in a natural habitat (esp. forest) that emerge from forest fragmentation by roads (Figure 3.11). Three main parameters determine the generated landscapes: the habitat cover, the number of roads crossing the landscape, and the field size. An additional parameter, maximum field disconnection, specifies whether and to what distance agricultural fields can be detached from roads or other fields. The model starts with a 100 % forest landscape and then creates roads that lead straight through the landscape, converting the forest into "non-forest". Roads are generated until the number of roads reaches the desired number, unless the forest cover reaches the target value specified by the user. Once all roads have been generated, agricultural fields are separated from them by a random movement of simulated "farmers". All fields have a square shape (same length and height), the size of which is derived from a uniform distribution between one and the maximum length specified by the user. Field expansion is a per-step process that can stop when the potentially converted cells are beyond the map extent or when the desired forest cover is reached. EFForTS-LGraf (Dislich *et*

al., 2018) is an extended version of *G-RaFFe*, which additionally includes two different land uses and households (Figure 3.11). Households can own several fields of different sizes with different land uses.

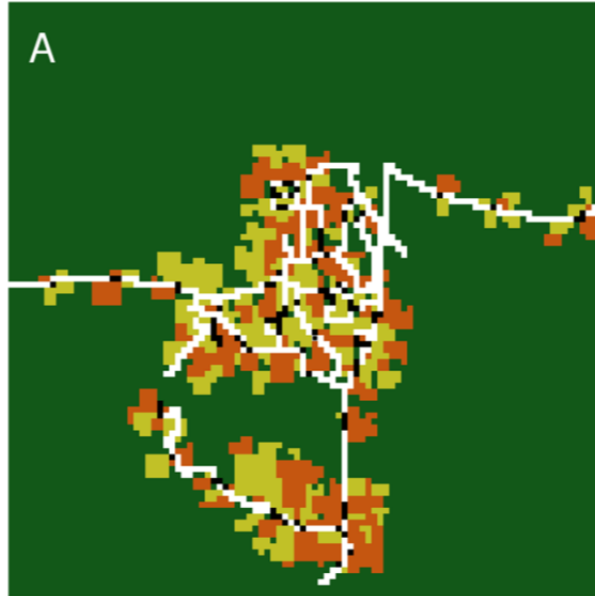


Figure 3.11: Virtual landscape generated by EFForTS-Lgraf (Dislich *et al.*, 2018), an extended version of *G-RaFFe* (Pe'er *et al.*, 2013). Roads are marked in white, household home bases in black, oil palm plantations in orange, rubber plantations in dark yellow. Dark green is the area which is not used for agriculture.

Table 3.2: Configurational and compositional details of existing agricultural landscape generators (ALGs). The scope of application of an ALG is demonstrated with specific case studies. Thus, the table shows only a selection of compositional details; usually, many more application types are feasible.

| Publication | Configurational Details | | | Compositional Details | | | | | | Population module avail. |
|--------------------------------|----------------------------------|----------------------------|---|---|--------------|---|------------------------------|--------------------------------|---------------------------------|--|
| | Type of landscape generation | Map type | Input parameter | Case study | Study region | Crop types | Crop generation | Fringe structures | Semi-natural habitats | Taxa |
| Begg & Dye (2015) | Pattern-based | Grid-based | Field height Field width Number of fields | Begg & Dye (2015) | GB | Cereal crop Broad-leaf crop Wild bird seed mix Grass ley | Stochastic | Grass margin Hedgerow | Conservation headland Forest | <i>Perdix perdix</i> , Carabid, Parasitoid, Aphid |
| Engel <i>et al.</i> (2012) | Pattern-based | Grid-based | Mean field size Number of crops Crop types | Everaars <i>et al.</i> (2014) | DE | Alfalfa Barley Beets Grassland Maize Oat Oilseed rape Potato Summer Rye Winter Rye Ryegrass Set-aside Sunflower Triticale Wheat | Stochastic | Field margin In-field strip | Integrated Biodiversity Area | <i>Alauda arvensis</i> , <i>Motacilla flava</i> , <i>Miliaria calandra</i> , <i>Vanellus vanellus</i> |
| Gaucherel <i>et al.</i> (2006) | Process-based / Pattern-based | Vector-based Grid-based | Depends on the process being modeled | Gaucherel <i>et al.</i> (2006)a, Gaucherel <i>et al.</i> (2006)b | FR | Maize Fallow land Permanent grassland Temporary grassland Cereal field Vegetable field | Stochastic, Gibbs process | Hedgerow River Road | Forest | - |
| Inkoom <i>et al.</i> (2017) | Pattern-based | Vector-based Grid-based | Cell size Initial split Initial split tolerance Split algorithm Split algorithm tolerance Area size Centre point Median line | Inkoom <i>et al.</i> (2017) | GH | Grassland Legumes Maize Millet Rice | Statistic, Stochastic | - | Mixed Vegetation Trees | - |

3 AGRICULTURAL LANDSCAPE GENERATORS FOR SIMULATION MODELS

| | | | | | | | | | | |
|---------------------------------|---------------|--------------|---|--|----------------|--------------------------|------------|----------|--------|---------------------------|
| Le Ber <i>et al.</i> (2009) | Pattern-based | Vector-based | Seed choice (original, simulated, random) Tessellation choice Cropping pattern choice (random, stochastic) | Le Ber <i>et al.</i> (2009) | FR | Coupling with crop model | Stochastic | - | - | - |
| Papaïx <i>et al.</i> (2014) | Pattern-based | Vector-based | Number of fields Surface of field Field surface variability Square-like field shapes | Papaïx <i>et al.</i> (2014) | - | Coupling with crop model | Stochastic | - | - | Plant pathogen |
| Pe'er <i>et al.</i> (2013) | Process-based | Grid-based | Map extent Desired habitat cover Number of roads Field size Max. field disconnection Density of farming households Household size Fraction of land uses (Road width) | Pe'er <i>et al.</i> (2011), Pe'er <i>et al.</i> (2013), Dislich <i>et al.</i> (2018) | AR, PY, BR, ID | Oil palm, Rubber | n.i. | Road | Forest | Hypothetical bird species |
| van Strien <i>et al.</i> (2016) | Pattern-based | Grid-based | Proportion of landscape component Number of patches Maximum edge length Patch size Patch maximum perimeter Patch edge contrast Shape of the bounding box of a patch | Slager & de Vries (2013) | NL | Maize | - | Hedgerow | - | - |

3.11.4 *Composition*

“Composition” here refers to the assignment of landscape elements (configuration) to different land cover types or structures. However, not all of the generators reviewed allow a finer differentiation in this respect (Table 3.2). The generated landscapes of *G-RaFFe* consist only of forest and agricultural fields, in which ‘agricultural field’ is not further specified. However, agricultural fields can be covered with oil palm or rubber plantations in the extended version *EFForTS-LGraf*. The composition of the generated landscape described by van Strien *et al.* (2016) is defined by various land use categories. Regarding agricultural landscapes, one case study on maize farmland with hedgerows has been carried out so far (Slager & de Vries, 2013).

GenExP-LandSiTes and presumably *Ddal* can be coupled with external crop rotation models such as *CarrotAge* (Le Ber *et al.*, 2006), whereby a wide range of crops can be taken into account. The data mining software *CarrotAge* is based on high-order hidden Markov models for analysing spatio-temporal cropping patterns. Many crop rotation approaches work with Markov models to achieve a change in landscape configuration or composition. Markov models provide matrices with transition probabilities between different crop types; similar matrices have been widely used for representing succession in forests (Horn *et al.*, 1975). These models are descriptive, not mechanistic, but they can be a starting point for realistic depictions of existing composition dynamics. Different policies can be implemented by manipulating the transition probabilities. In *Ddal* (Papaix *et al.*, 2014), no explicit crop types have been implemented so far. The number of land use types (host types), the proportions they cover and their level of spatial aggregation can be varied by applying a stochastic algorithm.

The other four generators work with pre-defined crop types or land use classes, which are distributed to the fields mostly according to stochastic rules of crop successions. The landscape mosaic generator described by Begg & Dye (2015) describes crop rotations as first-order Markov chains (Usher, 1992). Only four crop types have been implemented so far, but different land use types such as hedgerows, flowering margins and conservation headlands can be chosen. The number and type of 15 different crops can be varied in the landscape generator of Everaars *et al.* (2014) to build different cropping scenarios. Crops are allocated randomly or with a probability that equals the relative proportion to the agricultural fields for multiple subsequent scenarios. In addition, fields can be allocated with integrated biodiversity area (IBA), defined as semi-natural habitat. *DYPAL* simulates deterministic or stochastic crop successions within farms, while other landscape elements such as hedgerows, forests and rivers can be depicted. In Gaucherel *et al.* (2006), land use types are assigned to patches using the Gibbs process, which is derived from statistical physics (Caldiera & Presutti, 1974) and describes the local interactions between landscape units. It is also possible to apply the Gibbs

process to landscape configurations (Gaucherel, 2008). This can be achieved by editing the shape or size of the landscape patches or by selecting a Gibbs pair function to constrain the relative positions of the seeds. In SG4GISCAME (Inkoom *et al.*, 2017), a large number of land use classes can be specified as well as their relative amount. The distribution is based on transition probabilities and tolerable or intolerable neighbourhood settings. In addition to crop types, five of the ALGs can depict semi-natural habitats such conservation headlands (Begg & Dye, 2015), integrated biodiversity areas (Everaars *et al.*, 2014) and forest (Gaucherel *et al.*, 2006, Pe'er *et al.*, 2013, Begg & Dye, 2015, Inkoom *et al.*, 2017). Four of the ALGs were coupled with population modules (Pe'er *et al.*, 2011, Everaars *et al.*, 2014, Papaix *et al.*, 2014, Begg & Dye, 2015).

Additional crop rotation tools

As alternatives to *CarrotAge*, a range of other crop rotation tools exist that can be used as a supplement to a landscape generator. Some useful examples are presented as follows.

LandSFACTS (Landscape Scale Functional Allocation of Crops Temporally and Spatially) allocates a crop to each field for each simulation year in a GIS shape file (Castellazzi *et al.*, 2008, Castellazzi *et al.*, 2010). Fields are represented as polygons in vector format with fixed boundaries. The model is based on a stochastic process using the probabilities of crop-to-crop transitions (Markov chains) and rule-based constraints.

The linear optimisation model *CropRota* (Schönhart *et al.*, 2009, Schönhart *et al.*, 2011) integrates agronomic criteria and observed land use data at field, farm, or regional scales in order to generate typical crop rotations for the particular scale.

ROTAT (Dogliotti *et al.*, 2003) is a computer program that combines crops from a predefined list to generate all possible different rotations. A number of filters or rules based on explicit agronomic criteria and expert knowledge can be controlled by the user.

ROTOR (Bachinger & Zander, 2007) is a static rule-based model for generating and evaluating site-specific and agronomically sustainable crop rotations for organic farming systems in central Europe. ROTOR requires as input data field specific soil data, mean annual precipitation and mean precipitation during the winter half year.

NePoFarm (Horn, 2017) is a landscape generator that creates farmland scenarios as input files for the honeybee model BEEHAVE (Becher *et al.*, 2014). Field patches are allocated randomly in two British template landscapes and are characterised by crop type identity and crop diversity (crop type number and relative abundance). NePoFarm is based on GIS maps and is implemented in the freely available programming language R.

3.11.5 *Validation*

“Validation” here refers to testing whether landscapes generated by an ALG reproduce realistic landscape features. To validate the generated landscapes, five of the reviewed approaches compared certain landscape metrics with real landscapes (Gaucherel *et al.*, 2006, Le Ber *et al.*, 2009, Pe'er *et al.*, 2013, van Strien *et al.*, 2016, Inkoom *et al.*, 2017). Three of them (Pe'er *et al.*, 2013, van Strien *et al.*, 2016, Inkoom *et al.*, 2017) calculated the relevant landscape metrics of the real and computer-generated landscapes by using *FRAGSTATS* (McGarigal *et al.*, 2012). The calculated landscape metrics can also be used as input parameters for the ALG to approximate the computer-generated landscape to the real one. As a result, the generated landscapes preserve the main characteristics of the original landscape while being configurationally different. Inkoom *et al.* (2017) used a Turing Test to explore expert visual judgement in comparing neutral landscapes to real landscapes. The publications of the other approaches did not contain any evidence of validation.

3.11.6 *Evaluation of policy measures*

Here, we summarise to what extent and how ALGs were used to evaluate existing or prospective policy measures addressing agricultural landscapes. Everaars *et al.* (2014) simulated future scenarios of different land use changes due to policy-making and economic aspects of bioenergy production. The effectiveness of different mitigation strategies on farmland birds was analysed on the basis of the generated landscapes. *DYPAL* has been developed, inter alia, to assess the environmental consequences of agricultural policies affecting processes that drive changes in landscape patterns and ecological functioning. It was used to evaluate simplified CAP reform decisions such as changing maize and cereals to fallow and temporary grassland (Gaucherel *et al.*, 2006). Houet *et al.* (2010) used *DYPAL* to simulate plausible future states of landscape features such as hedgerows, riparian wetlands, and agricultural land covers based on hypotheses about future land management related to European policies. The AgBioscape modelling approach has the intention to develop an impact assessment and decision support tool for land management options, including agri-environmental schemes (AESs). The potential of such a tool is to assist land managers and policy makers in identifying effective management options. The landscape generator by Slager (2011) was initially developed to generate plausible landscape configurations for participatory spatial plan-making. The study focuses on the construction of so-called policy (plan) scenarios as a fundamental activity in spatial plan-making.

3.11.7 *Availability of the ALGs*

ALGs that have an executable version are mostly openly available on the internet (Table 3.3). However, only *DYPAL* has open source code. Almost none of the ALGs are documented in detail; instead, only summary descriptions of the algorithms and data used are provided, which also limits the level of detail by which we could characterise the ALGs above.

Table 3.3: Availability of agricultural landscape generators (ALGs).

| Publication | Name | Software application | Availability | Webpage / Download link | Code open source | Documentation |
|---------------------------------|---------------------------------|----------------------|------------------------|---|------------------|---------------|
| Begg & Dye (2015) | AgBioscape | Y | not open to the public | | N | Annex 1 |
| Engel <i>et al.</i> (2012) | Landscape generator | N | not open to the public | | N | Appendix S1 |
| Gaucherel <i>et al.</i> (2006) | DYPAL | Y | free to use | http://amap-collaboratif.cirad.fr/pages-logiciels/?page_id=70 | Y | n.i. |
| Inkoom <i>et al.</i> (2017) | SG4GISCA ME | Y | usage fee | http://www.giscame.com/giscame/english_giscame_giscame_suite_sg4giscame.html | N | N |
| Le Ber <i>et al.</i> (2009) | GENEXP-LANDSITES | Y | free to use | http://engees.unistra.fr/~fleber/Landsites/ | N | N |
| Papaix <i>et al.</i> (2014) | <i>Ddal</i> Landscape simulator | N | not open to the public | | N | N |
| Pe'er <i>et al.</i> (2013) | <i>G-RaFFe</i> | N | on request | | N | Y |
| van Strien <i>et al.</i> (2016) | Landscape Generator (LG) | Y | free to use | www.lg.ethz.ch | N | Y |
| n.i. | No information available. | | | | | |

3.11.8 *Other tools for generating neutral landscapes*

Our definition of ALGs is rather restrictive, as we require the potential to systematically vary landscape features in an automated way. Such generators have many advantages, but there are also software tools, or generators, that are not ALGs according to our definition but are still certainly useful for more specific purposes. Here, we give a brief overview of such tools that we found in our survey of the literature. They have in common that they do not explicitly address agricultural landscapes or land use types.

RULE is a software package for the generation of neutral landscape models and the analysis of landscape patterns (Gardner *et al.*, 1987, Gardner, 1999, Gardner & Walters, 2002). Landscape patterns are generated either as simple random processes (random maps), or as a result of

spatially correlated processes using algorithms derived from fractal geometry (multifractal maps). *QRULE* is a further development of *RULE*, retaining the essential features but providing statistical summaries based on area rather than pixel counts, improving the formats of ancillary data sets, and adding the potential for developing and analysing alternative neutral models (Gardner & Urban, 2007).

The *Fractal Realizer* (FR), developed by Hargrove *et al.* (2002), generates multiple-category synthetic landscape maps according to user specifications. The synthetic landscapes show statistical properties similar to those of a particular empirical landscape and can be used to generate replicated input to spatial simulation models. It generates fractal landscape patterns based on the midpoint displacement algorithm by Saupe (1988).

GradientLand (Cambui *et al.*, 2014) is a free software program for generating a wide range of habitat cover gradients as random and fractal neutral landscapes. In the fractal mode, varying the aggregation and land cover is realised by using the midpoint displacement algorithm. Completely random patterns are produced by using a uniform probability distribution.

NLMpy (Etherington *et al.*, 2015) is a Python software package for the creation of neutral landscapes within a general numerical framework. It integrates a range of NLM algorithms that differ in the spatial autocorrelation of the element values in a two-dimensional array. It is open source, can be used on any computer system and is easily combined with geographic information system (GIS) data.

NLMR and *landscapetools* (Sciaini *et al.*, 2018) are R packages for simulating and modifying neutral landscape models in a single environment. *NLMR* is a comprehensive collection of algorithms for creating neutral landscapes and *landscapetools* provides a utility toolbox which facilitates an easy workflow with neutral landscapes and other raster data.

Hiebeler (2000) describes a simple algorithm for generating landscapes with spatially structured habitat heterogeneities. The landscapes consist of rectangular lattices of sites, or patches, each characterised by a value indicating its habitat type. Hiebeler (2007) improved the landscape-generation algorithm by using stratified sampling of sites rather than simple random sampling.

Remmel & Fortin (2013) utilize a stationary random field simulator (Remmel & Csillag, 2003) to produce large numbers of binary landscapes with identical parameters. Clearly defined descriptors of spatial pattern (composition and configuration) can be parameterized within the R statistical computing environment.

3.12 OUTLINE OF A FUTURE GENERIC ALG

Our Review shows that, currently, no generic, commonly used or useable ALG exists, but isolated solutions have been developed in specific contexts with specific purposes. It seems impossible to design a single unifying ALG that is able to cover all past and future applications and questions. A generic ALG would have to perform the balancing act of being both versatile and adaptable for case specific application. In order to solve this dilemma, in the following we would like to suggest a modular design for generic ALGs.

Specific requirements

Our idea behind generic ALGs is the development of a software tool in modular design. The activation and deactivation of modules should be controllable with regard to the final result, because the design of the landscapes can vary considerably depending on the final use. Likewise, defined interfaces should exist for adding own, specific modules. The design depends above all on the simulation models to which the landscapes produced by the ALGs serve as an input. These can be different types of dynamic models, for example, LUCC models, spatial ecological models that analyse the effects of landscapes on certain ecological aspects (e.g. animal species), or agent-based land use models, which analyse farmer's decisions under the influence of institutional (markets, policies) and natural (e.g. soil type) framework conditions.

Basically, the generic ALGs create and systematically vary hypothetical agricultural landscapes (spatial configuration and composition of field mosaics). The following requirements should be fulfilled: (1) Pattern- and/or process-based generation. (2) The generation of a large number of random landscape maps in order to make general statements as well as the generation of specific landscapes. (3) Random and targeted distribution of landscape elements. Table 3.4 presents a tentative list of features that such a generic ALG should have. This list is our subjective merger of features that we, based on our review, consider essential. All features should be separately testable and controllable. Essential elements are required to adapt the landscapes to a wide range of target model types. Optional elements allow tailoring the landscape to specific purposes. The size and number of fields and the assignment of crop types are obligatory inputs. Regarding crop types, coupling with a software program that generates crop types or rotations (Dogliotti *et al.*, 2003, Bachinger & Zander, 2007, Schönhart *et al.*, 2009, Castellazzi *et al.*, 2010) can be useful. Additional landscape elements, e.g., semi-natural landscape elements and hedges, are optional, but can be decisive, as in the case of pollinators. Even the addition of abiotic (e.g., soil, runoff, relief) and socio-economic factors should be possible.

Table 3.4: Essential and optional features of agricultural landscape generated with a generic ALG.

| Essential features | Optional features |
|---|--|
| Field size | Natural and semi-natural landscape elements |
| Number of fields | Fringe structures, e.g., hedges, field margins |
| Shape of fields | Other land use types, e.g., set-aside, grassland |
| Crop types | Farm type |
| Spatial correlation (clustering, fragmentation, distribution) | Crop rotation schemes |
| | Abiotic factors, e.g., soil, runoff, relief |

A gradient from very simple to very complex landscapes should be possible. Landscape complexity can successively be increased by adding certain features or modules. The resulting landscape must have an adequate degree of complexity, which is not just a technical or methodological question but a practice-oriented one (Seppelt *et al.*, 2009). Because scale, grid type, resolution and the degree of complexity have to be compatible with the simulation model to which the landscapes serve as input. This also has an effect on the design of the landscape, since some landscape elements are not visible at a particular resolution, e.g., fine fringe structures.

Model and software architecture

The optimal generic ALG framework is open source, fully documented and easy to use. With regard to an integrative approach, other open source models can be integrated quickly and easily. According to Agarwal *et al.* (2002), initiating such an open-source modelling effort will require several components: (1) a web site to support modelling collaboration (e.g., data and interactions among individuals, such as bulletin boards and FAQs); (2) the establishment of one or more modelling “kernels” (core components of models using various technologies) that are designed in a modular fashion and allow participants to make enhancements with relative ease; and (3) the development of mechanisms for sharing model enhancements that encourage participation and provide incentives that are comparable. Experience with the generic forest succession model Landis II (Scheller *et al.*, 2007) shows that it is crucial to employ modern software engineering techniques for software that is intended to be generic and used by many people (Scheller *et al.*, 2010).

A modular model architecture meets the requirements for generic ALGs. It enables the integration of building blocks of existing ALGs that have proven to be useful, in the form of modules. All modules can be easily revised, such that the latest expert knowledge can always be integrated. Furthermore, new modules can be added with little effort. The ALGs should be

operated via an intuitive graphical user interface that consists of different toolboxes with open source code for model development. Ideally, the package concept of R would be adopted, but this would require the existence of a core architecture and scheduler. The algorithms and rationale of the ALGs have to be fully documented and a user manual and guided tour provided. The ALGs should not only be a stand-alone program but should also be usable as a library, i.e., it can be started from every simulation model and generate landscapes during the simulation process on the fly. Such coupling is important particularly for optimisation models. An interface to GIS should exist to be able to alter real imported maps automatically using the ALGs. Various software platforms or programming languages could be envisaged for developing generic ALGs; however, no single language will be accepted, and used, by all potential users. Still, if a certain widely used language is chosen, such as C++, Java or Python, programming interfaces should be provided that allow links to other languages, if possible. An alternative is to try to build on existing GIS software. One option is to use the ArcGIS ModelBuilder, but this might be suboptimal because this software is proprietary and still might not offer the full flexibility required.

A suitable solution might be based on a domain-specific visual dataflow programming approach. Visual dataflow programming (VDP) is a programming paradigm that represents a program as a directed graph of data flows between operations (Wikipedia, 2018). In visual dataflow programming, users can assemble a program by placing operations (nodes) and connecting their data inputs and outputs in a graphical user interface (Figure 3.12).

The appeal of VDP is that it combines high flexibility and extensibility with ease of use and program readability without programming knowledge. In the context of an ALG framework, operations (i.e., nodes) would include basic GIS operations such as a raster calculator, buffer, filters or Voronoi diagram calculation, as well as generators such as Perlin noise or random points. Finally, it would include output operations for different file formats and visualisation for debugging. Every operation can have input and output slots for defined data types (e.g., floating-point number, integer raster, vector layer).

The framework would be easily extensible through the addition of operations. Although some programming knowledge in the framework's implementation language would be necessary for the creation of new operations, their mutual independence would greatly benefit flexibility and facilitate the exchange of operations between users or a central repository for official and community-based extensions (operations or bundles thereof).

One important advantage of this approach would be that it combines ease of use, without having to learn a specific programming language, with modularity and extensibility based on a widely

used language. In the Supplementary Material, an example VDP program implemented in a prototype framework in Scala is explained in detail to further illustrate the concept of VDP.

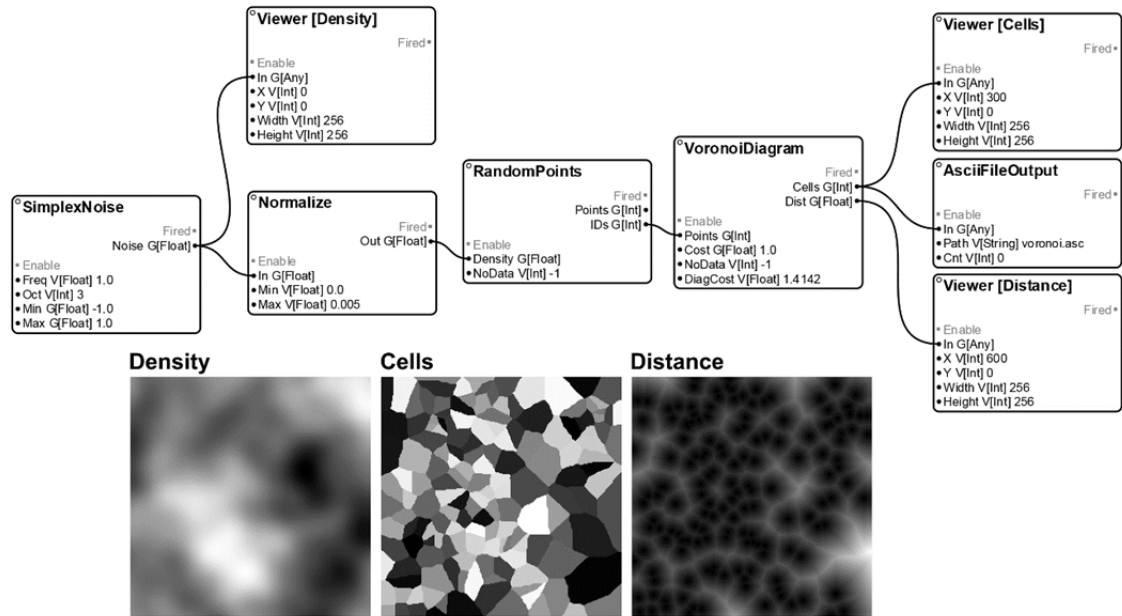


Figure 3.12: Example of Visual Dataflow Programming for generating a landscape based on Voronoi tessellation. Users compile programs by selecting and combining nodes that represent certain operations. Using Java, developers program further nodes. (See also Appendix B1)

Another generic approach to implementing modular generic ALGs are the so-called “pattern grammars” (Gaucherel *et al.*, 2012), where landscape features are described using a certain syntax. This approach has been widely used for functional-structural plant modelling (FSPM), using L-systems grammar (e.g., Godin & Sinoquet, 2005, Wang *et al.*, 2018). The ALG DYPAL (Gaucherel *et al.*, 2006) is based on such a grammar and is one of the most flexible existing ALGs.

3.13 DISCUSSION

The computer-aided generation of agricultural landscapes can provide a framework for understanding and evaluating how land use and land cover changes will take place and affect the environment. Being input to simulation models, the landscapes can serve as a basis for decision-making for policy makers or as support for discussion and negotiation. This especially concerns insights into the adequate scale of policies (national or more regionalised), but also into the relative importance of landscape structural elements for achieving societal goals with implications for the prioritisation of conservation activities. The results are useful for

communicating policies and the corresponding landscape changes and environmental effects to local actors and to the public.

Computer-generated landscapes offer a number of advantages: (1) they can fill the gap when real data are not available or are not at a suitable resolution, and they allow us (2) to test new landscape configurations, (3) to carry out systematic analyses of environmental gradients, and (4) to perform spatial sensitivity analyses as a basis for the regional transferability of the results. For these reasons, we believe that the future lies in the computational evolution of landscape patterns not limited to random change.

The aim of each ALG should be to design a plausible landscape with appropriate input parameters and algorithms. This means that the generated landscape should not be more complex than necessary to serve as input for a simulation model or to answer the scientific or policy question. Still, most existing ALGs represent rather simple agricultural landscapes via a few regularly shaped patches. Configurational changes are often realised by transition probabilities. Important questions, though, exist that would require more-complex landscapes by, for example, adding semi-natural habitats or applying advanced design rules which acknowledge the relationship between abiotic site conditions (e.g., soil, runoff, relief) and crop choice. In this way, all processes that lead to significant changes in configuration and use can be included.

Process-based approaches

The landscapes of process-based ALGs are the result of the implemented process and are therefore strongly dependent on the input parameters. Users thus need to know and fully understand the effect of each input parameter to design specific landscapes. An advantage of process-based or mechanistic ALGs is that the underlying processes can be explicitly addressed, so these landscapes are more likely to be relevant for the study of policy measures. The disadvantage is that it can be difficult to quantify all the necessary parameters.

We found only two process-based ALGs developed so far. *DYPAL* is the most complex and most advanced one. It integrates numerous algorithms as a basis for various processes. While neutral models are already implemented for the composition, landscape configuration is currently based on real landscapes. That's the reason why this approach does not fully meet our selection criteria and cannot be compared very well with the other approaches. Nevertheless, we have included it because it shows the possibilities of a process-based generator. The possibility to generate landscape configurations in a systematic and automated way would make the application of *DYPAL* much more versatile and flexible. *G-RaFFe* simulates the highly significant process by which primary forest is transformed into arable land. The conversion is

performed by simulated farm establishment subsequent to the generation of roads. Unfortunately, agricultural fields cannot be assigned to different crops, so this generator can only be used for the investigation of landscape dynamics rather than for agricultural questions.

Pattern-based approaches

Pattern-based ALGs usually require fewer parameters and less computing time than process-based ones. There are a variety of landscape metrics that can be used as input parameters, e.g., the number and size of fields or the proportion of landscape elements. Most ALGs integrate only a few landscape metrics, which limits the design of the landscape pattern and, thus, the range of possible applications. To generate realistic agricultural landscapes, a set of different landscape metrics is needed. However, one should consider that more input parameters as well as a larger grid size lead to more-complicated algorithms and longer computing time. To solve this problem, efficient algorithms become important.

The strength of the AgBioScope landscape mosaic generator is that it is already coupled with four population modules (a ‘conservation’ species, an agricultural pest, and two functionally distinct natural enemies) to investigate the influence of management and land use patterns. The generator can be used to generate simple field patterns from rectangular fields with fringe structures and to assign four different crop types to the fields. The landscape generator of Engel *et al.* (2012), Everaars *et al.* (2014) also designs simple field patterns, which can be assigned to 15 different crop types. The focus is on the variation of crop proportions and the mean field size. However, it cannot vary the range of field sizes, leading to quite artificial landscapes composed of square fields. Using the ALG developed by van Strien *et al.* (2016), a differentiated landscape can be generated by integrating different landscape metrics that can be applied at either the field or class level. The number of different land use classes can be defined, but no specific crop types have been implemented so far.

With the tessellation methods applied in *GenExp-LandSiTes*, *SG4GISCAME* and the landscape simulator by Papaix *et al.* (2014), irregular geometric field patterns are generated without fringe structures. Tessellations have the advantage that the general geometrical character as well as the spatial distribution of the agricultural landscape can be preserved. The difficulty is in controlling important landscape features, such as field sizes and shapes or distances between tessellation seeds. While the tessellation methods allow one to simulate numbers of fields and average field sizes that are similar to those of real landscapes, they do not correctly depict the shapes of the fields or the variability of these shapes within the landscape (Le Ber *et al.*, 2009). *GenExp-LandSiTes* produces slightly too-compact fields with little variability, while the rectangular tessellation produces over-elongated fields with too-high variability. As a result, this

ALG generates landscapes with configurations of limited realism, and landscape dynamics cannot be investigated very well. In contrast, *SG4GISCAME* provides a better representation of field shapes through higher flexibility and refinement algorithms.

Simulating crops

In most existing ALGs, crop types are defined only marginally (*Le Ber et al.*, 2009, *Papaix et al.*, 2014, *Begg & Dye*, 2015, *van Strien et al.*, 2016, *Dislich et al.*, 2018) or not at all (*Pe'er et al.*, 2013). This means that although there are various land use patterns from agricultural fields, there are few specific farming systems. However, representing land cover in more detail is essential to answer many questions regarding agricultural landscapes. The tessellation method, for example, offers little possibility for handling attributes of landscape composition, but it can be combined with crop rotation models. Statistical modelling of crop rotations in general and Markov models in particular are suitable tools for predicting crop types. However, Markov models per se are empirical, based on observed transitions of land use types, or are fully hypothetical. Therefore, they should be constrained by conditional rules based on expert knowledge.

Evaluating policy measures

By using computer-generated landscapes in simulation models, agricultural policies can be evaluated quickly and effectively at the local or regional scale. This is an advantage over field observations and long-term field experiments, which are more time-consuming but obtain higher precision and validity. Both methods have their pros and cons and should be used and supplemented according to their capabilities. The rapid evaluation and prediction of environmental effects related to policies are a great strength of simulation models and are essential to propose and implement sustainable and efficient environmental policies. However, since the so-far generated landscapes are often rather simple, the application as a tool for evaluating policy measures is still limited because the results are only partially transferable to reality. Validation not only of the simulation models used but also of the ALG is crucial in this context. Here, validation means providing evidence that ALG-generated landscapes are able to capture essential features of existing, and planned, landscapes.

Challenges & Limitations

We have tried to describe existing ALG approaches in the same depth and with regard to the same criteria. Unfortunately, not only are the approaches themselves very different in terms of

methodology, but they are also often incomplete in their description, which makes them difficult to compare. The approaches are not described in the same way, terminologies differ, and much of the information we have been looking for is not available. This leads to incompleteness in the description of some approaches and, possibly, to biases. ALG descriptions following a standardised protocol would be extremely helpful and a desirable standard for publications in the future. For example, the ODD protocol, which is a standard format for describing individual- or agent-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010), could be adopted for this purpose.

The ALGs presented here have mostly only been used within the research group that developed them. Thus, they were not designed for general application and availability, nor were they designed with user friendliness in mind. Generic ALGs will require well-designed software and detailed documentation so that the user can quickly become familiar with the ALG's functionality and understand exactly which application possibilities are available. In our opinion, the generator developed by van Strien *et al.* (2016) comes closest to meeting these demands. A well-documented open source code can be further developed and enriched by the scientific community, and it can be used for other models. Until now, most ALGs have been developed in isolation. Because no consistent terminology regarding landscape generators exists, and because we had to focus on ISI-listed publications, we might have overlooked further relevant ALGs, although we could not find references to any further ALGs in the publications we reviewed.

Our review shows that the development of computer-generated agricultural landscapes is still in its infancy. Most generators generate simple landscapes, which limits the range of application. In most cases, the main focus is on either the spatial configuration or the composition, not on both in a balanced way. All approaches still have great potential for further development towards broader applicability. To address the multi-functionality of landscapes, generic ALGs should include other land use types such as forests or settlements. Pattern-oriented modelling can be used, for example, to identify relevant landscape metrics. The alignment of computer-generated landscapes with real landscapes still has much potential for improvement. This can be made possible by the further development of specific algorithms and calibration or validation with high-resolution data on cultivation systems and abiotic factors. An important data input for future ALGs will be remote sensing data (e.g., Pettorelli *et al.*, 2016), which open up new approaches for identifying land use types (e.g., Joshi *et al.*, 2016).

Outlook

As a result of our review, we derived requirements for generic future ALGs that have the potential to be widely used in landscape science. Environmental questions can be examined on certain spatial scales and transferred to other scales that are not feasible to explore in reality. However, the difficulty of computer-generated landscapes is that they represent few landscape features well simultaneously. Each extension leads to a more complicated algorithm and longer calculation time. This leads to the classical modeller's dilemma of when functionality falls victim to complexity. Therefore, the complexity of the model has to be carefully considered as well as how versatile the ALG can and should be. It is important to give the user the possibility of prioritising, e.g., which landscape features should be exact and which can be approximate. Generic ALGs thus need to have a modular and preferably open architecture. In the Supplement, we outline one possible solution, but other solutions certainly exist. In any case, although the architecture of generic ALGs might be set up by individual groups of researcher, e.g. the approach that we outline above and in the supplement, or approaches based on pattern grammar (Gaucherel *et al.*, 2006, Gaucherel *et al.*, 2012), establishing a modular framework would have to be a community activity. Ideally, national or European funding agencies would initiate such joint projects, similar to the EU initiative to standardize models of the fate of pesticides in surface waters (FOCUS, 2001).

3.14 CONCLUSION

Systematically generating variable virtual landscapes as a basis for spatially explicit assessment opens up new ways of exploring environmental issues. There is an enormous field of application, particularly with regard to the evaluation of policy measures. Critical threshold values of environmental effects can be identified at an early stage, and suitable mitigation measures can be developed. Due to the enormous application potential, the significance of landscape generators as a basis for spatial simulation models will continue to grow in the future, and they will be a useful complement to real landscapes and long-term field studies. However, considerable development work is still needed to improve and generalise the generators, which would be feasible in a joint project in the open source context. We expect that 5-10 years are needed to develop, successively, such a generic ALG framework and that considerable manpower and data sources are needed. In Europe, this would ideally be the scope of EU-funded projects. Hot topics such as the decline of pollinators such as honeybees (Potts *et al.*, 2010, Horn, 2017), evaluating and improving the effectiveness of the CAP reform (Pe'er *et al.*, 2014), or the safe provisioning of the full bundle of ecosystem services (Raudsepp-Hearne *et*

al., 2010) emphasise that investing in developing a generic, modular ALG would not only pay off well but might actually be crucial.

3.15 ACKNOWLEDGEMENTS

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4 MITIGATING BIOENERGY-DRIVEN BIODIVERSITY DECLINE: A MODELLING APPROACH WITH THE EUROPEAN BROWN HARE

This chapter is based on a manuscript:

Langhammer, M., Grimm, V. (2019): Mitigating bioenergy-driven biodiversity decline: a modelling approach with the European brown hare. *Ecological Modelling* (in review).

4.1 ABSTRACT

The cultivation of energy crops leads to direct and indirect land use changes that impair the biodiversity of the agricultural landscape. In our study, we analyse the effects of mitigation measures on the European brown hare (*Lepus europaeus*), which is directly affected by ongoing land use change and has experienced widespread decline throughout Europe since the 1960s. Therefore, we developed a spatially explicit and individual-based ecological model to study the effects of different landscape configurations and compositions on hare population development. As an input, we used two 4×4 km large model landscapes, which were generated by a landscape generator based on real field sizes and crop proportions. The crops grown annually are evaluated in terms of forage suitability, breeding suitability and crop diversity for the hare. In six mitigation scenarios, we investigated the effects of a 10 % increase in the following measures: (1) mixed silphie, (2) miscanthus, (3) grass-clover ley, (4) alfalfa, (5) set-aside, and (6) general crop diversity. All mitigation measures had significant effects on hare population development. Compared to the base scenario, the relative change in hare abundance ranged from a factor of 0.56 in the grass-clover ley scenario to -0.16 in the miscanthus scenario. The mitigation measures of mixed silphie, grass-clover ley and increased crop diversity led to distinct increases in hare abundance in both landscapes (> 0.4). The results show that both landscape configuration and composition have a significant effect on hare population development, which responds particularly strongly to compositional changes. The increase in crop diversity, e.g., through the cultivation of alternative energy crops such as mixed silphie and grass-clover ley, proves to be beneficial for the brown hare.

4.2 INTRODUCTION

The increased cultivation of energy crops in Germany and Europe in recent years has led to extensive direct and indirect land use changes, which have an important but not yet quantified impact on biological diversity (Dauber *et al.*, 2010). In particular, land competition triggered by biomass cultivation affects other forms of land use, such as conventional food production, organic farming, set-aside and biotope connectivity (Harvey & Pilgrim, 2011, Steinhauser *et al.*, 2015, Dauber & Miyake, 2016). The associated land use changes lead to reduced habitat diversity (heterogeneity), and increasing field margins and fringe structures are lost due to the expansion and merging of fields (Butler *et al.*, 2010, Brandt & Glemnitz, 2014).

In connection with the ongoing intensification of agriculture, many animal species are threatened in their habitats (e.g., de Chazal & Rounsevell, 2009, Sauerbrei *et al.*, 2014). While there are numerous studies on the effects of land use change on birds (e.g., Lemoine *et al.*, 2007,

Butler *et al.*, 2010), studies on mammals are rare. The European brown hare (*Lepus europaeus*) is an important representative of the agricultural landscape, and its population has been declining in Europe since the 1960s. Studies have shown that the brown hare has been directly affected by the intensification of agriculture and its side effects in recent decades; these impacts include a higher proportion of monocultures on larger fields, the loss of crop diversity and semi-natural habitats and more intensive management activities (e.g., Smith *et al.*, 2005, Baldi & Farago, 2007, Pépin & Angibault, 2007).

However, there is still a considerable need for research to clarify the causes of these impacts. Despite extensive wildlife studies in recent decades, estimates and evaluations of population trends are still not sufficiently possible due to the lack of long-term and large-scale population data. To understand the ecological significance of agricultural effects on brown hare populations and the causes of their widespread decline, habitat use in space and time must be studied more intensively.

Agricultural fields serve as both foraging and reproduction habitat for the brown hare. For foraging, hares select arable crops (e.g., wheat, barley and sugar beet) and weeds (e.g., clover and corn poppy), especially after cereal crops are harvested (Reichlin *et al.*, 2006). During most of the breeding season, hares prefer arable crops and habitat structures that provide cover from predators and unfavourable weather conditions, and this practice is particularly important for the survival of leverets (Smith *et al.*, 2004). Thus, their life cycle is directly dependent on the configuration (landscape structure) and composition (arable crops and other land use types) as well as the management of the fields.

The proportion of land that is composed of cultivated energy crops in Germany has risen considerably in the last 10 years. In 2015, an additional 0.6 million ha of land was needed for energy crops compared to the value in 2008 (Destatis, 2018). However, recent crop cultivation data show that biomass production from energy crops has remained almost unchanged for the past four years (Destatis, 2018). Energy crops are mainly used for biogas and biofuel production. The most important crop for biogas plants is maize, but biogas substrates are also supplied by cereal crops and grain cereals, grasses from arable and permanent grassland, sugar beet and other energy crops. Oilseed rape is the most important energy plant for biofuels, and biodiesel is obtained from it. However, cereals, sugar beets and maize are also used for biofuel production. Maize (18.2% of arable land in 2017), winter rape (11.2%), and winter wheat (26.6%) dominate German agriculture (Destatis, 2018). However, most of the maize is silage maize for feed production.

The negative effects of the large-scale cultivation of energy crops and the associated land use change on biodiversity have been described in numerous studies (e.g., Gevers *et al.*, 2011,

Everaars *et al.*, 2014, Petrovan *et al.*, 2017). Maize and rape are often cultivated in large monocultures, and above a certain height of vegetation, they are not only not suitable for foraging but also too dense for hares. As a consequence, large areas of their home ranges are rendered useless, and hares have to move longer distances to more favourable habitats (Lewandowski & Nowakowski, 1993). An additional effect of the increased proportion of energy crops is a lower overall diversity of arable crops on the landscape and the expansion of arable land to include marginal lands. Both crop diversity and marginal lands are important habitat characteristics for the brown hare (Mayer *et al.*, 2018).

The European Union is trying to limit the negative effects of land use change on agricultural biodiversity through the use of various policies, such as the greening of farming (Regulation (EU) No 1307/2013). Farmers receive an area-based payment for various farming practices that benefit the environment and the climate, including diversifying crops, maintaining permanent grassland and dedicating 5% of arable land to ecologically beneficial elements (i.e., ecological focus areas, EFAs). However, recent studies suggest that the current measures are not sufficient to adequately protect the biodiversity of agricultural landscapes (Pe'er *et al.*, 2014, Pe'er *et al.*, 2017).

In this study, we want to analyse and compare the benefits of a range of different greening measures that are eligible as EFAs in the framework of the EU agricultural subsidy for the brown hare. In particular, this is the cultivation of the alternative energy crops of mixed silphie (*Silphium perfoliatum*), miscanthus (*Miscanthus x giganteus*) and grass-clover ley, the cultivation of the legume alfalfa (*Medicago sativa*), and the increase of set-aside and crop diversification.

We selected mixed silphie, miscanthus and grass-clover ley as alternative energy crops because they are considered to be more environmentally friendly than annual energy crops. The Asteraceae silphie (*Silphium perfoliatum*) is bee-friendly and can remain in the field for up to ten years. Under good conditions, mixed silphie has a similar yield to that of maize and is therefore a realistic alternative for biogas production. The reed grass miscanthus (*Miscanthus x giganteus*), sometimes called "elephant grass", has a harvest period of over twenty years. With its high biomass yield, it is also a remarkable alternative for biofuel production. By 2018, both mixed silphie and miscanthus are eligible for use on greening areas as a result of the mid-term review of the Common Agricultural Policy (CAP). It can therefore be assumed that the proportion of both energy crops will continue to increase in the coming years. For example, the silphie cultivation has more than doubled to over 3,000 ha in 2017 over than value in 2016. Grass-clover ley is a mix of legumes and grasses, which allows multiple harvesting with a high

yield level of biomass. It is used as livestock feed as well as for energy production in biogas plants.

Alfalfa (*Medicago sativa*) is a forage legume for hares, and it becomes important in the spring-summer when the digestibility of cereals is reduced due to maturation or harvest that has taken place (Santilli *et al.*, 2014). Set-aside is considered a particularly high-quality ecological measure, which on the one hand, creates valuable areas of protection and on the other hand, opens up many possibilities for the cross-linking of biotopes. It has been identified in many studies as a favourable habitat for many animal species on the agricultural landscape and for the brown hare, as it often has a high diversity of plants and is structurally heterogeneous (Reichlin *et al.*, 2006, Gevers *et al.*, 2011, Meichtry-Stier *et al.*, 2014, Langhammer *et al.*, 2017).

Empirically investigating land use scenarios on a larger spatial scale is very time-consuming and is associated with a high effort. Therefore, spatially explicit simulation models are useful tools for testing and analysing different configurations and compositions of agricultural landscapes. By using a defined parameter set, different agricultural landscape mosaics can be generated, which serve as a basis for controlled simulation experiments (Langhammer *et al.*, 2019).

Using a modelling approach, we want to answer the following questions: (1) What effects do selected mitigation measures have on long-term hare population development? (2) Is an individual-based simulation model that works with simplified generated landscapes able to produce robust predictions for hare population development? For this purpose, the effects of different crop distributions on hare population abundance were analysed using three habitat evaluation criteria: suitability as forage habitat, suitability as breeding habitat and regional crop diversity. The crop distributions are based on data from a reference landscape in Brandenburg and the average crop distribution for Germany in 2017. Based on the results, specific solutions for sustainable mitigation measures and the protection of the brown hare will be identified.

4.3 METHODS

We analysed the effects of different mitigation measures in agricultural landscapes on the brown hare. Therefore, we developed an individual-based simulation model, which was implemented in NetLogo (Wilensky, 1999). Input included landscape configurations, which differed in the size and spatial distribution of fields, created by the landscape generator from Engel *et al.* (2012) and Everaars *et al.* (2014).

4.3.1 *Landscape generation*

The applied landscape generator was originally developed to evaluate the impacts of cropping scenarios on different farmland bird species (Engel *et al.*, 2012, Everaars *et al.*, 2014). The model workflow consists of several subsequent steps, whereby only a part of the workflow was used for landscape generation in this study. A complete model description can be found in the original publications.

The landscape generator generates a mosaic of agricultural fields with varying shapes, sizes and edge lengths (Figure 4.1), whereby the landscape configuration depends on the mean field size (in ha). The generation takes place in two steps. First, fields are placed randomly on the landscape grid until all of the area is covered. Second, a correction algorithm replaces all fields that are too small by merging them with neighbouring fields. The emerging field mosaic is adapted to the specified mean field size. For this study, the landscape extent is 4×4 km with a resolution of 10×10 square metres (400×400 grid cells).

4.3.2 *Reference landscapes*

The configuration of the reference landscape *Uckermark* is based on data from a 213 km² area in Brandenburg, north-eastern Germany. The area is part of the long-term research platform *AgroScapeLab Quillow* (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the BioMove Research Training Group (DFG GRK 2118/1). *Uckermark* is characterised by large fields with an average field size of 27.5 ha and a simple landscape structure (Ullmann *et al.*, 2018).

For comparison, a second reference landscape was created from the average data of Germany. The literature provides no average field sizes for Germany, but Brady *et al.* (2012) assumes that there is a correlation between field size and farm size. In 2016, the average farm size in Germany was 61 ha of agricultural land (Destatis, 2018). Accordingly, we assume an average field size of 6.8 ha for our model landscape *Germany*. This makes the field mosaic in *Germany* much more small-scaled and heterogeneous than that in *Uckermark* (Figure 4.1).

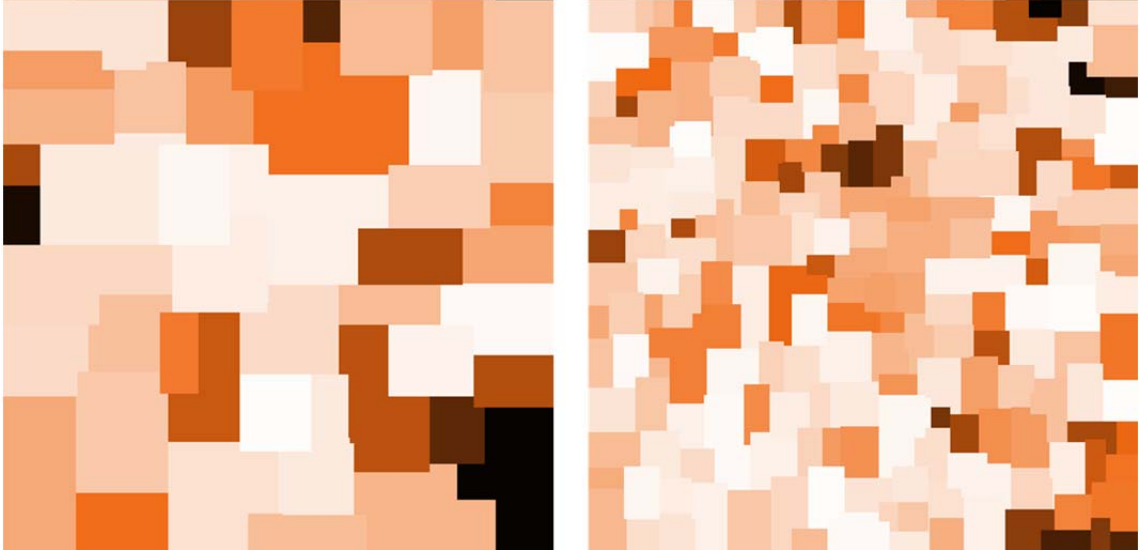


Figure 4.1: Generated agricultural landscapes with an area of 4×4 km. (Left) *Uckermark* reference landscape with an average field size of 27.5 ha. (Right) *Germany* reference landscape with an average field size of 6.8 ha. The colours mark the fields and can be assigned to different crop types.

4.3.3 *Hare model*

The generated agricultural landscape mosaics serve as an input for the individual-based hare model (Figure 4.4). A detailed model description following the ODD protocol (overview, design concepts, details) for describing individual-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010) can be found in the Appendix.

In each time step, which represents one year, crops are assigned to the fields according to the determined crop proportions for each landscape and scenario. Fourteen different crop types are available for selection: alfalfa, barley, beets, grassland, grass-clover ley, maize, miscanthus, oilseed rape, pasture, rye, set-aside, mixed silphie, triticale and wheat. The selection of the crop type per field remains the same throughout each simulation run for each scenario. Thus, as in reality, crops are assigned to the fields each year, and an evaluation for the hare population takes place.

Each grid cell of the landscape is evaluated on the basis of three suitability criteria, which we assumed to be significant for the hare population: (1) suitability as forage habitat F_H , (2) suitability as breeding habitat B_H and (3) regional crop diversity D_C . The values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on expert knowledge drawn from the literature (Figure 4.2, Table 4.2). An overview of the literature on the ecology of the brown hare, which we have used to assess foraging and breeding preferences, is given in the Appendix. Suitability as a foraging habitat specifies the suitability of each crop type as a food source. Suitability as breeding habitat is defined as the probability that a hare will give birth. The value

is related to crop density, crop height and management activities. Crop diversity indicates the distribution and quantity of all crop types in the landscape. The geometric mean of all three variables (F_H , B_H , D_C) results in the habitat suitability value (S_H) for each individual grid cell (Figure 4.2).

$$S_H = \sqrt[3]{F_H \times B_H \times D_C}$$

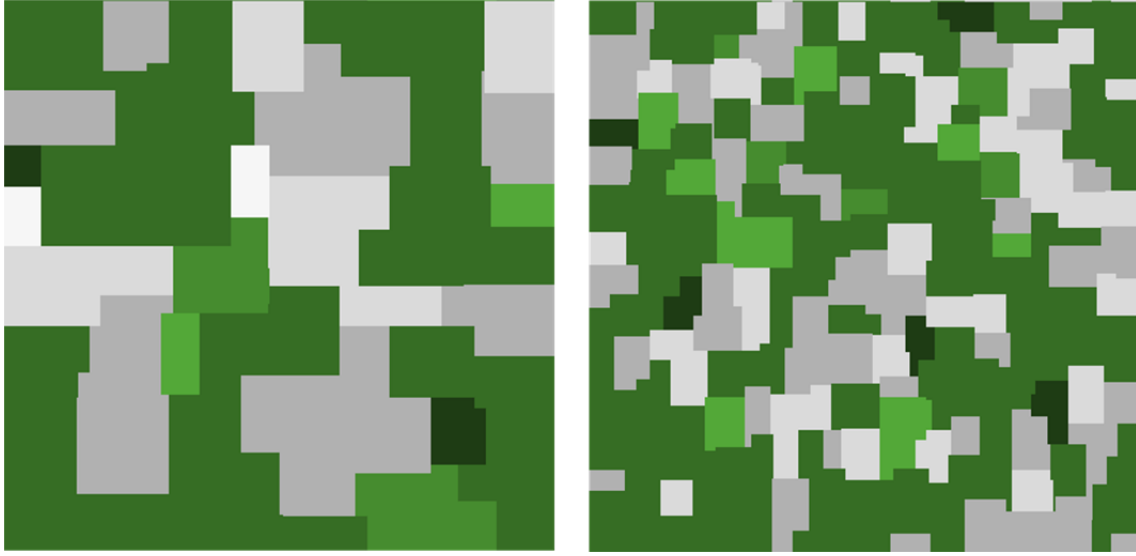


Figure 4.2: Habitat suitability of the base scenarios in *Uckermark* (left) and *Germany* (right) as a result of the geometric mean of suitability as forage habitat, suitability as breeding habitat and crop diversity. The green colours show habitats above the suitability threshold of 0.5. The grey colours show habitats below the suitability threshold of 0.5. Darker green indicates higher suitability, and lighter grey indicates lower suitability.

In the next step, the general suitability of the current hare home ranges is evaluated by calculating the mean value of all habitat suitability values within the home range. Each adult hare has a home range of a given radius, which is, for reasons of simplification, constant and the same for the entire population. In the model, we assume that the home ranges of up to 10 hares can overlap (Figure 4.3). For each additional hare that marks a cell belonging to its home range, the habitat suitability value of the cell is reduced by 0.02. In the next step, the habitat suitability value of the home range is compared to the habitat suitability threshold of 0.5, which indicates the probability of survival. After crop cultivation each year, all hares search within their home range for a suitable position. If this is not possible due to unsuitable habitat quality or a population density that is too high within the search radius, the hares still have two attempts to find a new suitable home range. If they fail all three times, they die. Juveniles that mature are searching for a home range within a larger search radius of 150 cells (1.5 km) prior to the assignment of new crop types. The rules applied here are similar to those for adults: they search for a suitable grid cell, defined by suitability and the requirement that no more than nine hares

use this cell as part of their home range. Then, if the suitability of the entire home range is, such as with the adults, too low, they try again, but die after the third unsuccessful attempt. Thus, the number of adults alive before reproduction takes place is determined by habitat suitability, which in turn, depends on crop types, field configurations, and the density of conspecifics. These factors affect hare distribution and abundance two times per year, for establishing juveniles, and, after new assignments of crops, for established adults.

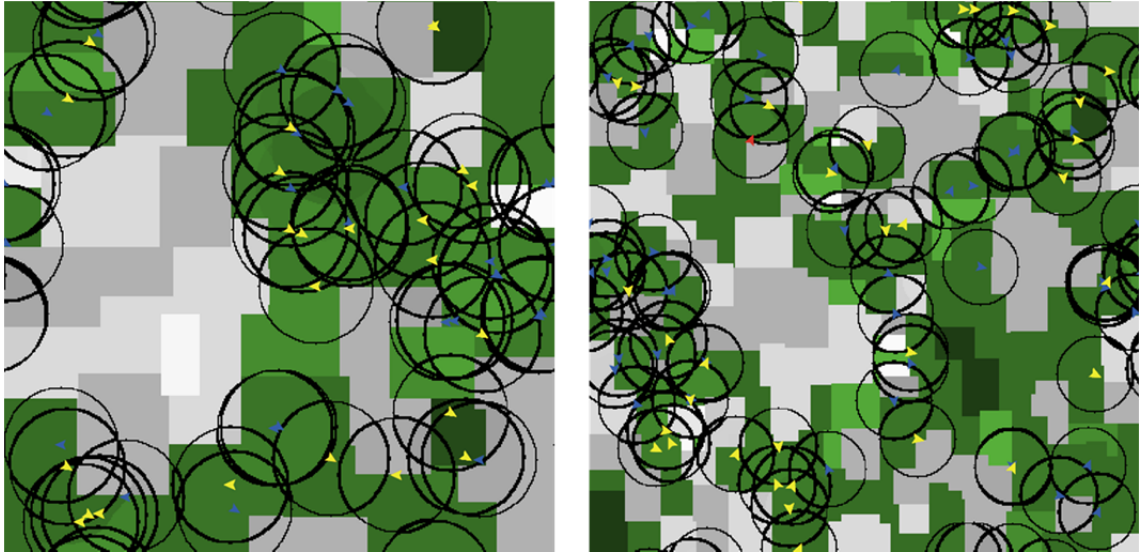


Figure 4.3: Hare home ranges in the base scenarios in *Uckermark* (left) und *Germany* (right). Blue arrows mark males, red arrows indicate females and yellow arrows indicate females with juveniles. The home ranges are represented as circles surrounding the hares. The green colours show habitats above the suitability threshold of 0.5. The grey colours show habitats below the suitability threshold of 0.5. Darker green indicates higher, and lighter grey indicates lower suitability. Note the tracking of habitat suitability by the distribution of hare home ranges and the partly high overlap of home ranges.

At the end of a time step, reproduction takes place, and mortality rates are applied for juveniles and adults. The mortality rates reflect losses due to predation, environmental impacts (e.g., weather conditions) and accidents and are derived from the investigations of Marboutin & Peroux (1995).

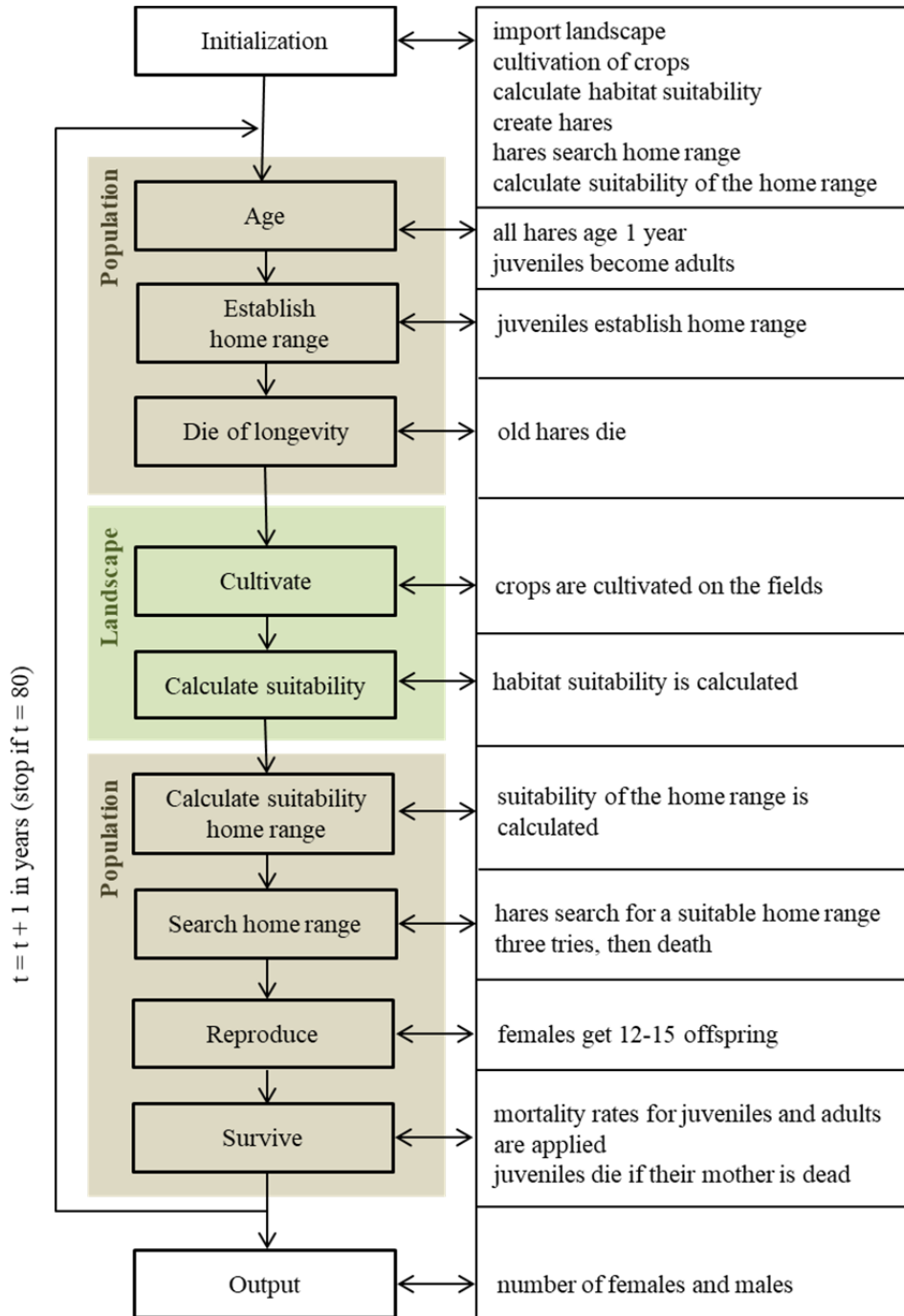


Figure 4.4: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 7 *Sub-models* in Appendix C1.

4.3.4 Hare parameterization

It is undisputed that the configuration and composition of crops in an agricultural landscape have a significant effect on the brown hare population, but there are only a few studies that quantitatively demonstrate the importance of specific crops for the hare. Based on these studies,

we derived crop suitability values for forage and breeding habitat (Table 4.1). If we did not find any information about a certain crop, we derived the value of a similar crop (e.g., for cereals) or assumed a mean value of 0.5.

Table 4.1: Habitat characteristics of the crop types considered in this study. The suitability values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on the literature. Values in italics have an intermediate value of 0.5 due to a lack of information to estimate them. Details can be found in the Appendix C2.

| Crop type | Suitability as forage habitat (F_H) | Suitability as breeding habitat (B_H) |
|------------------|---|---|
| Alfalfa | 0.75 | 0.25 |
| Barley | 0.75 | 0.75 |
| Beets | 0.75 | <i>0.50</i> |
| Grassland (ext.) | 0.75 | 0.75 |
| Grass-clover ley | 0.75 | 0.50 |
| Maize | 0.50 | 0.25 |
| Miscanthus | 0.00 | 0.25 |
| Oilseed rape | 0.25 | 0.25 |
| Pasture (int.) | 0.25 | 0.25 |
| Rye | <i>0.50</i> | <i>0.50</i> |
| Set-aside | 1.00 | 1.00 |
| Mixed silphie | <i>0.50</i> | 0.75 |
| Triticale | <i>0.50</i> | <i>0.50</i> |
| Wheat | 0.75 | 0.75 |

The literature shows that the preference of forage crops is strongly dependent on the season and the general landscape structure. For this reason, general statements regarding a crop type can be made only to a limited extent. For our analyses, we assumed a spring to summer situation because this is the period in which most breeding takes place (Tapper, 1987, Flux & Angermann, 1990). Because our model landscape consists solely of fields with crops, we have not considered wild grasses and herbs, which are also important food plants for hares and occur primarily in other landscape structures, such as field margins or unused areas. To assess the suitability of crops as breeding habitats, we considered conditions such as crop height and management activities in spring and summer. We have not taken into account other landscape structures that also represent important breeding habitats, such as field margins. We have also not included other important factors for breeding success, such as weather conditions (Hackländer *et al.*, 2002, Smith *et al.*, 2005) or pesticides. The influence of predators is indirectly considered by the height of vegetation and the survival rates.

Many studies show that habitat diversity, in general, including crop diversity, has a clear positive effect on hare populations (Tapper & Barnes, 1986, Lewandowski & Nowakowski, 1993, Reichlin *et al.*, 2006, Santilli & Galardi, 2016). Crop diversity not only results in a richer food supply but also results in a spatial and temporal separation of management activities, which limits the impact on the mortality of the leverets. Following this, we related the crop diversity value to the number of crops in three levels (Table 4.2).

Table 4.2: Crop diversity in terms of the number of crop types in the model landscapes. The crop diversity value ranges from 0.0 (not suitable) to 1.0 (very well-suited).

| Number of crops types | Crop diversity D_c |
|-----------------------|----------------------|
| 5 – 10 | 0.60 |
| 11 – 13 | 0.80 |
| > 14 | 1.00 |

The hare home ranges in the model landscapes are distributed in a circle around the individuals. In reality, the sizes of hare home ranges depend on the landscape structure and food supply, and the literature shows significant variations in mean home range sizes during the breeding season (Broekhuizen & Maaskamp, 1981, Tapper & Barnes, 1986, R  he & Hohmann, 2004, Smith *et al.*, 2004, Bertolino *et al.*, 2013). In small-scale heterogeneous landscapes, home ranges are smaller than those in landscapes with large monocultures. Following Ullmann *et al.* (2018), we set the hare home ranges in the Brandenburg scenarios to 55 ha. Another landscape in South Germany, Bavaria, investigated by Ullmann *et al.* (2018) with an average field size of 3 ha, showed an average hare home range of 19 ha. Based on these data, we interpolated the presumed average value of Germany to be 25 ha. This value is comparable to the values of 21 ha in R  he & Hohmann (2004) and 29 ha in Broekhuizen & Maaskamp (1981). A home range of 25 ha corresponds to a radius of 28 grid cells (280 m) in the model (*Uckermark*), i.e., a home range of 55 ha to 42 grid cells (420 m) in *Germany*.

Home ranges also vary over the course of a year. Bertolino *et al.* (2013) determined mean home range sizes of 30.5 – 33.8 ha in summer and 49.5 – 85.9 ha in winter. Despite these relative adaptations to spatial conditions and seasons, hares are a sedentary species, and studies show that they do not significantly expand their home range if their energy requirements are not covered (Smith *et al.*, 2005, Bray *et al.*, 2007). Thus, the hares in the model search only within their home ranges for a new, more suitable place, from which the new home range is created. Females and males have the same home range sizes in the model, although this value can be different in reality.

As in reality, the home ranges of several individuals can overlap in the model. However, a grid cell can only be assigned to the home range of a maximum of ten hares. This method indirectly simulates competition for habitat and avoids unnatural clumping of too many individuals per area. The overlap of home ranges of individual hares fluctuates strongly in reality; in densely populated areas, there is a strong overlap (Rühe & Hohmann, 2004).

Each year, all females have 12 to 15 offspring (Marboutin *et al.*, 2003). Because the model calculates in annual steps, juveniles do not have their own home range in the year of birth. In the following year, they are considered sexually mature and are looking for their own home range.

Sensitivity analysis

We conducted sensitivity analysis to understand how the variation in key parameters affects model predictions. Focal parameters were the radius of the home range and the threshold for habitat suitability. To test the sensitivity, we varied the values of the two parameters in the base scenario *Uckermark* and calculated the resulting hare population abundance. The *threshold suitability* parameter was varied from 0 to 1 in 0.1-interval steps. The parameter *home range radius* varied from 10 to 50 grid cells in steps of five. Furthermore, we performed sensitivity analysis by reducing the weighting of the crop diversity criterion. Instead of weighting one-third compared to forage and breeding suitability, we tested one-quarter, one-sixth and zero. To test the influence of hare home range overlap, we varied the number of possible overlaps from 0 to 10 hares in steps of two. The sensitivity analyses were based on 100 replicates with the same input parameters as that of field size and number of crops.

4.3.5 *Scenarios*

The basis for our simulations are two recent crop distributions, one of the reference landscapes in Brandenburg (UM, *Uckermark*), Germany and one average distribution for Germany in 2017 (GER, *Germany*). The crop data for *Uckermark* (GIS InVeKoS, 2015) were provided by the Leibniz Centre for Agricultural Landscape Research (ZALF). Because the proportions of the rarely cultivated crops (< 1%) were too small to be consistent in the model landscape, we selected the ten most common crops (in total 97%) cultivated in this landscape for the base scenario (UM). The data for the German average scenario are derived from the Federal Statistical Office Germany (Destatis, 2018). To compare both landscapes, we also selected the ten most common crops for the base scenario (GER). In both landscapes, the proportions of the

ten most common crops were recalculated for the entire area (Table 4.3). However, because the fields cannot be filled to the exact percentage, there are minor deviations from the set values.

Maize and winter oilseed rape are the most frequently cultivated energy crops in *Uckermark* as well as in *Germany*. A total of 14.5% of maize is cultivated in the reference landscape in Brandenburg. Most of it is silage maize for feed production (97%), and 3% is used for biogas production. However, there is a high proportion of winter oilseed rape (18.1%), mainly used for biofuel production. The German average maize cultivation in 2017 was 15.8% of agricultural land, but locally, the proportion can be much higher. Approximately 5% of this is cultivated land is used for biogas production. In contrast, the German average of oilseed rape cultivation (7.4% of agricultural land) is much lower than the percentage in the reference landscape in Brandenburg.

Table 4.3: The simulated crop proportions for each of the 14 crops and for each scenario. The two base scenarios (UM, GER) match the crop distributions in the reference landscape Uckermark and the average distribution in Germany 2017 for the ten most common crops. For each base scenario, six mitigation strategies are explored: three alternative energy plant scenarios and three crop composition scenarios. For the alternative energy plant scenarios (AE1-AE3), the proportions of mixed silphie, miscanthus and grass-clover ley were increased by 10% in each case. For the first two crop composition scenarios (CC1, CC2), the proportions of alfalfa and set-aside were increased by 10% in each case. Crop composition scenario 3 (CC3) integrates all 14 crops in the landscape. Key changes are displayed in bold. Further details on the scenarios are provided in the Methods section.

| | Crop proportion [%] | | | | | | | | | | | | | |
|------------------|---------------------|-------------|-------------|-------------|-------------|-------------|------|------|-------------|-------------|-------------|-------------|-------------|------|
| | UM | AE1 | AE2 | AE3 | CC1 | CC2 | CC3 | GER | AE1 | AE2 | AE3 | CC1 | CC2 | CC3 |
| Wheat | 37.5 | 37.5 | 37.5 | 37.5 | 37.5 | 37.5 | 23.2 | 20.7 | 20.7 | 20.7 | 20.7 | 20.7 | 20.7 | 14.0 |
| Oilseed rape | 18.7 | 18.7 | 8.7 | 18.7 | 10.2 | 10.2 | 11.6 | 8.3 | 8.3 | 0.0 | 8.3 | 0.0 | 0.7 | 5.6 |
| Maize | 15.0 | 5.0 | 15.0 | 5.0 | 15.0 | 15.0 | 9.3 | 17.8 | 7.8 | 16.1 | 7.8 | 16.1 | 17.8 | 12.0 |
| Barley | 9.2 | 9.2 | 9.2 | 9.2 | 9.2 | 9.2 | 5.9 | 11.3 | 11.3 | 11.3 | 11.3 | 11.3 | 11.3 | 7.7 |
| Grassland (ext.) | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.0 | 12.5 | 12.5 | 12.5 | 12.5 | 12.5 | 12.5 | 8.5 |
| Pasture (int.) | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.0 | 18.1 | 18.1 | 18.1 | 18.1 | 18.1 | 18.1 | 12.3 |
| Beets | 4.5 | 4.5 | 4.5 | 4.5 | 4.5 | 4.5 | 5.0 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 5.0 |
| Alfalfa | 1.5 | 1.5 | 1.5 | 1.5 | 10.0 | 1.5 | 5.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 5.0 |
| Set-aside | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 10.0 | 5.0 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 10.0 | 5.0 |
| Rye | 1.4 | 1.4 | 1.4 | 1.4 | 1.4 | 1.4 | 5.0 | 3.6 | 3.6 | 3.6 | 3.6 | 3.6 | 3.6 | 5.0 |
| Triticale | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 5.0 |
| Silphie | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 |
| Miscanthus | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 5.0 |
| Grass-clover ley | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 5.0 |

To mitigate the negative effects of a high proportion of maize and oilseed rape on the brown hare, we investigated various mitigation measures. Three of these measures focus on the effects of alternative energy plants (mixed silphie AE1, miscanthus AE2 and grass-clover ley AE3) and three on the effects of more beneficial crop compositions (alfalfa CC1, set-aside CC2 and crop diversity CC3). For the first five scenarios, we increased the proportion of the respective crop or set-aside to 10% each and reduced the proportion of maize (mixed silphie and grass-clover ley scenario) and oilseed rape (miscanthus, alfalfa and set-aside scenario) accordingly. The percentage of each crop in each scenario is shown in Table 4.3. For the crop diversity scenario (CC3), we integrated all 14 crops into the landscape, with a proportion of at least 5% each.

As a result, we compared the six strategies regarding their mitigating effects to provide management recommendations for the protection of the brown hare.

4.3.6 Data analysis

We ran each scenario for a total of 80 years. However, the population abundance was determined after only 30 years because the population had to stabilise in the first years. Thereafter, the number of adults (females and males) was recorded annually. From each scenario, 100 replicates were run. Each replicate differed in the initial distribution of hares and crops in the landscape. The total number of simulations was 1600.

Boxplots show the effects of the mitigation measures on the hare abundance for each landscape. To compare and rank the effects of different mitigation measures, we calculated the relative change of hare densities compared to the base scenario. Mann–Whitney U tests were performed for each scenario to test the significance of the changes. All statistical calculations were carried out with R 3.4.3. (R Core Team, 2017).

4.4 RESULTS

The hare abundance in the base scenario *Uckermark* (3.9 individuals per 100 ha) is comparable to the hare counts in the reference landscape of 5 individuals per 100 ha (data provided by the BioMove Research Training Group DFG GRK 2118/1). In *Germany*, the mean abundance in the base scenario is approximately twice as high as that in *Uckermark* (8.2 individuals per 100 ha). Comparisons with average data for Germany are difficult because hare densities can differ greatly between regions. Strauß *et al.* (2008) showed average population densities between 5.4 individuals per 100 ha in East Germany and 23.9 individuals per 100 ha in Northwest Germany.

The average German hare density in 2016 was 12 individuals per 100 ha (Greiser *et al.*, 2018). All mitigation measures had significant effects ($P \leq 0.001$) on the hare population abundance (Table 4.4, Figure 4.5). However, the relative effect of the mitigation measures was slightly smaller in *Uckermark* (max. 0.41) than in *Germany* (max. 0.56). In general, the mean standard deviation of all scenarios was slightly higher in *Germany* (0.5 individuals per 100 ha) than in *Uckermark* (0.4 individuals per 100 ha).

Table 4.4: Factors by which hare abundances changed relative to the base scenarios.

| Landscape | Scenario | Individuals per km ² | Abs. change | Rel. change |
|-----------|----------|---------------------------------|-------------|-------------|
| Uckermark | Base | 5.4 | | |
| | AE1 | 7.4 | 1.92 | 0.35 |
| | AE2 | 6.7 | 1.24 | 0.23 |
| | AE3 | 7.4 | 1.92 | 0.35 |
| | CC1 | 5.5 | 0.08 | 0.01 |
| | CC2 | 6.4 | 0.96 | 0.18 |
| | CC3 | 7.4 | 1.94 | 0.36 |
| Germany | Base | 8.3 | | |
| | AE1 | 14.9 | 6.58 | 0.79 |
| | AE2 | 7.8 | -0.51 | -0.06 |
| | AE3 | 14.9 | 6.61 | 0.79 |
| | CC1 | 8.9 | 0.54 | 0.07 |
| | CC2 | 11.0 | 2.64 | 0.32 |
| | CC3 | 16.3 | 7.99 | 0.96 |

Impact of alternative energy crops

The relative effect of the alternative energy crops was significantly different in both landscapes. In *Uckermark*, the increase of the energy crops of mixed silphie and grass-clover ley influenced the hare abundance most positively (each 0.41). In comparison, the energy crop of miscanthus had a minor positive effect (0.14). Additionally, in *Germany*, the increase of mixed silphie and grass-clover ley had the largest positive effect on hare abundance (0.56). In contrast to *Uckermark*, miscanthus had a negative effect in *Germany* (-0.16).

Impact of modified crop compositions,

The relative effects of the other crop composition modifications were again smaller in *Uckermark* (max. 0.26) than in *Germany* (max. 0.53). The most positive effect in both landscapes included the crop diversity scenario, but that in *Uckermark* was only approximately

half as that in *Germany* (0.26 in *Uckermark*, 0.53 in *Germany*). Alfalfa had a minor positive effect in both landscapes (0.08 in *Uckermark*, 0.12 in *Germany*), while the increase in set-asides had a moderate effect of 0.19 in *Uckermark* and 0.26 in *Germany*.

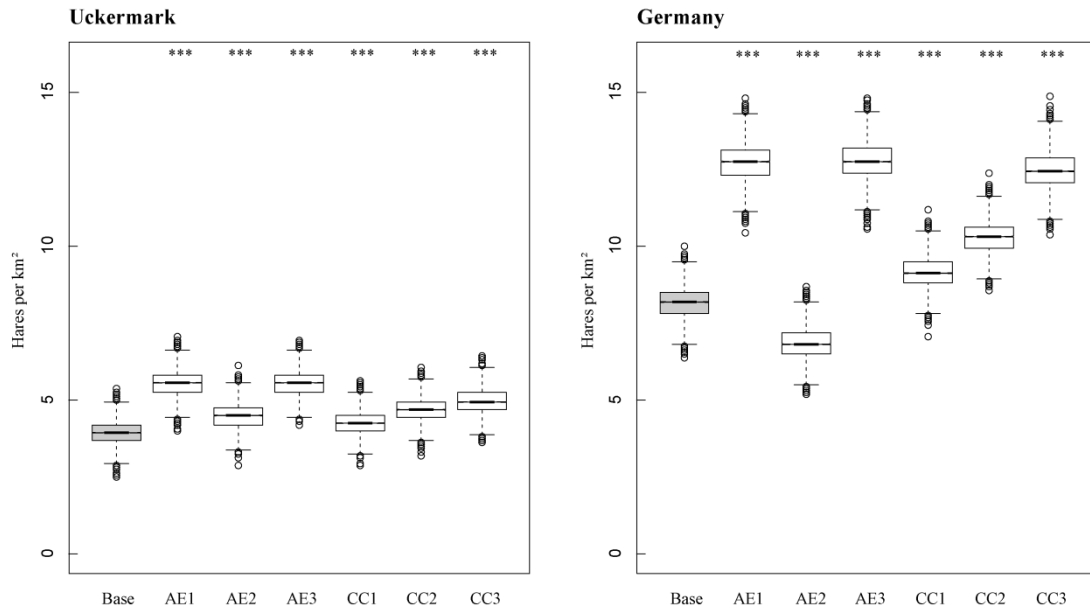


Figure 4.5: Effect of the implemented mitigation scenarios on hare abundance. Stars specify the level of significance, *** $P \leq 0.001$, for each scenario relative to the base scenario.

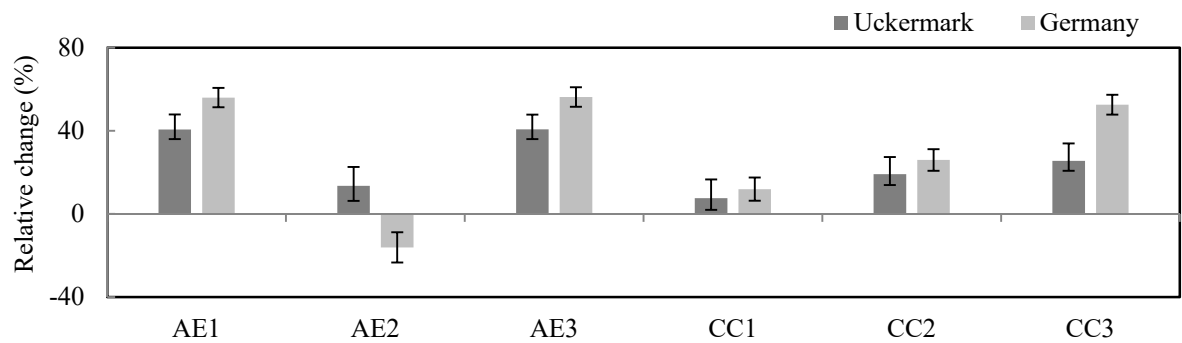


Figure 4.6: Relative changes in hare densities from the base scenario values. Bars indicate standard deviation of the replicates.

Overall, the mitigation measures of mixed silphie, grass-clover ley and increased crop diversity led to distinct increases in hare abundances in both landscapes (> 0.4).

Sensitivity analyses

Figure C 2 in the Appendix shows that a reduction of the hare home range radius in the model correlates with an increase in population abundance ($R = -0.73$). A small home range of 3.1 ha (corresponding to a radius of 10 grid cells in the model) leads to a hare density of 84.2 individuals per 100 ha. In turn, a large home range of 78.5 ha (corresponding to a radius of 50 grid cells in the model) leads to low hare densities of 6.1 individuals per 100 ha.

The threshold for habitat suitability strongly influences hare population development ($R = -0.95$). At a threshold higher than 0.5, the population abundance decreases rapidly until it dies out at a threshold of 0.9 (Figure C 3). Below a threshold of 0.5, the hare population stabilises at a density of 6-7 individuals per 100 ha in the base scenario *Uckermark*.

Furthermore, there is a strong correlation between the number of potential home range overlaps per grid cell in the model and the hare abundance ($R = 0.9$). A huge maximal overlap of 10 hare home ranges per grid cell leads to a population density of 6.4 individuals per 100 ha in the base scenario *Uckermark* (Figure C 4). On the other hand, when no overlap was allowed, it led to a population density of 0.4 individuals per 100 ha.

In contrast to the previous model parameters and settings, a reduction in the weighting of the crop diversity criterion had almost no effect on the hare population abundance (Figure C 5). It was weighted with one-third in comparison to the forage and breeding suitability of a crop in the default settings of the model. A reduction to one-quarter, one-sixth or zero weighting did not lead to any significant changes in hare population abundance.

4.5 DISCUSSION

We used an individual-based model to investigate the influence of mitigation measures in agricultural landscapes on the brown hare. The results show that it is possible to predict population development under modified habitat conditions using the model. The examined scenarios resulted in different responses of the hare population, from minor to large responses. It turned out that not only the composition of the landscape (the number and proportion of crops) but also the configuration (the field sizes) play an important role in hare population development.

The model landscapes used in this study vary in field size and the proportion and distribution of crops. In the German average landscape, where the field sizes are significantly smaller than those in the *Uckermark*, mitigation measures had a stronger impact. This result was mainly caused by the smaller hare home ranges in *Germany*, which allowed an overall higher

population abundance on the landscape. Because the habitat requirements of hares are met more easily in small-scale heterogeneous landscapes, hares do not have to move long distances, as in landscapes with large monocultures (Broekhuizen & Maaskamp, 1981, Tapper & Barnes, 1986, R  he & Hohmann, 2004, Smith *et al.*, 2004, Bertolino *et al.*, 2013). Within smaller home ranges, hares benefit more quickly from mitigation measures, as the probability of favourable crop types in their home range is higher. Thus, smaller field sizes can be regarded as mitigation strategies by themselves. In contrast, the probability of favourable crop types decreases in landscapes with large fields. The model results show that not only the configuration of the landscape affects hare population development but also the composition, i.e., the number and distribution of the crop types. Bennett *et al.* (2006) found that spatial configuration had less influence on biota than did the composition of a landscape. In comparison, Fahrig *et al.* (2011) recommend the consideration of a ‘functional landscape heterogeneity’, in which compositional heterogeneity and configurational heterogeneity were examined separately and were species-related. To evaluate the crop types for the brown hare in the model, we based our assessment on the literature. Unfortunately, there were few concrete data available; thus, we mostly had to translate qualitative assessments into foraging and breeding values. In the following, we discuss the model results with regard to their consistency in relation to the literature references.

In *Uckermark*, the proportion of wheat, which is a favourable crop for hares, is much higher (37.5%) than that in *Germany* (20.7%). Winter wheat in the form of seedlings is especially important in spring (Pepin & Angibault, 2007, Bertolino *et al.*, 2011). Although the proportion of maize and rape in *Uckermark* is comparably high (33.7%), the negative effects are compensated by wheat. Therefore, the addition of 10% hare-friendly crops had a lower overall effect than that in *Germany*. In total, the mitigation measures had a more moderate effect in *Uckermark* and a stronger effect in *Germany*. This result indicates that the general composition of the landscape must be considered when mitigation measures are planned. The mitigating effect depends not only on one crop replacement but also on the proportion and distribution of other crops in the landscape.

Energy crop cultivation can be diversified with alternative energy crops. The alternative energy scenarios show that mixed silphie and grass-clover ley have a strong positive effect on hare population development, while miscanthus has a little to a negative effect, which is dependent on the landscape. Mixed silphie offers coverage for hares from the beginning of April. If the stands are harvested by mid-September, the rootstock will form new rosette leaves until snow falls. These scenarios offer good cover in autumn (e.g., protection from wind, rain and predators). A perennial grass-clover ley offers a high level of cover and forage availability to hares (Santilli, 2006) and is more attractive than pastures (Frylestam, 1986). Clover as a forage legume becomes especially important in spring and summer when cereals start to ripen and their

digestibility is reduced (Santilli *et al.*, 2014) or after they are harvested (Reichlin *et al.*, 2006). The bioenergy crop miscanthus, even the young sprouts, are entirely avoided as food (Petrovan *et al.*, 2017).

The second part of crop composition measures also showed different effects, i.e., from low to high. The addition of the legume alfalfa had a minor effect in both landscapes. Although alfalfa is a forage plant for hares, harvesting takes place several times a year, leading to high leveret losses, represented in the model by low breeding habitat suitability. Increasing set-asides had a moderate positive effect in both landscapes. Set-asides with low to medium height and favourable plant composition are a very important foraging habitat for hares (Reichlin *et al.*, 2006, Gevers *et al.*, 2011, Meichtry-Stier *et al.*, 2014, Langhammer *et al.*, 2017). These landscapes offer a high amount and variety of wild herbs and grasses, which are an essential part of the hare diet. However, if the vegetation becomes too high and dense, hares avoid these areas (Schai-Braun *et al.*, 2013). The strongest positive effect of the crop composition measures in both landscapes was the increase in crop diversity from 10 to 14 crops, with at least a 5% proportion for each crop. Many studies demonstrate that brown hare populations are strongly positively influenced by habitat diversity (variety of crops), as they need protection and forage plants year round (e.g. Tapper & Barnes, 1986, Lewandowski & Nowakowski, 1993, Vaughan *et al.*, 2003, Santilli & Galardi, 2016).

Our results show that an increase in crop diversity in the landscape has a beneficial effect on hares, as they have more opportunities to find year-round forage and cover. One way to achieve this benefit is to cultivate alternative energy crops that are beneficial for hares. The extent to which the proportion of mitigation measures in a real landscape should be increased to stabilise the population in the long term would have to be investigated more precisely in further studies. Oppermann *et al.* (2012) suggest 10% and Meichtry-Stier *et al.* (2014) at least 14% of areas should be covered by high-quality agri-environmental measures or semi-natural habitats to sustainably protect agricultural biodiversity.

Using the individual-based hare model, controlled simulation experiments can be performed, and useful predictions can be made. The results show that it is possible to achieve reliable results with the model even without a profound data background. Nevertheless, the model is based on many simplifying assumptions, which are often a compromise between resolution and data availability. For example, the landscapes are quite artificial and contain no landscape structures other than agricultural fields. Although hares are mainly found in fields (> 70%), they also use other habitats, such as meadows, woodlands, shrubby habitats, and spontaneous vegetation (27.5%) (Reichlin *et al.*, 2006, Bertolino *et al.*, 2011). Additionally, field margins are a favourite foraging and breeding habitat due to the often higher diversity and height of growth.

In principle, it is possible to represent landscape structure and dynamics with higher resolution, e.g., by using a complex simulation system for hares and other animal species, ALMaSS (Topping *et al.*, 2003), which simulates population development based on real landscapes at a spatial resolution up to 1 m². One advantage of ALMaSS is that even narrow landscape structures, such as field margins, can be mapped, and the high temporal resolution of one day enables the precise representation of animal and management activities. However, due to the complexity, the model is rather difficult to modify, parameterize, and analyse.

The implementation of mitigation measures in the model also represents a simplification. In reality, eligible greening measures are not implemented equally because farmers can choose among several options. For example, ecologically valuable edge structures, such as field edges and buffer strips, are implemented much less frequently than is the cultivation of eligible crops, such as nitrogen-fixing crops (Pe'er *et al.*, 2017).

In the model, a time step represents one year, even if the spring/summer conditions are assumed. In reality, crops are mainly used on a seasonal basis. Wheat is especially important in spring, maize in spring and summer and stubble in autumn. Bertolino *et al.* (2011) and Reichlin *et al.* (2006) show that in May, more than 75% of the food supply consists of cereals. In summer, when the cereals have been harvested, hares shift to other crops such as Fabaceae, grasses and herbs. However, the seasonal characteristics of crops are indirectly included in the model in the form of forage and breeding estimates. We could not parameterize the weighting of the three criteria for forage, breeding and crop diversity because there are no data available for them. However, the sensitivity analysis shows that a reduction in the weighting of the crop diversity criterion had almost no effect on hare population abundance. Other important population influencing factors are indirectly included as mortality rates in the model, such as predation, weather conditions and diseases.

The hare home ranges in the model do not emerge dynamically but are fixed with a certain radius. It follows that, despite relative adaptations to spatial conditions and seasons, hares are a sedentary species, and studies show that they do not significantly expand their home range if their energy requirements are not covered (Smith *et al.*, 2005, Bray *et al.*, 2007). There are other models that use fixed home ranges for species, e.g., for birds in Scherer *et al.* (2016) and Everaars *et al.* (2014). Nevertheless, there is a natural variation in home range size, which depends on the landscape structure and food supply. Following this, the home ranges in *Uckermärk* are much larger than those in *Germany*.

Estimates of the effects of mitigation measures on population development are usually related to agri-environment schemes (e.g. Kleijn & Sutherland, 2003, Donald & Evans, 2006, Kleijn *et al.*, 2006) or other taxa, such as plants, birds or insects (e.g. Pryke & Samways, 2015, Hille *et al.*,

2018). With regard to agri-environmental measures, there are few studies analysing the effects on brown hare populations (Zellweger-Fischer *et al.*, 2011, Petrovan *et al.*, 2013, Meichtry-Stier *et al.*, 2014). As CAP reform's greening measures are a comparatively young policy instrument (introduced by the 2013 CAP reform), reliable evaluations are rare. A survey among 88 ecologists from 17 European countries in Pe'er *et al.* (2017) resulted in recommendations for improved ecological effectiveness of greening measures. Gocht *et al.* (2017) estimate the environmental impacts of biodiversity-friendly farming practices in the context of CAP greening as small, although some regions are more positively affected than others.

Regarding the brown hare, one modelling approach exists that evaluates the effectiveness of ecological focus areas in Danish landscapes (Langhammer *et al.*, 2017). The study found that a 5% coverage of an ecological focus area is insufficient to improve the living conditions of the brown hare to a substantial degree. Permanent set-aside was identified as the most favourable ecological focus area, with a relative increase in female abundance by a factor of 3.6. Altogether, more studies on the regional implementation and impact of greening measures are needed to make reliable assessments for the brown hare. Although the model presented here can be used to quickly assess rough trends of policy measures, it does not replace the long-term monitoring of hares.

4.6 CONCLUSION

The hare model presented here opens up new possibilities to answer environmental questions. In due time, the impact of mitigation and policy measures on hare population development can be estimated on the basis of simplified generated landscapes. Furthermore, the use of a landscape generator in combination with a species model allows the investigation of numerous landscape compositions and configurations. The results show that both have a significant effect on the hare population, whereby they respond particularly strongly to compositional changes. The cultivation of alternative energy crops, e.g., mixed silphie and grass-clover ley, allows the increase of diversity in the landscape, which has proven to be highly beneficial for the brown hare. The reduction of field sizes is also a strategy to positively affect hare population development, as it increases local heterogeneity.

The future lies in agricultural landscape generators able to reproduce landscapes in even more detail to make more realistic predictions (Langhammer *et al.*, 2019). Based on such tools and appropriate data sets, assessment schemes that cover a range of landscapes, management practices and species can be developed. This purpose requires both the further development, parameterization and testing of such spatial models and the collection of data and long-term

monitoring of species. Together, both enable targeted analyses and predictions for the protection of biodiversity in agricultural landscapes.

4.7 ACKNOWLEDGEMENTS

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5 CONCLUSION AND OUTLOOK

5.1 SUMMARY OF MAIN RESULTS

The aim of this thesis was to investigate the effects of changes in land use mosaics, especially through policy measures, on the biodiversity of agricultural landscapes. Since such effects are virtually impossible to investigate empirically due to the scales and complexity involved, modelling is an indispensable tool. A main focus of my thesis, therefore, was methodology: in two case studies, different modelling approaches (a complex one and a simplified one) were applied and compared in order to identify the possibilities and potential of spatial simulation models to explore the effects of land use change and policy on biodiversity. A special focus was placed on the agricultural landscapes underlying the models and the extent to which their design and complexity determine the scope of the simulation models used. For this purpose, I compared different “Agricultural Landscape Generators” (ALG), pointed out their advantages and limitations, and developed a concept for a future-oriented generic tool for the generation of agricultural landscapes.

In this chapter, I discuss my findings with regard to their contribution to the current state of research and the methodological approach. Based on the approaches and findings presented here, I will give conclusions and an outlook on the future perspectives of the research field and draw general conclusions for biodiversity research in agricultural landscapes.

5.1.1 *A complex simulation model for the assessment of policy measures*

In the first study of this thesis, Chapter 2, I investigated the effects of greening measures on hare abundances using the Animal, Landscape and Man Simulation System (ALMaSS, Topping et al., 2003). Greening measures were introduced with the current reform of the Common Agricultural Policy (CAP) for 2014-2020 to make agriculture in the European Union more sustainable and environmentally friendly. To achieve this, the EU is financing various mandatory measures that have environmental benefits, such as Ecological Focus Areas (EFAs) but also voluntary agri-environmental measures, through green direct payments.

I developed and implemented different greening scenarios and investigated their effects on hare abundances in three different Danish landscapes. I selected EFA types that I assume to have positive effects on hare habitat: the cultivation of legumes, such as (1) peas and (2) beans, (3) permanent and (4) rotational set-asides, (5) permanent extensive grasslands, and (6) herbaceous and (7) woody field margins. As specified in the greening regulations, their proportions were increased to 5 % of the total agricultural area, and the effects on hare population development were investigated over a period of 30 years. The following research questions were the focus of the study: How does the brown hare population respond to an increased proportion of EFA types in the landscape? Are there differences between the EFA types with regard to their effectiveness? Are the measures sufficient to achieve stable hare population densities? According to Homolka & Zima (1999), I defined 10 females per km² as the lower limit for a stable population.

To investigate these questions, I applied the complex spatial simulation model ALMaSS, which is in development since 1998, has been applied in numerous studies so far (e.g., Jepsen *et al.*, 2005, Høye *et al.*, 2012, Malawska & Topping, 2016) and is well documented (ALMaSS Model Documentation, 2014). A number of arable species are already parameterised for ALMaSS (e.g., Bilde & Topping, 2004, Topping *et al.*, 2010, Topping *et al.*, 2012), including the brown hare (Topping *et al.*, 2010).

The results show that all EFA types analysed had moderate positive effects on the development of hare populations. Stable population densities, however, were achieved only by permanent set-asides, and with an average of 11 females per km² only at the lower limit. Herbaceous field margins and extensive grassland also led to a smaller but significant increase in population density. These results are in line with other studies that consider diverse landscapes that provide year-round forage and protection to be particularly favourable for the brown hare (e.g., Tapper & Barnes, 1986, Smith *et al.*, 2004, Pépin & Angibault, 2007).

Model complexity

ALMaSS works with very high spatial and temporal resolutions. Landscape structures are represented with a resolution of 1 m², agricultural management practices in 1-day steps and behavioural changes of individuals with an even finer resolution. Additionally, the model integrates weather information, which includes daily records for mean temperature, mean wind speed and total daily precipitation, in combination with seasonal vegetation growth models for each vegetation type and crop, supplying vegetation height, green and total biomass. Information on soil type can also be imported into the model to improve the simulation of

vegetation growth. The result is a dynamic model of an agricultural landscape with all vegetation growing in response to the weather.

This landscape model forms the basis for the individual-based animal models in ALMaSS, which are behaviour-based on a state/transition principle (Topping *et al.*, 2003), including elements of discrete-event simulation in, e.g., Operations Research (Zeigler *et al.*, 2000). This means that a change of behaviour to another state takes place when certain predefined conditions are fulfilled, e.g., certain probabilities and internal or external events. A software agent called the “population manager” controls the individuals by executing the respective behaviour, e.g., foraging, with a temporal resolution of up to 1-minute time steps. The most important behaviours are movement (dispersal/foraging), growth, lactation and starvation. Thus, the individuals move in the landscape, whereby their energy state is the primary driving force. The assessment of foraging quality is based on the combination of vegetation type, vegetation age and vegetation structure. Agricultural activities directly influence the individuals through changes in habitat composition and direct disturbances.

Representation of landscape

I used three different 10 x 10 km Danish landscapes for my analyses (Figure 5.1). The creation of these landscapes and their implementation in ALMaSS are described in detail in Topping *et al.* (2016). Since the model works with a high resolution of 1 m², it needs adequate landscape maps as inputs to classify all types of landscape elements. However, most land use maps are available at a coarser spatial resolution of e.g., 100 x 100 m (CORINE Land Cover, EEA maps), and landscape elements are less finely categorised (Topping *et al.*, 2016). These maps are therefore unsuitable as a basis for the model. Alternatively, aerial images could be digitised manually, which is very time-consuming, prone to errors and impractical for larger landscapes. To solve this problem, a large number of vector maps have been combined to produce a single high-resolution raster map for ALMaSS. The entire process consists of three steps: First, the input vector data are converted into the raster format. Then, the single raster layers are combined to form thematic maps (e.g., streets and paths), which are then placed one above the other in a useful order (e.g., streets above fields, etc.). The mapping process was programmed in a Python script that is freely available on Github⁶.

However, this method is time-consuming and error-prone, as well, due to the use of a large number of different data sources; it can lead to inconsistencies in the raster map if the vector maps were created independently and/or if they were created in different points in time. In most

⁶ <https://github.com/au-bios/python-landscapegen/tree/ERA2015>

cases, these inconsistencies are caused by the spatial displacement of vector layers, which can lead to overlaps or gaps between landscape elements (Topping *et al.*, 2016).

Land cover in ALMaSS is classified in 64 different polygon types with specific properties and characteristics. The polygons are exported as a text file from ArcGIS and get their own IDs and coordinates. Basically, a distinction is made between non-planted areas, such as roads or streams, and planted areas, such as arable land or field margins. I changed the land cover by modifying the polygon reference file, which is the input for ALMaSS, e.g., by assigning other cover types to certain polygons.

Farms are managed by an integrated software agent called *FarmManager*, which defines units, farm types and individual cropping plans for all arable land. Each type of farm (e.g., conventional arable farming) has a specific crop rotation programme that determines the replacement of crops on a field. Crops grow from sowing and respond to management events such as harvest and cutting. A general overview of the agricultural management processes in ALMaSS is provided by Topping *et al.* (2016) in Appendix 2.

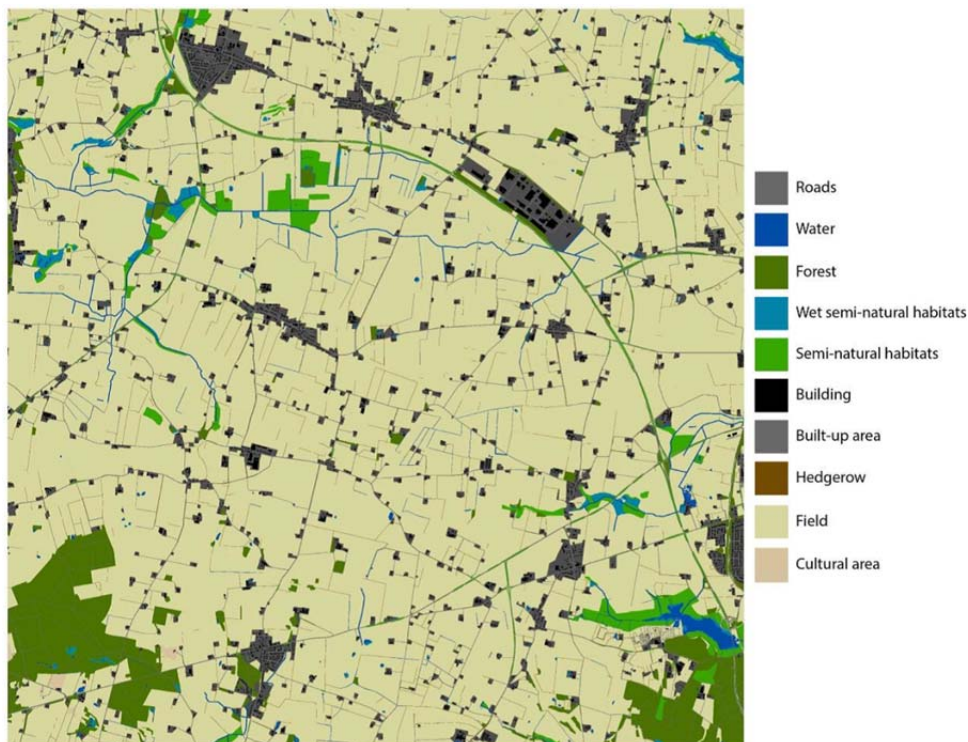


Figure 5.1: A 10 x 10 km landscape map with a resolution of 1 m² in ALMaSS. The landscape is based on vector maps from a region in Denmark, Mors.

Conclusions

ALMaSS is complex enough to realistically analyse environmental impacts and reproduce the interactions between landscape, management practices, weather and individuals. It offers many

possibilities to answer environmental questions on different landscape scales and for different animal species.

A disadvantage of the complexity is that the model is not easily adaptable, e.g., to new landscapes because the creation of the input maps is quite elaborate. In addition, the farm management characteristics of the new landscape must be implemented, which is currently only possible at the source code level and thus requires knowing and understanding the software architecture of ALMaSS, which in turn requires professional skills in programming in C++ and software engineering.

A further limitation is that the model uses high-resolution landscapes that are based on real maps, i.e., local or regional landscape and management characteristics. To increase the validity of the results, ALMaSS can be used, as shown in this study, with several landscapes that differ, for example, in farm types and field sizes. However, it is not possible to avoid the context dependence on local landscapes and agricultural characteristics limiting the generalisation of results (Topping, 2011, Topping *et al.*, 2016). Thus, this model is particularly suitable for regional case studies.

5.1.2 *Agricultural landscape generators for spatial simulation models*

Based on my experiences with ALMaSS, in the third chapter of this thesis I am looking for tools that can generate variations of land use mosaics, i.e., artificial landscapes, as input for spatial simulation models. I compared existing tools, called Agricultural Landscape Generators (ALGs), with regard to their objectives, design and features. Furthermore, based on this information, I compiled requirements for a generic ALG and suggested a possible software architecture.

As for my other two chapters on the situation of hares in agricultural landscapes indicate, there is an increasing need to assess land use changes and policy measures using simulation models. So far, such models have mostly used either landscape maps from geographical information systems (GIS) or strongly simplified virtual landscapes that were generated using algorithms. To increase the range of application of simulation models and to achieve transferable results, the use of ALGs that generate realistic but simplified representations of land cover in agricultural landscapes is needed. Variations of artificial agricultural land cover mosaics in the spatial resolution of individual fields and for certain parameter sets are created. We call these tools “generators” because they can systematically and automatically generate different landscape configurations (spatial arrangement of land cover) and compositions (type and proportion of

land cover). If the distribution of the landscape characteristics is based on the distributions in real landscapes, realistic landscape structures can be designed.

The literature research showed that so far only eight landscape generators have been developed that meet our definition. Regarding the methodological approach, I differentiate between pattern-based and process-based generators.

Pattern-based generators, also known as neutral landscape models, are based on generic algorithms and produce virtual landscapes regardless of the underlying ecological or social processes (Gardner *et al.*, 1987, With & King, 1997). Regarding complexity, they range from pure neutral models to more realistic models in terms of landscape structure (Johnson *et al.*, 1999, Gaucherel *et al.*, 2014). Pattern-based ALGs typically require fewer parameters and less computation time than process-based ALGs. There are a variety of landscape metrics that can be used as input parameters, such as the number and size of fields or the proportion of landscape elements.

Process-based generators, also known as mechanistic models, produce landscape patterns as a result of ecological or socioeconomic processes that are explicitly integrated into the model (Jackson *et al.*, 2000, Cuddington *et al.*, 2013). The advantage of these models is that the underlying processes can be addressed directly, so that these landscapes are suitable, for example, for the investigation of political measures. A disadvantage is that the effect of each individual input parameter must be known in order to design specific landscapes, but it can be difficult to quantify all the necessary parameters.

With regard to their objectives, the approaches found can be distinguished by the general directions they take. While some approaches aim to gather theoretical understanding and foster theory development, the others are designed for application, for example, to predict the ecological consequences of landscape dynamics or to give policy advice. With regard to landscape configuration, most ALGs integrate only a few landscape metrics and design simple regularly shaped fields, which limits the design of the landscape pattern and thus the range of applications. The composition of the landscape is also very simplified for most ALGs, i.e., only a few land use types can be selected. However, a more detailed description of land cover is essential to answer many questions about agricultural landscapes. One solution would be to combine the ALG with additional crop rotation tools, of which a selection is presented in Chapter 3.

Conclusions

Existing ALGs already contain helpful components that can be used for specific purposes. However, most of the approaches are still very simple in their technical implementation, which limits the application possibilities. On the basis of the results and the needs that can be read from them, I have collected the main features and criteria of generic software tools that can design landscapes with more comprehensive and variable configuration and composition. A generic ALG should have the potential to be widely used in landscape research for a variety of scenarios, regions and model types, enable the investigation of environmental questions on many spatial scales and be easily adaptable. Therefore, I propose a modular design and a preferably open architecture, where the user is given the opportunity to switch individual components on and off. A prototype for such a generic tool, which was developed in my department, is presented in Appendix B1. The program implemented in Scala is an example of a Visual Dataflow Programming (VDP) framework, which generates a simple patchy landscape with a spatially heterogeneous patch size.

5.1.3 *A simplified simulation model for the assessment of policy measures*

To clarify whether there are more generalisable model approaches to assess the impact of policy measures on biodiversity, in the third part of this thesis, Chapter 4, I investigated mitigation effects in bioenergy-driven landscapes using a much simpler individual-based model that I developed myself and that works with automatically generated artificial landscapes. The increasing cultivation of energy crops for biogas and biofuel production in Germany in recent years has led to extensive direct and indirect land use changes and thus to habitat modification of agricultural species (Dauber *et al.*, 2010). In particular, the increasing land demand for biomass cultivation has led to the loss of valuable land, such as semi-natural habitats, extensive grassland or field margins, and it has reduced the overall diversity of agricultural landscapes (Butler *et al.*, 2010, Brandt & Glemnitz, 2014).

Since the brown hare is particularly affected in its habitat by the changes mentioned above, I have investigated the effects of different mitigation measures that are eligible as EFA in the framework of the EU agricultural subsidy on population development. In contrast to the first study, I have selected measures that are alternatives to the large-scale cultivation of the energy crops maize and rape. In particular, these are the cultivation of the alternative energy crops mixed silphie (*Silphium perfoliatum*), miscanthus (*Miscanthus x giganteus*) and grass-clover ley, the cultivation of the legume alfalfa (*Medicago sativa*), the increase of set-asides and of the general crop diversity. The investigations were based on two different landscapes with a high

proportion of the energy crops maize and winter rape. Maize and oilseed rape are often cultivated in large monocultures in Germany, and above a certain height of vegetation, they are not only not suitable for foraging but also too dense for hares. As a consequence, large areas of their home ranges are rendered useless, and hares have to move longer distances to more favourable habitats (Lewandowski & Nowakowski, 1993).

I developed a spatially explicit and individual-based ecological model in NetLogo to study the effects of the different mitigation scenarios. The focus was on the following questions: What effects do the selected mitigation measures have on long-term hare population development? Is an individual-based simulation model working with simplified generated landscapes able to produce robust predictions for hare population development? As input, I used two 4 x 4 km automatically generated model landscapes with different landscape configurations (size and spatial arrangement of fields). For the scenarios, the proportion of maize or winter rape was reduced in the annual crop allocation scheme, and in return, the proportion of mitigation measures was separately increased. The effects on hare population abundance were analysed using three habitat evaluation criteria: suitability as forage habitat, suitability as breeding habitat and regional crop diversity.

All mitigation measures had significant effects on hare population development. The alternative energy crops mixed silphie and grass-clover ley as well as increased crop diversity had the strongest positive influence. In comparison, the other measures had rather moderate (alfalfa, set-asides) or even negative effects (miscanthus). Furthermore, the investigations showed that not only did the composition of the landscape (proportion of crops) but also its configuration (size of fields) affect hare population development.

Model complexity

In comparison to ALMaSS, the simplified simulation model has a rather coarse spatial resolution of 10 x 10 m and a temporal resolution of one year. Although the evaluation of crops in the hare model is based on spring/summer conditions, in reality, the crops are mainly used on a seasonal basis by hares. For example, cereals are particularly important in spring, while in summer after harvesting, hares shift to other crops such as Fabaceae, grasses and herbs (Reichlin *et al.*, 2006, Bertolino *et al.*, 2011). The seasonal use of crops is indirectly included in the hare model in the form of forage and breeding estimates.

While the hares in ALMaSS can move realistically in the landscape in time steps of up to 1 minute, and there is a constant alignment of the foraging and dispersal activity with the energy demand, the hares in this model have fixed home ranges by which the state of the hare is

determined. Hares only move in space when the quality of the home range is no longer sufficient, e.g., due to changes in crop cultivation or changes in local hare density. However, even then, they only search within their home ranges for a more suitable central position for their activities because hares, despite their ability to adapt relatively to spatial conditions and seasons, are a sedentary species and do not significantly expand their home range if their energy needs are not met (Smith *et al.*, 2005, Bray *et al.*, 2007). However, since the size of the home range depends on the landscape structure and food supply, the home ranges in the two model landscapes differ in size.

As in reality, the individuals in the hare model age annually, reproduce and die either due to age or by fixed mortality rates symbolising predation, diseases and accidents.

Representation of landscape

In contrast to the high-resolution realistic landscapes in ALMaSS, the landscapes generated by the landscape generator are rather abstract, with no other landscape elements than fields (Figure 5.2). This is another simplification, as hares also use other habitats such as meadows, forests, bushes and field margins, which are not represented in this model. However, studies have shown that they actually stay in agricultural fields for over 70 % of the time (Reichlin *et al.*, 2006, Bertolino *et al.*, 2011).

The generation of the landscapes takes place in two steps: First, the fields are randomly placed on the landscape grid until the entire area is covered. Second, a correction algorithm replaces all fields that are too small by merging them with adjacent fields. The resulting field mosaic is adapted to the specified average field size, which is based on real landscape data in this case. For this study, the landscapes are 4 x 4 km with a resolution of 10 × 10 m (400 by 400 raster cells).

In addition to the average field size, the model landscapes differ in the proportion and distribution of crops. There are 14 different crop types to choose from, which differ in terms of forage and breeding suitability and are allocated annually to the fields according to predefined proportions for each landscape and scenario.

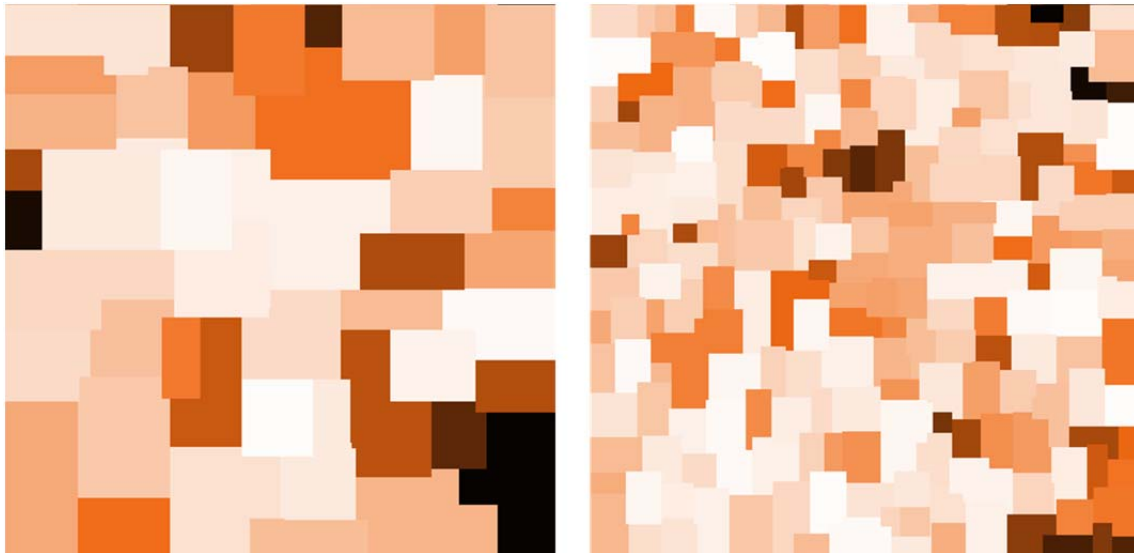


Figure 5.2: Generated agricultural landscapes with an area of 4 x 4 km. (Left) *Uckermark* reference landscape with an average field size of 27.5 ha. (Right) *Germany* reference landscape with an average field size of 6.8 ha. The colours mark the fields and can be assigned to different crop types.

Conclusions

Despite its simplifications, the NetLogo model allows robust predictions of the development of hare populations in changing land use patterns. Furthermore, the automatically generated landscapes enable a fast and systematic variation of land use patterns. In comparison to ALMaSS, the high degree of abstraction allows more general statements about specific mechanisms and dynamics to be made than targeted case analyses. Since the models are so different in their structure and design, the results for the individual measures cannot be directly compared with each other. Nevertheless, both model approaches lead to meaningful results for their scope of application. The use of the landscape generator and the simpler model structure compared to ALMaSS enable quick adaptations to new questions. Altogether, the NetLogo model is much simpler but also much more flexible and easily extendable. For example, an increase in landscape complexity through the implementation of further land use types or fringe structures such as field margins is possible.

5.2 CONCLUSIONS FOR THE PROTECTION OF THE BROWN HARE

Both simulation studies show that the most favourable measures for the development of hare populations are those that provide year-round forage and protection at the landscape level. This requires a diverse and heterogeneous habitat, especially in intensively managed landscapes. The diversification of landscapes can be achieved through permanent set-asides as shown in the first

study, or through crop diversification, as shown in the second study. One way to achieve crop diversification is to cultivate alternative energy crops such as silphie and grass-clover ley, which are more favourable for hares than maize or oilseed rape in large monocultures. Additionally, an increase in crop diversity through the cultivation of legumes such as peas and beans, which are forage plants for hares, has a positive effect on hare populations.

The results also indicate that the composition of the whole landscape must be considered when planning measures. A certain measure can have a great effect in one landscape and only a moderate effect in another, depending on the prior composition or what land use type was replaced by what. Furthermore, it turned out that not only the landscape composition (number and proportion of crops) but also its configuration (field sizes) plays an important role in hare population development. Since the habitat requirements are more easily met in small-scale heterogeneous landscapes, hares do not have to move as far in landscapes with large monocultures (e.g., Broekhuizen & Maaskamp, 1981, R  he & Hohmann, 2004). Furthermore, hares benefit faster from mitigation measures in small-scale landscapes, as the probability of favourable areas in their home range is higher. This also implies that smaller field sizes can be regarded as mitigation strategies themselves. Altogether, the results indicate that analysing the starting situation of the landscape is indispensable, and tailor-made measures for certain landscape compositions and configurations would be beneficial. This estimation is in line with Fahrig *et al.* (2011), who propose the consideration of a “functional landscape heterogeneity”, in which compositional and configurational heterogeneity are considered separately and are species-related.

The results of Chapter 2 indicate that a 5 % proportion of ecological focus areas is not sufficient to improve the habitat conditions of the brown hare to the necessary extent. Since the CAP greening measures are a relatively young policy instrument (introduced by the 2013 CAP reform), there are not yet many reliable assessments. Gocht *et al.* (2017) estimate the environmental impact of CAP greening measures as low, even if some regions are affected more positively than others. Two other evaluation studies also come to the conclusion that the greening measures are insufficient to protect the biodiversity of agricultural landscapes (Pe'er *et al.*, 2014, Pe'er *et al.*, 2017). Oppermann *et al.* (2012) propose that 10 % and Meichtry-Stier *et al.* (2014) that at least 14 % of areas should have valuable agri-environmental measures or semi-natural habitats for the sustainable protection of agricultural biodiversity. The extent to which the proportion in a real landscape should be increased in order to stabilise the population in the long term would have to be investigated in more detail in further studies for the specific landscapes.

Overall, more studies on the regional implementation and impact of greening measures are needed to provide reliable assessments for the brown hare. Although the simulation models presented here allow an assessment of rough trends and a comparison of measures, they do not replace the long-term monitoring of hares. The comparison of the obtained results with studies on other animal species or animal groups of the agricultural landscape would help determine smart solutions that benefit a wide range of species.

5.3 REFLECTIONS ON METHODOLOGICAL APPROACHES

5.3.1 *Spatial simulation models as assessment tools*

Empirically assessing the impact of policies on different landscapes is very time-consuming and requires numerous case studies. This thesis demonstrates that policy measures can be quantitatively evaluated with reasonable effort and within a short period of time by using spatial simulation models. It is possible to carry out controlled simulation experiments on the basis of variable landscapes. Chapter 4 shows that even a simplified model with a less profound data background can produce meaningful results, which is particularly important in cases where the data situation is insufficient. This illustrates one advantage of simulation models, namely, that they nevertheless allow quantitative assessments based on reasonable assumptions, for example, on the basis of expert knowledge.

As this thesis demonstrates, agent-based models (ABMs) are particularly suitable for species-related assessments because they simulate how the structure and dynamics of populations derive from first principles such as adaptive behaviour and energy budgets (Grimm *et al.*, 2005, Grimm & Berger, 2016). ABMs allow the combination of physiological and behavioural processes at the individual level with demographic processes at the population level, as in ALMaSS, but they can also be based on more aggregated empirical rules, as in my NetLogo model (Railsback & Grimm, 2012). By using complex and high-resolution ABMs such as ALMaSS, the consideration of both various landscape features, including agricultural practices, and the precise representation of population ecological processes is possible. However, the more complex the model becomes, the more difficult it is to modify and parameterise.

Nevertheless, simulation models are always more or less a strong simplification of reality, and their results are an approximation. In reality, greening or mitigation measures, for example, would never be implemented as equally distributed with a certain percentage in the landscape as in the scenarios of these studies. Farmers have multiple options that are not necessarily always hare-friendly. For example, ecologically valuable fringe structures such as field margins and

buffer strips are implemented much less frequently than the cultivation of eligible crops, such as nitrogen-fixing crops, which accounted for 70.7 % of all EU greening measures in 2015 (Pe'er *et al.*, 2017, Agrar-Atlas, 2019).

By using an assessment scheme based on complex spatial simulation models, specific measures for a range of species and landscape types can be evaluated, as well as the optimisation of existing measures. Critical threshold values of environmental impacts can be identified at an early stage, and suitable mitigation measures can be developed. This could support the European Commission in promoting biodiversity in the European Union through more environmentally friendly farming practices. Involving policymakers and relevant stakeholders in the process of developing and applying such assessment tools would have great potential to determine targeted and tailor-made solutions.

5.3.2 *Generalisation of landscapes*

The computer-based generation of agricultural landscapes can provide a framework for understanding and assessing how land use and land cover changes take place and affect the environment. Computer-generated landscapes offer a number of advantages: they can close the gap if data is not available or not available in a suitable resolution (for example land use data), and they allow the investigation of different landscape configurations and compositions, a systematic analysis of environmental gradients as well as spatial sensitivity analyses.

The tools available so far, however, usually create quite simple landscapes, which limits the application range, since the results are only partially transferable to reality. Usually, the focus is on either the spatial configuration or the composition, not on both in a balanced way. All approaches still have great potential for further development towards broader applicability. The particular challenge in developing such tools lies in the fact that any increase in complexity (e.g., through the integration of new landscape features) is accompanied by more complicated algorithms and a longer computing time. This is the classic modeller's dilemma, at which point functionality falls victim to complexity. Therefore, the complexity of a tool must be carefully weighed with regard to the range of application. Against this background, a validation of the generators, i.e., the verification of whether significant characteristics of existing landscapes are reproduced, is essential.

5.3.3 *Future perspectives of the simulation of agricultural landscape*

This work shows that the development of computer-generated agricultural landscapes is still in its infancy. However, there are important open questions that require more complex landscapes or to include advanced design rules, for example, to consider the relationship between abiotic site conditions (e.g., soil, runoff, relief) and crop selection. To take the multifunctionality of landscapes into account, simulation models should be able to map the diversity of the landscape and the major processes that lead to significant changes in configuration and composition.

Therefore, the future lies in smart simulation models that are able to reproduce landscapes in more detail in order to make more realistic predictions and multifunctionality assessments. Agricultural landscapes are basically multifunctional, as they fulfil other functions in addition to food and raw material production, such as habitat for species, production of groundwater and recreational area. The models must be regionally transferable, predictive and adaptable, and there are already many approaches that can be used for the further development of spatial simulation models. Pattern-oriented modelling, for example, can help identify relevant landscape metrics. Remote sensing can be used to provide models with high-resolution data on crop systems and abiotic factors or to identify configuration and composition patterns. Due to the enormous application potential, the importance of landscape generators as a basis for spatial simulation models will continue to increase in the future and be a valuable complement to real landscapes and long-term field studies. However, considerable development work is still required to improve and generalise the generators.

The further development of spatial simulation models for the integrated analysis of causal relationships requires the combination of data on different spatial scales. Since this involves the considerable input of data and work, it would be helpful to collaborate on this within the scientific community. Interdisciplinary collaboration (including, e.g., ecology, geography, physics) would improve the understanding of the relationships within the complex and multifunctional landscape system. This requires funding mechanisms that support integration, continuity and maintenance, shared learning and permanent innovation (Reidsma *et al.*, 2018). Synthesis products offer the chance to free individual approaches that already exist from isolation and combine the knowledge and skills of many scientists, leading to new insights. Regarding simulation models, a well-documented modular and open source code can be edited and enriched by the scientific community and used for further models. In this way, simulation models can be further developed with efficient algorithms, parameterised and tested. A proper research goal and the result of interdisciplinary collaboration could be the development of a new generation of large-scale land use systems that combine different modelling concepts in a unified framework. Ideally, such a framework would consist of different modules that can be

coupled directly or indirectly by importing and exporting data. For example, standardised sub-models could be used for a wide range of species, systems, and environments with minor amendments (Grimm & Berger, 2016). The coupling of bottom-up and top-down models to capture macro-level dynamics would allow a consistent analysis of the land system and its interactions as a whole (Rounsevell *et al.*, 2012). The strengths of existing approaches could be used without having the disadvantages of a complex model such as ALMaSS, which tries to represent the whole system but is difficult to handle. Combined with data collection and long-term observations of species, such new approaches would enable targeted analyses and more accurate predictions for the protection of biodiversity in agricultural landscapes.

With regard to the strategy of model building, trade-offs must be found between generalisation, precision and realism (Levins, 1966). This work proves that a single model can hardly do justice to all three aspects; therefore, generality is sacrificed for realism and precision (similar to ALMaSS), precision for generality and realism, and realism for generality and precision (similar to the NetLogo model). The future lies in modular systems that unite all three aspects and, depending on the question, can be used in any of the directions.

5.4 SYNTHESIS AND OUTLOOK

After having started the energy transition, a comprehensive and profound agricultural transition is needed. There is an urgent need for agricultural practices that reconcile food production with the promotion of biodiversity, ecosystem services and climate mitigation. European agricultural policy, with its control instruments, is the main influencing actor on agriculture in Europe and the first addressee for change requests. To promote an agricultural transition towards more environmentally friendly and sustainable agricultural production, it is essential to evaluate the EU control instruments, i.e., greening measures.

This thesis makes a contribution towards agricultural transition, as it presents approaches and tools that open up new possibilities for evaluating policy measures in agricultural landscapes. First, a complex simulation system (ALMaSS) is used to show how realistic simulations can be carried out in high-resolution landscapes and how detailed case studies can be conducted (Chapter 2). Second, this thesis demonstrates that also a simplified spatial simulation model without a profound data background is able to quickly evaluate and predict environmental impacts (Chapter 4). Third, this work clearly shows how versatile and powerful spatial simulation models are in combination with automatically generated landscapes. At the same time, it points out how many development needs still exist (Chapter 3).

The potential benefits of the presented approaches and tools were only shown for a small number of scenarios. Valuable insights into the effects of greening and mitigation measures on brown hare populations could be gained, for example, which crop types are particularly favourable. Further impact assessments of policy measures on biodiversity in agricultural landscapes, for example, for other animal species, should be conducted using the instruments presented, which offers a great opportunity for the development of general assessment schemes of EU policy instruments. After all, computer-based assessments of urgent topics, such as insect decline, climate mitigation and adaptation, and future food security, could not only become important but decisive in the future.

It would be my pleasure if this thesis could mark a piece on the way to let the vision of the European Commission become reality:

“In 2050, we live well, within the planet’s ecological limits. Our prosperity and healthy environment stem from an innovative, circular economy where nothing is wasted and where natural resources are managed sustainably, and biodiversity is protected, valued and restored in ways that enhance our society’s resilience. Our low-carbon growth has long been decoupled from resource use, setting the pace for a safe and sustainable global society.”

(7th EAP - General Union Environment Action Programme to 2020)

APPENDICES

A APPENDIX OF CHAPTER 2

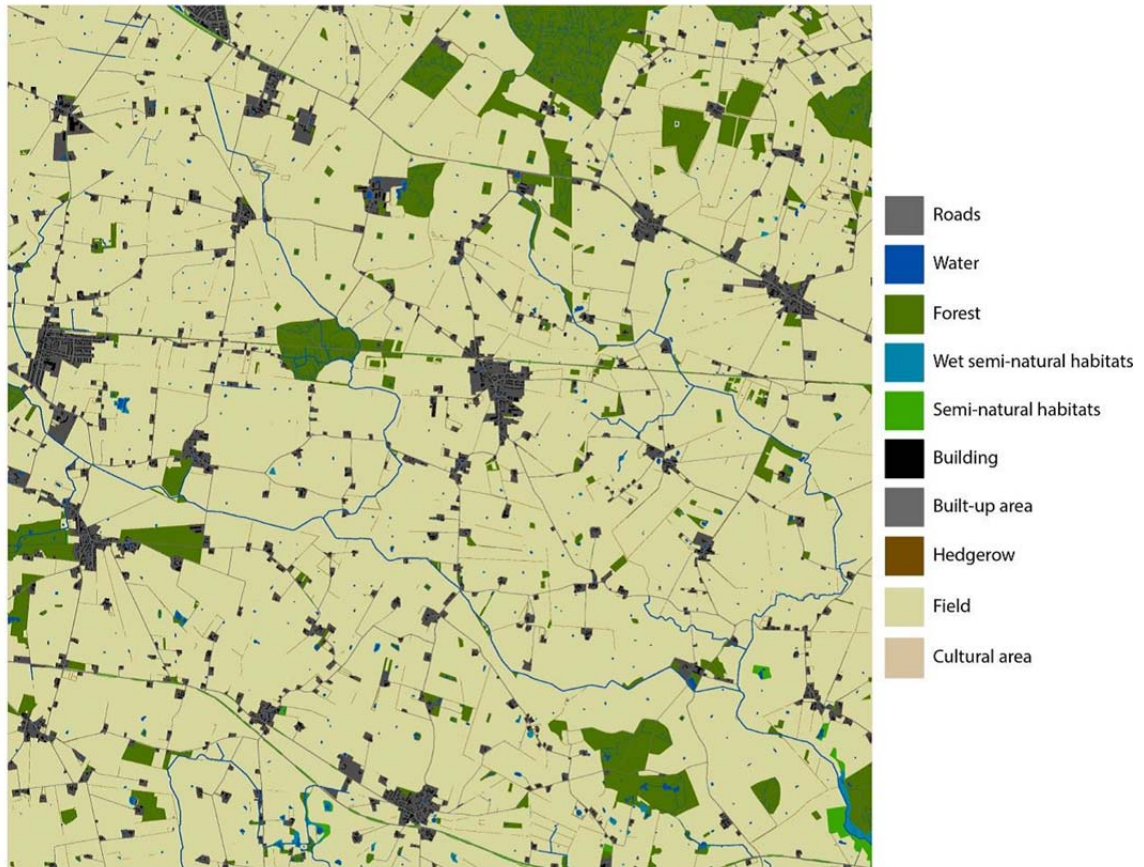


Figure A 1: Visual overview of Naestved, 10 x 10 km, mapping the basic elements of the landscape visible at this scale.

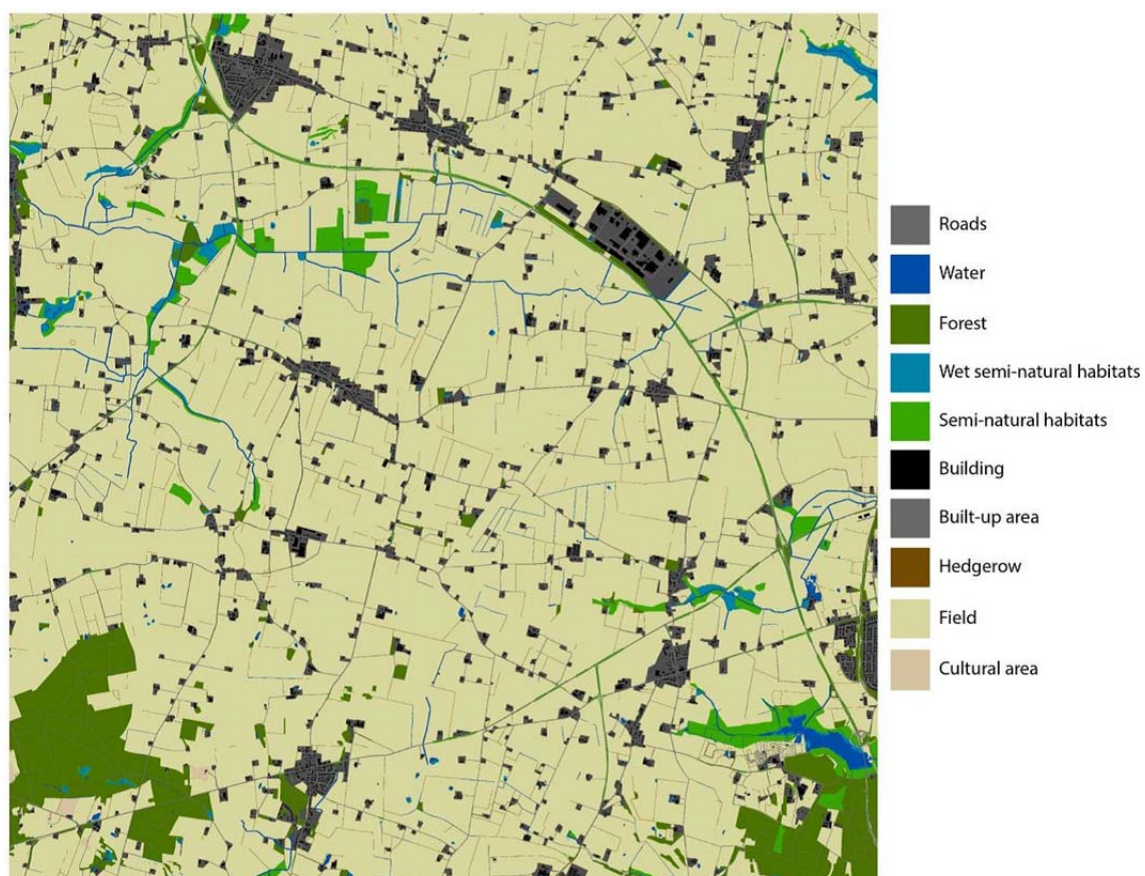


Figure A 2: Visual overview of Odder, 10 x 10 km, mapping the basic elements of the landscape visible at this scale.

Table A 1: The amount of all landscape elements in Mors.

| Polygon type in ALMaSS | Landscape element | Area [m ²] | % | %* |
|------------------------|---------------------|------------------------|--------|--------|
| 5 | Building | 1416036 | 1.42 | 1.42 |
| 8 | Rural residential | 762835 | 0.76 | 0.76 |
| 11 | Garden | 4206600 | 4.21 | 4.21 |
| 12 | AmenityGrass | 338061 | 0.34 | 0.34 |
| 13 | RoadsideVerge | 561749 | 0.56 | 0.56 |
| 20 | Field | 75154612 | 75.15 | 69.89 |
| 27 | PermPastureTussocky | 132395 | 0.13 | 0.11 |
| 33 | PermanentSetaside | 271002 | 0.27 | 0.24 |
| 35 | PermPasture | 1807788 | 1.81 | 1.61 |
| 40 | DeciduousForest | 19776 | 0.02 | 0.02 |
| 41 | Copse | 313888 | 0.31 | 0.31 |
| 50 | ConiferousForest | 74594 | 0.07 | 0.07 |
| 55 | YoungForest | 6192 | 0.01 | 0.01 |
| 56 | Orchard | 14781 | 0.01 | 0.01 |
| 60 | MixedForest | 4998688 | 5.00 | 5.00 |
| 70 | Scrub | 1380 | 0.00 | 0.00 |
| 90 | Freshwater | 431233 | 0.43 | 0.43 |
| 94 | Heath | 31943 | 0.03 | 0.03 |
| 95 | Marsh | 800206 | 0.80 | 0.80 |
| 96 | River | 374849 | 0.37 | 0.37 |
| 98 | RiversidePlants | 318040 | 0.32 | 0.32 |
| 110 | NaturalGrassDry | 24591 | 0.02 | 0.02 |
| 115 | ActivePit | 142018 | 0.14 | 0.14 |
| 121 | LargeRoad | 564084 | 0.56 | 0.56 |
| 122 | SmallRoad | 1104618 | 1.10 | 1.10 |
| 123 | Track | 1062506 | 1.06 | 1.06 |
| 130 | Hedges | 689938 | 0.69 | 1.01 |
| 140 | HedgeBank | 962945 | 0.96 | 0.64 |
| 150 | Chamaeleon | | 0.00 | 5.52 |
| 160 | FieldBoundary | 536650 | 0.54 | 0.54 |
| 201 | RoadsideSlope | 292045 | 0.29 | 0.29 |
| 203 | Carpark | 17872 | 0.02 | 0.02 |
| 204 | Churchyard | 37495 | 0.04 | 0.04 |
| 205 | NaturalGrassWet | 294879 | 0.29 | 0.29 |
| 206 | Saltmarsh | 2159 | 0.00 | 0.00 |
| 207 | Stream | 39709 | 0.04 | 0.04 |
| 208 | HeritageSite | 6967 | 0.01 | 0.01 |
| 209 | Wasteland | 2007325 | 2.01 | 2.01 |
| 210 | NaturalGrassDry | 57416 | 0.06 | 0.06 |
| 211 | WindTurbine | 243 | 0.00 | 0.00 |
| 212 | Pylon | 6791 | 0.01 | 0.01 |
| 216 | WoodyEnergyCrop | 113100 | 0.11 | 0.10 |
| Σ | | 99999999 | 100.00 | 100.00 |

Table A 2: The amount of all landscape elements in Naestved.

| Polygon type in ALMaSS | Landscape element | Area [m ²] | % | %* |
|------------------------|---------------------|------------------------|--------|--------|
| 5 | Building | 868071 | 0.87 | 0.87 |
| 8 | Rural residential | 336990 | 0.34 | 0.34 |
| 11 | Garden | 3597150 | 3.60 | 3.60 |
| 12 | AmenityGrass | 266573 | 0.27 | 0.27 |
| 13 | RoadsideVerge | 383294 | 0.38 | 0.38 |
| 16 | BuiltUpWithParkland | 1840 | 0.00 | 0.00 |
| 20 | Field | 77567804 | 77.57 | 72.83 |
| 33 | PermanentSetaside | 378691 | 0.38 | 0.31 |
| 35 | PermPasture | 810581 | 0.81 | 0.73 |
| 40 | DeciduousForest | 26133 | 0.03 | 0.03 |
| 41 | Copse | 252947 | 0.25 | 0.25 |
| 50 | ConiferousForest | 63645 | 0.06 | 0.06 |
| 55 | YoungForest | 487715 | 0.49 | 0.44 |
| 56 | Orchard | 1225444 | 1.23 | 1.14 |
| 60 | MixedForest | 5389529 | 5.39 | 5.39 |
| 70 | Scrub | 8572 | 0.01 | 0.01 |
| 90 | Freshwater | 510837 | 0.51 | 0.51 |
| 94 | Heath | 499 | 0.00 | 0.00 |
| 95 | Marsh | 316911 | 0.32 | 0.32 |
| 96 | River | 440500 | 0.44 | 0.44 |
| 98 | RiversidePlants | 416838 | 0.42 | 0.42 |
| 101 | SandDune | 54 | 0.00 | 0.00 |
| 110 | NaturalGrassDry | 16285 | 0.02 | 0.02 |
| 118 | Railway | 113101 | 0.11 | 0.11 |
| 121 | LargeRoad | 325521 | 0.33 | 0.33 |
| 122 | SmallRoad | 875933 | 0.88 | 0.88 |
| 123 | Track | 679586 | 0.68 | 0.68 |
| 130 | Hedges | 601033 | 0.60 | 0.88 |
| 140 | HedgeBank | 910501 | 0.91 | 0.63 |
| 150 | Chamaeleon | | 0.00 | 5.02 |
| 160 | FieldBoundary | 486048 | 0.49 | 0.49 |
| 201 | RoadsideSlope | 70829 | 0.07 | 0.07 |
| 203 | Carpark | 1881 | 0.00 | 0.00 |
| 204 | Churchyard | 14916 | 0.01 | 0.01 |
| 205 | NaturalGrassWet | 74800 | 0.07 | 0.07 |
| 207 | Stream | 62107 | 0.06 | 0.06 |
| 208 | HeritageSite | 2989 | 0.00 | 0.00 |
| 209 | Wasteland | 2205689 | 2.21 | 2.21 |
| 210 | NaturalGrassDry | 5804 | 0.01 | 0.01 |
| 211 | WindTurbine | 279 | 0.00 | 0.00 |
| 212 | Pylon | 2287 | 0.00 | 0.00 |
| 214 | PlantNursery | 30272 | 0.03 | 0.03 |
| 216 | WoodyEnergyCrop | 169525 | 0.17 | 0.15 |
| Σ | | 100000004 | 100.00 | 100.00 |

Table A 3: The amount of all landscape elements in Odder.

| Polygon type in ALMaSS | Landscape element | Area [m ²] | % | %* |
|------------------------|---------------------|------------------------|--------|--------|
| 5 | Building | 725515 | 0.73 | 0.73 |
| 6 | UrbanNoVeg | 209059 | 0.21 | 0.21 |
| 11 | Garden | 2958120 | 2.96 | 2.96 |
| 12 | AmenityGrass | 656848 | 0.66 | 0.66 |
| 13 | RoadsideVerge | 309657 | 0.31 | 0.31 |
| 20 | Field | 67611303 | 67.61 | 63.54 |
| 27 | PermPastureTussocky | 29180 | 0.03 | 0.03 |
| 33 | PermanentSetaside | 565184 | 0.57 | 0.53 |
| 35 | PermPasture | 4002591 | 4.00 | 3.61 |
| 40 | DeciduousForest | 4574 | 0.00 | 0.00 |
| 41 | Copse | 224329 | 0.22 | 0.22 |
| 55 | YoungForest | 975076 | 0.98 | 0.89 |
| 56 | Orchard | 22710 | 0.02 | 0.02 |
| 60 | MixedForest | 12231602 | 12.23 | 12.23 |
| 90 | Freshwater | 323990 | 0.32 | 0.32 |
| 94 | Heath | 16893 | 0.02 | 0.02 |
| 95 | Marsh | 1282697 | 1.28 | 1.28 |
| 96 | River | 180819 | 0.18 | 0.18 |
| 98 | RiversidePlants | 670666 | 0.67 | 0.67 |
| 101 | SandDune | 8505 | 0.01 | 0.01 |
| 110 | NaturalGrassDry | 200716 | 0.20 | 0.20 |
| 118 | Railway | 61145 | 0.06 | 0.06 |
| 121 | LargeRoad | 302465 | 0.30 | 0.30 |
| 122 | SmallRoad | 997203 | 1.00 | 1.00 |
| 123 | Track | 920064 | 0.92 | 0.92 |
| 130 | Hedges | 319456 | 0.32 | 0.47 |
| 140 | HedgeBank | 487054 | 0.49 | 0.34 |
| 150 | Chamaeleon | | 0.00 | 4.59 |
| 160 | FieldBoundary | 433704 | 0.43 | 0.43 |
| 201 | RoadsideSlope | 129378 | 0.13 | 0.13 |
| 203 | Carpark | 583 | 0.00 | 0.00 |
| 204 | Churchyard | 14939 | 0.01 | 0.01 |
| 205 | NaturalGrassWet | 485102 | 0.49 | 0.49 |
| 206 | Saltmarsh | 1086 | 0.00 | 0.00 |
| 207 | Stream | 192434 | 0.19 | 0.19 |
| 208 | HeritageSite | 721 | 0.00 | 0.00 |
| 209 | Wasteland | 2433652 | 2.43 | 2.43 |
| 210 | NaturalGrassDry | 3979 | 0.00 | 0.00 |
| 211 | WindTurbine | 63 | 0.00 | 0.00 |
| 212 | Pylon | 2322 | 0.00 | 0.00 |
| 216 | WoodyEnergyCrop | 4617 | 0.00 | 0.00 |
| Σ | | 100000001 | 100.00 | 100.00 |

* Landscapes with widened edge structures

Table A 4: Farm types in the three model landscapes.

| Farm types in ALMaSS | Number of farms | | |
|-------------------------------|-----------------|----------|-------|
| | Mors | Naestved | Odder |
| <i>ConventionalPig</i> | 35 | 11 | 28 |
| <i>ConventionalCattle</i> | 37 | 23 | 38 |
| <i>ConventionalArable</i> | 35 | 75 | 34 |
| <i>ConventionalHobby</i> | 51 | 39 | 38 |
| <i>ConventionalMixedStock</i> | 4 | 17 | 5 |
| <i>ConventionalBeet</i> | | 2 | |
| <i>ConventionalVeg</i> | | 1 | |
| <i>OrganicMixedStock</i> | | 1 | |
| <i>OtherFarmTypes</i> | 4 | 5 | 2 |

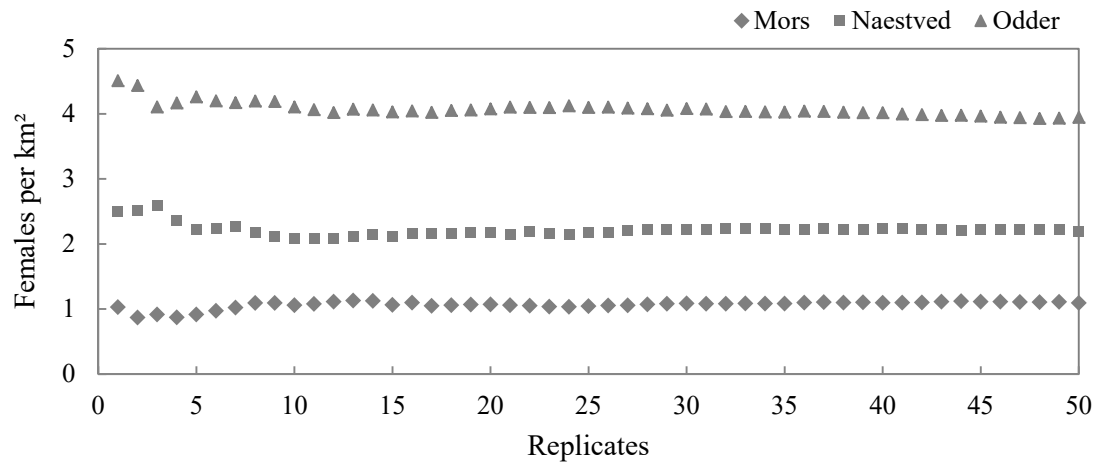


Figure A 3: Effect of increasing number of replicates on the mean female abundance for the baseline scenarios in Mors, Naestved and Odder.

Table A 5: Changes in the crop rotations of the conventional farm types for each scenario.

| Crop type in ALMaSS | Farm types in ALMaSS | | | | | | | | | | | | | | | | | | | |
|--------------------------------|----------------------|---|---|---|--------------------|---|---|---|--------------------|---|---|---|-------------------|---|---|---|------------------------|---|---|---|
| | ConventionalPig | | | | ConventionalCattle | | | | ConventionalArable | | | | ConventionalHobby | | | | ConventionalMixedStock | | | |
| Scenario | B | P | B | R | B | P | B | R | B | P | B | R | B | P | B | R | B | P | B | R |
| <i>SpringBarleyCloverGrass</i> | 4 | 4 | 4 | 4 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 9 | 9 | 9 | 9 |
| <i>SpringBarley</i> | 2 | 2 | 2 | 2 | | | | | 3 | 3 | 3 | 3 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 3 |
| <i>SpringBarleySpr</i> | 6 | 6 | 1 | 6 | 6 | 6 | 1 | 6 | 7 | 7 | 2 | 7 | 2 | 2 | 7 | 2 | 26 | 6 | 1 | 6 |
| <i>SpringWheat</i> | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 |
| <i>Oats</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>WinterBarley</i> | 3 | 3 | 3 | 3 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 0 |
| <i>WinterWheat</i> | 9 | 9 | 9 | 9 | 2 | 2 | 2 | 2 | 7 | 7 | 7 | 7 | 4 | 4 | 4 | 4 | 5 | 5 | 5 | 5 |
| <i>WinterRye</i> | 3 | 3 | 3 | 3 | | | | | 3 | 3 | 3 | 3 | 1 | | | | 1 | 1 | 1 | 2 |
| <i>WinterRape</i> | 5 | 0 | 0 | 0 | 9 | 4 | 4 | 4 | 5 | 0 | 0 | 0 | 4 | 9 | 9 | 9 | 22 | 7 | 7 | 7 |
| | 4 | 4 | 4 | 4 | 2 | 2 | 2 | 2 | 4 | 4 | 4 | 4 | 3 | 3 | 3 | 3 | 5 | 5 | 5 | 5 |
| | 1 | 1 | 1 | 1 | | | | | 1 | 1 | 1 | 1 | | | | | | | | 0 |
| | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 4 | 4 | 4 | 4 | 8 | 8 | 8 | 8 |
| <i>SpringRape</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>FieldPeas</i> | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 |
| <i>BroadBeans</i> | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 |
| <i>Setaside</i> | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 |
| <i>SeedGrass1</i> | 3 | 3 | 3 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 9 | 9 | 9 | 9 |
| <i>Potatoes</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>CloverGrassGrazed1</i> | 4 | 4 | 4 | 4 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 11 | 1 | 1 | 1 |
| <i>SpringBarleySilage</i> | 0 | 0 | 0 | 0 | 6 | 6 | 6 | 6 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 |
| <i>MaizeSilage</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 3 | 3 |
| <i>Carrots</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Triticale</i> | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>SugarBeet</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 2 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 8 | 3 | 8 |
| Σ | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 10 | 0 | 0 | 0 |
| | | | | | | | | | | | | | | | | | | | | 9 |

B = Baseline, P = Peas, B = Beans, RS = Rotational set-asides

Table A 6: Changes in the crop rotations of the organic and other farm types for each scenario.

| Crop type in ALMaSS | Farmtypes in ALMaSS | | | | | | | |
|------------------------------|--------------------------|----|----|----|-----------------------|----|----|----|
| | <i>OrganicMixedStock</i> | | | | <i>OtherFarmTypes</i> | | | |
| Scenario | B | P | B | RS | B | P | B | RS |
| <i>OBarleyPeaCloverGrass</i> | 12 | 12 | 12 | 12 | 17 | 17 | 12 | 17 |
| <i>OSpringBarley</i> | 13 | 13 | 13 | 13 | 0 | 0 | 0 | 0 |
| <i>SpringBarleySpr</i> | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| <i>OSpringWheat</i> | 8 | 8 | 8 | 8 | 0 | 0 | 0 | 0 |
| <i>OOats</i> | 17 | 17 | 17 | 17 | 3 | 3 | 3 | 3 |
| <i>OWinterBarley</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>OWinterWheat</i> | 4 | 9 | 9 | 9 | 4 | 4 | 4 | 4 |
| <i>OWinterRye</i> | 11 | 11 | 11 | 11 | 0 | 0 | 0 | 0 |
| <i>OWinterRape</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>OSpringRape</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>OFieldPeas</i> | 6 | 1 | 1 | 1 | 0 | 5 | 0 | 0 |
| <i>BroadBeans</i> | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| <i>Setaside</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>OSeedGrass1</i> | 5 | 5 | 5 | 5 | 0 | 0 | 0 | 0 |
| <i>OPotatoes</i> | 0 | 0 | 0 | 0 | 5 | 5 | 5 | 5 |
| <i>OCloverGrassGrazed1</i> | 19 | 19 | 19 | 19 | 67 | 62 | 62 | 62 |
| <i>OSpringBarleySilage</i> | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| <i>OMaizeSilage</i> | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| <i>OCarrots</i> | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>OTriticale</i> | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>OSugarBeet</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Σ | 100 | | | | 100 | | | |

We tried as far as possible to implement the rotation scenarios equally. The replacement decisions were made with regard to agricultural restrictions on the crop rotations.

Table A 7: Changes in the polygon types for permanent set-asides and permanent extensive grasslands [%].

| Scenario | Mors | | | Naestved | | | Odder | | |
|--|-------|-------|-------|----------|-------|-------|-------|-------|-------|
| | B | PS | PEG | B | PS | PEG | B | PS | PEG |
| Field | 75.15 | 70.41 | 72.09 | 77.57 | 72.94 | 73.39 | 67.61 | 63.17 | 66.64 |
| Permanent set-asides (<i>PermanentSetaside</i>) | 0.27 | 5.01 | 0.27 | 0.38 | 5.00 | 0.38 | 0.57 | 5.00 | 0.57 |
| Intensive grasslands (<i>PermPasture</i>) | 1.81 | 1.81 | 0.00 | 0.81 | 0.81 | 0.00 | 4.00 | 4.00 | 0.00 |
| Extensive grasslands (<i>PermPastureTussocky</i>) | 0.13 | 0.13 | 5.00 | 0.00 | 0.00 | 4.99 | 0.03 | 0.03 | 5.00 |

B = Baseline, PS = Permanent set-asides, PEG = Permanent extensive grasslands

In the case of permanent extensive grasslands, we first converted all intensive grasslands into extensive grasslands and then filled in the missing amount with field area.

Table A 8: Changes in the polygon types for the field margin scenarios [%].

| Scenario | Mors | | | Naestved | | | Odder | | |
|--|-------|-------|-------|----------|-------|-------|-------|-------|-------|
| | B | HFM | WFM | B | HFM | WFM | B | HFM | WFM |
| Field | 75.15 | 76.21 | 76.68 | 77.57 | 78.08 | 78.47 | 67.61 | 67.61 | 67.61 |
| Herbaceous field margins (<i>FieldBoundary</i>) | 0.54 | 5.00 | 0.54 | 0.49 | 5.00 | 0.49 | 0.43 | 5.02 | 0.43 |
| Woody field margins (<i>Hedges</i>) | 1.01 | 1.01 | 5.01 | 0.88 | 0.88 | 5.00 | 0.47 | 0.47 | 5.06 |
| <i>Chameleon</i> | 5.52 | 0.00 | 0.00 | 5.02 | 0.00 | 0.00 | 4.59 | 0.00 | 0.00 |

B = Baseline, HFM = Herbaceous field margins, WFM = Woody field margins

Table A 9: Absolute and relative changes in female abundances for all three landscapes.

| | Baseline | Legumes | | Set-asides | | Grasslands | Field margins | |
|-------------|----------|---------|-------|------------|-----------|------------|---------------|-------|
| | | Peas | Beans | Rotational | Permanent | Extensive | Herbaceous | Woody |
| Mors | 1.1 | 1.6 | 5.9 | 6.4 | 10.1 | 7.9 | 8.8 | 4.1 |
| Abs. change | | 0.5 | 4.9 | 5.3 | 9.0 | 6.9 | 7.8 | 3.1 |
| Rel. change | | 0.5 | 4.6 | 5.0 | 8.5 | 6.5 | 7.3 | 2.9 |
| Naestved | 2.1 | 3.1 | 7.7 | 8.0 | 10.8 | 10.1 | 10.9 | 5.7 |
| Abs. change | | 1.1 | 5.6 | 5.9 | 8.7 | 8.0 | 8.8 | 3.6 |
| Rel. change | | 0.5 | 2.7 | 2.8 | 4.2 | 3.8 | 4.2 | 1.7 |
| Odder | 4.1 | 5.1 | 9.2 | 9.4 | 12.1 | 10.4 | 12.7 | 9.3 |
| Abs. change | | 1.0 | 5.1 | 5.3 | 8.0 | 6.3 | 8.6 | 5.1 |
| Rel. change | | 0.2 | 1.2 | 1.3 | 1.9 | 1.5 | 2.1 | 1.3 |

APPENDICES

Table A 10: Absolute and relative changes in yearling abundances for all three landscapes.

| | Baseline | Legumes | | Set-asides | | Grasslands | Field margins | |
|-------------|----------|---------|-------|------------|-----------|------------|---------------|-------|
| | | Peas | Beans | Rotational | Permanent | Extensive | Herbaceous | Woody |
| Mors | 2.6 | 3.9 | 14.7 | 16.1 | 26.7 | 20.6 | 18.8 | 8.9 |
| Abs. change | | 1.3 | 12.1 | 13.5 | 24.1 | 18.0 | 16.2 | 6.3 |
| Rel. change | | 0.5 | 4.7 | 5.2 | 9.3 | 7.0 | 6.3 | 2.4 |
| Naestved | 5.3 | 7.9 | 19.4 | 21.0 | 29.6 | 27.2 | 25.4 | 12.9 |
| Abs. change | | 2.5 | 14.0 | 15.6 | 24.2 | 21.8 | 20.0 | 7.5 |
| Rel. change | | 0.5 | 1.8 | 2.9 | 4.5 | 4.1 | 3.7 | 1.4 |
| Odder | 10.5 | 13.0 | 23.6 | 25.2 | 34.4 | 28.5 | 31.4 | 22.2 |
| Abs. change | | 2.6 | 13.1 | 14.8 | 23.9 | 18.0 | 20.9 | 11.8 |
| Rel. change | | 0.2 | 1.3 | 1.4 | 2.3 | 1.7 | 2.0 | 1.1 |

Table A 11: Female abundances at percentage increase of the EFA types permanent set-asides and extensive grasslands in Mors.

| Scenario | Percentage of the EFA type | | | |
|----------------------|----------------------------|------|------|------|
| | 5 % | 7 % | 10 % | 15 % |
| Permanent set-asides | 10.1 | 12.4 | 14.3 | 15.3 |
| Absolute change | | 2.3 | 4.2 | 5.2 |
| Relative change | | 0.2 | 0.4 | 0.5 |
| Extensive grasslands | 7.9 | 12.4 | 14.6 | 15.2 |
| Absolute change | | 4.5 | 6.7 | 7.3 |
| Relative change | | 0.6 | 0.8 | 0.9 |

B APPENDIX OF CHAPTER 3

B1 List of ALG publications

Table B 1: List of publications in which the ALGs are described and / or applied.

| Name of the ALG | Main publication | Additional publications |
|---------------------------------|---------------------------------|--|
| AgBioscape | Begg & Dye (2015) | |
| Landscape generator | Engel <i>et al.</i> (2012) | Everaars <i>et al.</i> (2014) |
| <i>DYPAL</i> | Gaucherel <i>et al.</i> (2006) | Gaucherel <i>et al.</i> (2006), Gaucherel <i>et al.</i> (2010), Houet <i>et al.</i> (2010), Gaucherel <i>et al.</i> (2012), Houet <i>et al.</i> (2014), Bonhomme <i>et al.</i> (2017), Gaucherel <i>et al.</i> (2017) |
| <i>SG4GISCAME</i> | Inkoom <i>et al.</i> (2017) | Inkoom <i>et al.</i> (2017) |
| <i>GENEXP-LANDSiTES</i> | Le Ber <i>et al.</i> (2009) | Lavigne <i>et al.</i> (2008), Colbach <i>et al.</i> (2009), Le Ber & Mari (2013) |
| <i>Ddal</i> Landscape simulator | Papaïx <i>et al.</i> (2014) | |
| <i>G-RaFFe</i> | Pe'er <i>et al.</i> (2013) | Pe'er <i>et al.</i> (2011) Dislich <i>et al.</i> (2018) |
| Landscape Generator (LG) | van Strien <i>et al.</i> (2016) | Slager (2011), Slager & de Vries (2013), van Strien & Grêt-Regamey (2016) |

B2 VDP Example

To illustrate the concept of visual dataflow programming (VDP) within the context of agricultural landscape generators (ALGs), the simple example program shown in Fig. 12 is explained in detail. The figure shows a screenshot from a prototype VDP framework implemented by the authors in Scala. The purpose of the example program is to generate a simple patchy "landscape" with a spatially heterogeneous patch size ("Cells" in Fig. 12).

Operations/Nodes

Each box in Fig. 12 represents an operation, afterwards called a node. Nodes can be seen as functions taking parameters (called inputs) and returning results (called outputs). Taking the left-most node *SimplexNoise* as an example, the inputs are the black items on the left in the node, while the outputs are the black items on the right.

SimplexNoise has four inputs (*Freq*[ency], *Oct*[aves], *Min* and *Max*). The accepted data type is noted in short form (e.g., *V[Float]* for floating-point value or *G[Int]* for an integer grid) behind the name of the input. In this example node, none of the inputs is wired from another node, and their values are all set to constants.

SimplexNoise has one output named *Noise*, which has the type floating-point grid. This node generates the image "Density" (Fig. 12).

In addition to the black inputs and outputs, nodes have so-called triggers (left) and ports (right) shown in grey. This special type of "inputs" and "outputs" handles simple trigger signals instead of data, allowing for complex control structures such as iterations and feedback loops. For more details, see Mosconi & Porta (2000).

Data Flow

Data flows from outputs to inputs are shown as curved connections in Fig. 12. As soon as a node has all its inputs available, it "fires" by calculating its outputs and sending the results to all nodes wired to the outputs. In this way, data are propagated through the graph and transformed by nodes until no node has to fire anymore.

In the example in Fig. 12, the program works as follows:

1. Tick

SimplexNoise has all inputs available. It fires and generates the map "Density". The result is propagated to nodes *Normalize* and *Viewer [Density]*.

2. Tick

Viewer [Density] has all inputs available. It fires by opening a new window showing the image "Density" with the screen position and dimensions given by its inputs (*X*, *Y*, *Width*, and *Height*). *Viewer [Density]* generates no output.

Normalize fires and normalizes the output of *SimplexNoise* to the range [0, 0.005]. The result is propagated to *RandomPoints*

3. Tick

RandomPoints fires and generates a grid initially filled with -1 (input *NoData*). Then, each grid cell is set to a unique ID with the probability given by input *Density* (received from node *Normalize*). The result (*IDs*) is propagated to *VoronoiDiagram*. The additional output *Points* (1/0 for point/no point) is not used further.

4. Tick

VoronoiDiagram fires and constructs a Voronoi diagram (output *Cells*) for the point IDs generated by *RandomPoints*, i.e., each grid cell receives the ID of its closest point. Additionally, the distance to the closest point is generated as output *Distance*. *Cells* is propagated to nodes *Viewer [Cells]* and *AsciiFileOutput*. *Distance* is propagated to node *Viewer [Distance]*.

5. Tick

Viewer [Cells] shows image "Cells".

Viewer [Distance] shows image "Distance".

AsciiFileOutput writes the Voronoi tessellation to file *voronoi.asc* in Esri ASCII raster format.

6. Tick: No node can fire, so the program is completed and ends.

Note that points a, b, ... of each tick have no particular order and can inherently be processed in parallel, taking advantage of multi-core architectures.

Note that points a, b, ... of each tick have no particular order and can inherently be processed in parallel, taking advantage of multi-core architectures.

Groups

A feature not shown in the example is "node groups". A node group is an assemblage of nodes encapsulated to be handled as the node itself. Node groups can have inputs and outputs just like ordinary nodes and can be collapsed/minimized in the GUI to appear like nodes.

The purpose of node groups is twofold:

1. Closely related nodes in a program can be grouped to sub-programs and minimised to make the graph clearer.
2. Node groups can be saved to a file and exchanged between users. Later, they can be added to a program graph like ordinary nodes, making VDP programs more modular and reusable.

Automation

In the context of ALGs, a VDP program would often have to run many times, with or without parameter variation. Through the above-mentioned iterations and loops, such automation can be accomplished in the VDP program itself. However, because the program graph and its components (nodes, links) are accessible as a hierarchical data structure that can be manipulated from Java code at runtime, more-convenient means of automation can be easily implemented. Desired possibilities include:

- Setting node inputs when running a program from the command line
- Parameter files that specify node inputs and their variations
- Adaptation of the user interface, allowing one to set variations for inputs

C APPENDIX OF CHAPTER 4

C1 Hare model: ODD protocol

Hare model: ODD protocol

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This documentation follows the ODD protocol (overview, design concepts, details) for describing individual-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010).

The design of the model is based in parts on the Animal Functional Type (AFT) model from Scherer *et al.* (2016) and on the model from Engel *et al.* (2012), which was further developed by Everaars *et al.* (2014).

1. Purpose

The model aims to evaluate the quality of different agricultural land use patterns for the European brown hare (*Lepus europaeus*). In two representative landscapes, the effectiveness of different mitigation measures in bioenergy-driven landscapes is explored. These measures include alternative energy crops and other measures to increase habitat diversity.

2. Entities, state variables and scales

The model includes two types of entities: square grid cells and individuals (hares). Table C 1 gives an overview of these entities and their state variables. Grid cells represent $10 \times 10 \text{ m}^2$ and are characterised by their coordinates and the variables assigned to them. Each grid cell is covered by one of 14 crop types determined by the variable *crop*, from which the variables (1) suitability as forage habitat (*foraging* F_H), (2) suitability as breeding habitat (*breeding* B_H), and (3) crop diversity (*diversity* D_C) are derived.

Suitability as forage habitat, F_H , specifies the suitability of each crop type as a food source. The F_H value ranges from 0.0 (not suitable) to 1.0 (very well-suited). Suitability as breeding habitat, B_H , is defined by the probability that a hare will give birth. The value depends on crop density, crop height and management activities. The B_H value ranges from 0.0 (not suitable) to 1.0 (very well-suited). Crop diversity, D_C , indicates the distribution and quantity of all crop types within the landscape. The D_C value ranges from 0.0 (not suitable) to 1.0 (very well-suited) and is determined according to the number of crop types within the whole landscape.

The geometric mean of all three variables (F_H , B_H , D_C) results in the habitat suitability value (S_H) for each individual grid cell.

$$S_H = \sqrt[3]{F_H \times B_H \times D_C}$$

Hares are characterised by the following state variables: identity number (*who*), location (coordinates x and y at the centre of the grid cell they are on), *age*, *status* (juvenile, female, male) and home range area (Table C 2). Adults are differentiated into females and males.

The hare home ranges in the model landscapes are distributed in a circular shape around the individuals. Females and males have the same home range size in the model, although it can be different in reality. Because the model proceeds in annual steps, juveniles do not have their own home range in the year of birth. In the following year, they are considered sexually mature and are looking for their own home range. The home ranges of several individuals can overlap. However, a grid cell can only be assigned to the home range of a maximum of 10 hares. This method indirectly simulates competition for habitat and avoids unnatural clumping of too many individuals per area. The resulting hare abundance in the base scenario *Uckermark* (3.9 individuals per 100 ha) is comparable to the hare counts in the reference landscape in Brandenburg of 5 individuals per 100 ha (data provided by the BioMove Research Training Group DFG GRK 2118/1).

The model landscapes represent 4×4 km and are composed of agricultural fields of 27.5 ha (*Uckermark*) or 6.8 ha (*Germany*) with a resolution of 10×10 m. To avoid edge effects, the grid is wrapped to a torus. The configuration of the reference landscape *Uckermark* is based on data from a 213 km² area in Brandenburg, North-eastern Germany. The area is part of the long-term research platform *AgroScapeLab Quillow* (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the BioMove Research Training Group (DFG GRK 2118/1). *Uckermark* is characterised by large fields with an average field size of 27.5 ha and a simple landscape structure (Ullmann *et al.*, 2018). For comparison, a second reference landscape was created from the average data of Germany. The literature shows

no average field sizes for Germany, but Brady *et al.* (2012) assumes that there is a correlation between field size and farm size. In 2016, the average farm size in Germany included 61 ha of agricultural land. Accordingly, we assume an average field size of 6.8 ha for our model landscape *Germany*. This makes the field mosaic in *Germany* much more small-scaled and heterogeneous than that in *Uckermark*.

A time step in the model represents one year, and simulations are usually run for 80 time steps.

Table C 1: Entities and state variables of the habitat-based hare model.

| Entity | Variable | Abbreviation | Description | Scale |
|-----------|---------------|--------------|---|------------------------------|
| Landscape | diversity | D_C | Crop diversity of the landscape | 0 – 1 |
| Patches | pxcor, pycor | | Spatial unit on the landscape grid | 1 – 399 |
| | crop | | Crop type of a patch | 1 – 14 |
| | foraging | F_H | Suitability as forage habitat | 0 – 1 |
| | breeding | B_H | Suitability as breeding habitat | 0 – 1 |
| | suitability | S_H | General habitat quality for the hare | 0 – 1 |
| | numberOwners | | Number of hares to whose home range the cell belongs to | 0 – 10 |
| | owner | | Hare to whose home range the cell belongs to | 0 – ∞ (theoretically) |
| Hares | xcor, ycor | | Spatial location of the hare on the landscape grid | 1 – 399 |
| | status | | Hare specification | juvenile / female / male |
| | age | a | Age of the hare | 1 – 13 |
| | home range | | Set of grid cells defined by homeRangeRadius | 2453 (GER), 5525 (UM) |
| | suithomeRange | | Habitat suitability of the home range | 0 – 1 |

Table C 2: Hare parameters of the habitat-based hare model are listed with their value for the standard parameter set.

| Parameter | Abbreviation | Description | Default value |
|----------------------|--------------|--|------------------|
| longevity | <i>a</i> | Maximum age | 13 ^a |
| maturity | <i>a</i> | Sexual maturity | 1 ^b |
| mortalityAdult | | Mortality rate of adults | 0.3 ^c |
| mortalityJuvenile | | Mortality rate of juveniles | 0.5 ^c |
| thresholdSuitability | | Threshold below which survival is not possible | 0.5 ^d |
| homeRangeRadiusUM | | Radius of the home range in <i>Uckermark</i> | 42 ^e |
| homeRangeRadiusGER | | Radius of the home range in <i>Germany</i> | 28 ^f |

^a Although the proportion of hares older than 7 years is very small (2.4 %), it has a potential life span of 13 years (Broekhuizen, 1979).

^b Although female hares born in early spring can reach sexual maturity in autumn, we assume that hares are usually sexually mature by the following year (Broekhuizen & Maaskamp, 1981).

^c Marboutin, E. and Peroux, R. (1995): Survival pattern of European hare in a decreasing population. *Journal of Applied Ecology* 32(4): 809-816.

^d Model validation showed that at a value of 0.5, the difference in population abundance between field data and model output is smallest.

^e Ullmann, W., Fischer, C., Pirhofer-Walzl, K., Kramer-Schadt, S. and Blaum, N. (2018): Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes. *Landscape Ecology* 33(9): 1505-1517.

^f Another landscape in South Germany, Bavaria, investigated by Ullmann *et al.* (2018) with an average field size of 3 ha, showed an average hare home range of 19 ha. Based on these data, we interpolated the presumed average value for Germany to 25 ha. This value is comparable to values of 21 ha in R  he & Hohmann (2004) and 29 ha in Broekhuizen & Maaskamp (1981). A home range of 25 ha corresponds to a radius of 28 grid cells in the model (*Uckermark*), a home range of 55 ha to 42 grid cells (*Germany*).

3. Process overview and scheduling

In each time step (tick), the following submodels are called in the specified order. The names of the corresponding submodels are printed in *italics* and are used both in the submodels section and in the NetLogo code in the appendix. A flowchart of the model process is depicted in Figure C 1.

First, all hares become one year older, and juveniles become adults (*aging*). New adults then try to establish a home range (*establish-home range*); they have three attempts to find a grid cell where they can establish a home range with a suitability about the *suitabilityThreshold*. If they fail, they die. Adults that reached their maximum age die (*die-of-longevity*). In the next step, the crop types are reassigned to all fields each year (*cultivation*). The selection of the crop type per field depends on the field size and the determined crop proportions for each scenario, i.e., no specific crop rotations are taken into account. However, the proportion of a crop type in the entire landscape remains the same throughout each simulation run for each scenario. Next, the landscape is evaluated from the perspective of the hare (*evaluation*). Depending on the crop type, the variables foraging, breeding and diversity are calculated for each grid cell (*calculate-suitability*). The mean value of all habitat suitability values (S_H) within the home range describes the general suitability of the home range as a habitat (*calculate-suithomeRange*). In the next step, all hares search within their home range for a suitable position (*search-homeRange*). To do this, the individuals search for suitable patches as start patches within the home range. The search radius is limited to the home range because hares are a sedentary species, and studies show that they do not significantly expand their home range if their energy requirements are not covered (Smith *et al.*, 2005, Bray *et al.*, 2007). The search patches must have a suitability above the *thresholdSuitability*, which indicates the probability of survival and be occupied by 7 individuals maximum. If these requirements are met, the individual moves to the selected patch and installs its home range. Then, the suitability of the entire home range is calculated. If the hare fails three times in finding a new home range, it dies. Failure occurs either through too low habitat quality or too many other individuals within the search radius. Thus, the number of juveniles and adults alive at the end of each time step is determined by the habitat suitability of the home ranges and the population abundance. Next, all females have 12 to 15 offspring (Marboutin *et al.*, 2003) (*reproduction*). Finally, mortality rates are applied for juveniles and adults (*survival*). Mortality rates reflect the loss due to predation, environmental impacts (e.g., weather conditions) and accidents and are similar to the investigations of Marboutin & Peroux (1995).

Each simulation run ends after 80 years or when the population becomes extinct. The individuals and grid cells are processed in a random order each time step to avoid priority effects.

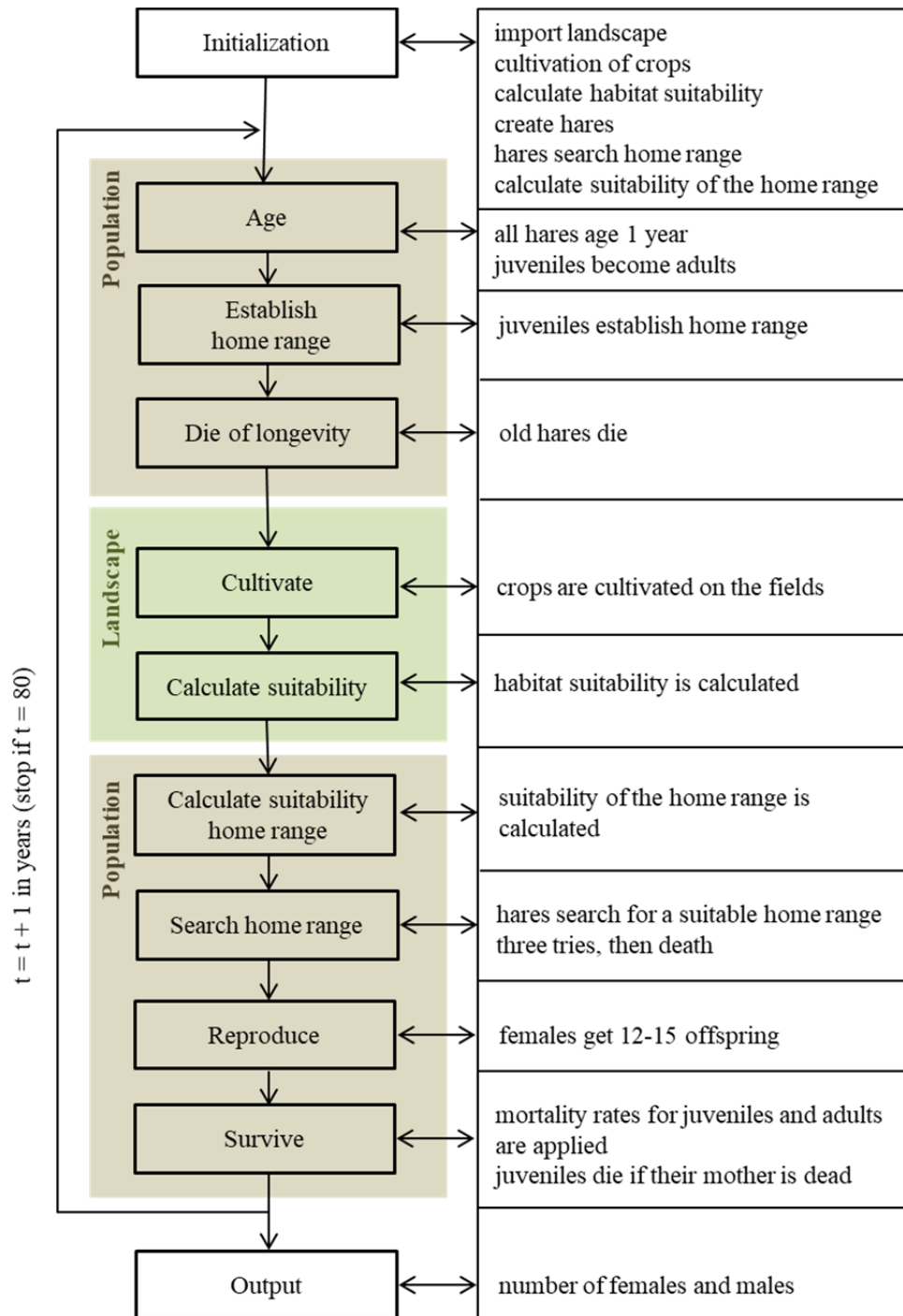


Figure C 1: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 7 *Sub-models*.

4. Design concepts

Basic principles

A basic principle of the model is to assign home ranges according to the quality of the habitat (e.g., Carter *et al.*, 2015) in contrast to home range models that are based on tracking data (e.g., Nabe-Nielsen *et al.*, 2014), although in a simplified way by assuming fixed home range sizes. The evaluation of habitat quality takes place within these fixed home ranges.

Emergence

Hare behaviour is largely imposed, in terms of both home range establishment and selection and demographic rates. Nevertheless, via the assessment of their potential or actual home ranges, the hares respond to changes in landscape structure and hare abundance in an adaptive way.

Adaptation

The hares have to adapt to changing habitat conditions due to a yearly changing crop pattern. Their home ranges are related to the habitat suitability of the arable crops. If they are juveniles or their habitat quality is not sufficient, they must disperse to find a more suitable habitat.

Sensing

The hares receive information about the habitat suitability of all cells of their home range. Furthermore, they know their status (juvenile, female or male) and age and are affected by the overall crop diversity within the model landscape (4×4 km²).

Interaction

An individual can occupy a new home range only if the total number of individuals on each cell of the respective area is less than 10. This means that the hares compete indirectly for available land. Juvenile hares trying to establish a home range only select grid cells as starting points, which are covered by less than 7 hare home ranges.

Stochasticity

The configuration and composition of the landscapes is partly random. (1) The agricultural fields are randomly distributed in the landscape by the landscape generator and (2) randomly assigned with crop types according to predefined percentages. (3) The hares are processed in a random order each time step to avoid priority effects. (4) The offspring are 50% female or male. (5) During dispersal, the target patch is randomly selected. (6) Females obtain a random number between 12 and 15 offspring. (7) Age is random between 1 and 13. All these elements of stochasticity are included to represent natural variation without going into the details of underlying mechanisms.

Observation

The main output value is the average number of females and males for the last 50 years after the end of the simulation. In the first 30 years, the population stabilises; therefore, they are not recorded.

5. Initialization

To initialize the model, a landscape derived from a landscape generator written in C++ using Embacadero RAD Studio 12.0 (available upon request) is imported as a text file. The file must contain numerical values in a space-separated table matching the dimensions of the model landscape from the graphical user interface (GUI). The file input workflow is similar to the method presented in Chapter 5 in Railsback & Grimm (2012).

The applied landscape generator was originally developed to evaluate the impacts of cropping scenarios on different farmland bird species (Engel *et al.*, 2012, Everaars *et al.*, 2014). The model workflow consists of several subsequent steps, whereby only a part of the flow was used for the landscape generation of this study. A complete model description can be found in the original publications. The landscape generator generates a mosaic of agricultural fields with varying shapes, sizes and edge lengths, whereby the landscape configuration depends on the mean field size (in ha). The generation takes place in two steps. First, fields are placed randomly on the landscape grid until all of the area is covered. Second, a correction algorithm replaces all fields that are too small by merging them with neighbouring fields. The emerging field mosaic is adapted to the specified mean field size. For this study, the landscape extent is 4×4 km with a resolution of 10×10 square metres (400×400 grid cells).

Crop types are then distributed to the fields according to the chosen scenario. From each crop type or rather the whole number of crops, the variables (1) suitability as forage habitat, (2) suitability as breeding habitat and (3) crop diversity are derived. The habitat suitability is calculated for each grid cell, and the cells are coloured on a green range with the darkest hue marking the best suitability (select “habitat suitability” view). Next, a number of hares are distributed in the landscape according to the variable *initialPopulation*. The default value is 80 hares corresponding to the data of the real landscape in Brandenburg, Germany. Age is assigned randomly between 1 and 13, and gender is either female or male with the same probability. After the first placement, the hares search for a suitable position with sufficient habitat suitability within their home range and claim it. If there is no position available, the hare is removed from the grid.

6. Input data

The model does not use any input data that would represent external factors that vary in time.

7. Submodels

Ageing

Because the model follows an annual rhythm, all individuals get one year older in each time step. Juveniles become adults and search within a radius of 150 grid cells for their own home range (*establish-home range*). If they do not succeed at three, they die. When individuals grow 13 years old, they die (*die-of-longevity*).

Cultivation

Each cell is assigned a new crop type. Fourteen different crop types are available for selection: alfalfa, barley, beets, grassland, grass-clover ley, maize, miscanthus, oilseed rape, pasture, rye, set-aside, mixed silphie, triticale and wheat. The proportion of a certain crop type in the landscape is defined by a cultivation probability. Table C 3 shows the cultivation probabilities of all crop types for each scenario.

Table C 3: The simulated crop proportions for each of the 14 crops and for each scenario. The two base scenarios (UM, GER) match the crop distributions in the reference landscape Uckermark and the average distribution in Germany 2017 for the ten most common crops. For each base scenario, six mitigation strategies are explored: three alternative energy plant scenarios and three crop composition scenarios. For the alternative energy plant scenarios (AE1-AE3), the proportions of mixed silphie, miscanthus and grass-clover ley were increased by 10% in each case. For the first two crop composition scenarios (CC1, CC2), the proportions of alfalfa and set-aside were increased by 10% in each case. Crop composition scenario 3 (CC3) integrates all 14 crops in the landscape. Key changes are displayed in bold. Further details on the scenarios are provided in the Methods section.

| | Crop proportion [%] | | | | | | | | UM | AE1 | AE2 | AE3 | CC1 | CC2 | CC3 |
|------------------|---------------------|-------------|-------------|-------------|-------------|-------------|------|------|-------------|-------------|-------------|-------------|-------------|------|------|
| | | | | | | | | | | | | | | | |
| Wheat | 37.5 | 37.5 | 37.5 | 37.5 | 37.5 | 37.5 | 23.2 | 20.7 | 20.7 | 20.7 | 20.7 | 20.7 | 20.7 | 20.7 | 14.0 |
| Oilseed rape | 18.7 | 18.7 | 8.7 | 18.7 | 10.2 | 10.2 | 11.6 | 8.3 | 8.3 | 0.0 | 8.3 | 0.0 | 0.7 | 5.6 | |
| Maize | 15.0 | 5.0 | 15.0 | 5.0 | 15.0 | 15.0 | 9.3 | 17.8 | 7.8 | 16.1 | 7.8 | 16.1 | 17.8 | 12.0 | |
| Barley | 9.2 | 9.2 | 9.2 | 9.2 | 9.2 | 9.2 | 5.9 | 11.3 | 11.3 | 11.3 | 11.3 | 11.3 | 11.3 | 7.7 | |
| Grassland (ext.) | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.0 | 12.5 | 12.5 | 12.5 | 12.5 | 12.5 | 12.5 | 8.5 | |
| Pasture (int.) | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.3 | 5.0 | 18.1 | 18.1 | 18.1 | 18.1 | 18.1 | 18.1 | 12.3 | |
| Beets | 4.5 | 4.5 | 4.5 | 4.5 | 4.5 | 4.5 | 5.0 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 5.0 | |
| Alfalfa | 1.5 | 1.5 | 1.5 | 1.5 | 10.0 | 1.5 | 5.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 5.0 | |
| Set-aside | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 10.0 | 5.0 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 10.0 | 5.0 | |
| Rye | 1.4 | 1.4 | 1.4 | 1.4 | 1.4 | 1.4 | 5.0 | 3.6 | 3.6 | 3.6 | 3.6 | 3.6 | 3.6 | 5.0 | |
| Triticale | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 2.4 | 5.0 | |
| Silphie | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | |
| Miscanthus | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 | 5.0 | |
| Grass-clover ley | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 5.0 | |

Evaluation

First, the variables (1) suitability as forage habitat (foraging F_H), (2) suitability as breeding habitat (breeding B_H) and (3) crop diversity (diversity D_C) are derived from each crop type or rather the whole number of crops. Table C 4 and Table C 5 give an overview of the assessment criteria. Suitability as a foraging habitat specifies suitability as a food source for each crop type. The F_H value ranges from 0.0 (not suitable) to 1.0 (very well-suited). Suitability as breeding habitat is defined by the probability that a hare will give birth. The value depends on crop density, crop height, production system and sudden alteration. The B_H value ranges from 0.0 (not suitable) to 1.0 (very well-suited). Crop diversity indicates the distribution and quantity of all crop types within the landscape. The D_C value ranges from 0.0 (not suitable) to 1.0 (very

well-suited) and is determined according to the number of crop types within the whole landscape.

The geometric mean of all three variables (F_H , B_H , D_C) results in the habitat suitability value (S_H) for each individual grid cell.

$$S_H = \sqrt[3]{F_H \times B_H \times D_C}$$

Based on this value, the mean habitat suitability of each hare home range is calculated.

Table C 4: Habitat characteristics of the crop types considered in this study. The suitability values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on the literature. Values in italics have an intermediate value of 0.5 due to a lack of information to estimate them. Details can be found in the Appendix C2.

| Crop type | Suitability as forage habitat (F_H) | Suitability as breeding habitat (B_H) |
|------------------|---|---|
| Alfalfa | 0.75 | 0.25 |
| Barley | 0.75 | 0.75 |
| Beets | 0.75 | <i>0.50</i> |
| Grassland (ext.) | 0.75 | 0.75 |
| Grass-clover ley | 0.75 | 0.50 |
| Maize | 0.50 | 0.25 |
| Miscanthus | 0.00 | 0.25 |
| Oats | <i>0.50</i> | <i>0.50</i> |
| Oilseed rape | 0.25 | 0.25 |
| Pasture (int.) | 0.25 | 0.25 |
| Rye | <i>0.50</i> | <i>0.50</i> |
| Set-aside | 1.00 | 1.00 |
| Silphie | <i>0.50</i> | 0.75 |
| Triticale | <i>0.50</i> | <i>0.50</i> |
| Wheat | 0.75 | 0.75 |

Table C 5: Crop diversity in terms of the number of crop types in the model landscapes. The crop diversity value ranges from 0.0 (not suitable) to 1.0 (very well-suited).

| Number of crops types | Crop diversity D_C |
|-----------------------|----------------------|
| 5 - 10 | 0.60 |
| 11 - 13 | 0.80 |
| > 14 | 1.00 |

Dispersal

After crop cultivation each year, all adult hares search within their home range for a suitable new position from where to establish a new home range. Therefore, the individual selects a suitable cell in the home range (habitat suitability ≥ 0.5 , number of owners ≤ 7) and moves there. Then, it calculates the mean habitat suitability for the prospective home range. If it is sufficient, the hare stays there and establishes its home range. As a consequence, habitat suitability is increased by 0.2 in all grid cells of the original home range and decreased by 0.2 in all cells of the new home range. If the conditions do not apply, the hare searches for a new target cell and tries to find a suitable home range in the same way. If that does not work either, it succeeds in the third try or dies.

Reproduction

Every year sexually mature females get 12 to 15 offspring (Marboutin *et al.*, 2003). The number of offspring is selected at random.

Survival

The individuals die after a maximum of 13 years of life. They die earlier if the habitat suitability is not sufficient to feed them and they cannot find a new position. Offspring in the first year die when the mother dies. In addition, there is a fixed mortality rate to reflect predation, environmental impacts (e.g., weather conditions) and accidents. The mortality rate for juveniles is 20 % higher than for adults (Marboutin & Peroux, 1995).

8. Acknowledgements

M.L. thanks Wiebke Ullmann for the provision of data of the research platform *AgroScapeLab Quillow* (Agricultural Landscape Laboratory Quillow) established by the Leibniz Centre for Agricultural Landscape Research (ZALF) as well as data gained by the BioMove Research Training Group (DFG GRK 2118/1). Furthermore, M.L. thanks Wiebke Ullmann for helpful knowledge on the ecology and behaviour of the brown hare.

C2 Hare-specific preferences

The following is an overview of the literature on the ecology of the European hare (*Lepus europaeus*), which we have used to assess foraging and breeding preferences.

Foraging

A study by Reichlin *et al.* (2006) has shown that hares prefer winter wheat and spring barley in spring, while in summer, when the grain is harvested, they switch to sugar beet, maize and sunflower. Wheat is especially important in spring in the form of seedlings of winter wheat (Pepin & Angibault, 2007, Bertolino *et al.*, 2011). Maize is a frequently used food plant in spring and summer but becomes more indigestible with increasing maturation (Bertolino *et al.*, 2011). High stocks of maize are avoided by hares. Lucerne and the other forage legumes as clovers become important in the spring-summer when the digestibility of cereals is reduced due to maturation or harvest took place (Santilli *et al.*, 2014). Oilseed rape is generally avoided by hares (Schai-Braun *et al.*, 2013). Frylestam (1986) suspects that the content of glucosinolates could be the reason. Hares tend to eat oilseed rape as seedlings (Lewandowski & Nowakowski, 1993) or in cases of a lack of alternatives, e.g., in monocultures (Frylestam, 1986). An eight-year study by Nyenhuis (1999) in north-west Germany showed that grain and maize fields have overall positive effects on the hare population, while areas where root crops such as sugar beet and potatoes dominate tend to have a negative effect. In a study by Vaughan *et al.* (2003), hares were relatively common on arable farms with wheat, beet or set-aside and less common on pastoral areas. Other studies have also shown that certain types of grassland are unfavourable for hares (Smith *et al.*, 2004, Smith *et al.*, 2005, Zellweger-Fischer *et al.*, 2011, Schai-Braun *et al.*, 2013). It is particularly unfavourable if it is often mowed or intensively grazed, such as pastures (Barnes *et al.*, 1983). Strong grazing pressure leads to a low heterogeneous structure and decreasing hare numbers (Smith *et al.*, 2004, Lush *et al.*, 2014). In contrast, unimproved grasslands with a heterogeneous structure or species-rich pastures lead to higher hare numbers (Schai-Braun *et al.*, 2013). The two crop types pasture and grassland in the model are intended to represent two intensity levels: pasture as intensively grazed area and grassland as extensively used area. A perennial grass-clover ley offers a high level of cover and forage availability to hares (Santilli, 2006) and is more attractive than pastures (Frylestam, 1986). Clover as forage legume becomes especially important in spring and summer when cereals start to ripen and their digestibility is reduced (Santilli *et al.*, 2014) or after they were harvested (Reichlin *et al.*, 2006). The same applies to peas, which are also considered to be forage legumes for hares (Chapuis, 1990, Vaughan *et al.*, 2003). Set-asides with low to medium height and favourable plant composition are a very important foraging habitat for hares (Reichlin *et al.*, 2006, Gevers *et al.*,

2011, Meichtry-Stier *et al.*, 2014, Langhammer *et al.*, 2017). It offers a high amount and variety of wild herbs and grasses, which are an essential part of the hare diet. However, if the vegetation becomes too high and dense, hares avoid these areas (Schai-Braun *et al.*, 2013). The bioenergy crop miscanthus is entirely avoided as food, even young sprouts (Petrovan *et al.*, 2017). For the new promising alternative to maize, mixed silphie, there are still no evaluations for hares. The study by Van Tassel *et al.* (2017) describes a forage quality comparable to alfalfa for cattle. For our study, we assume an average value of 0.5 for the forage quality of mixed silphie.

Breeding

Management activities and protection against predators are the two main drivers for breeding success in our model. Regarding management, crop harvesting operations are a notable source of mortality for leverets (Milanov, 1996). Kałuziński & Pielowski (1976) found that leveret losses were high in forage and grass fields (lucerne, grass meadow and clover) and much lower in arable crop fields (spring barley and winter wheat). This is mainly because forage crops for silage will be harvested starting in May. Lucerne harvesting takes place several times a year. Additionally, intensively used grassland is an unfavourable breeding habitat due to the multiple mowing (McLaren *et al.*, 1997). At the time of harvesting winter cereals, most young hares are old enough to escape (Kałuziński & Pielowski, 1976). Pepin (1989) found that leverets have a good survival rate until April, as there are enough forage plants and fewer disturbances by agricultural practices. However, if the landscape consists mainly of spring cereals, maize or potatoes, breeding success is limited by harrowing and rolling in March-April (Durdik, 1981). Kałuziński & Pielowski (1976) found maximum densities of leverets in March on ploughed fields. Harvesting not only has a mechanical influence by machines but also leads to a lack of protection against predators and weather conditions (Pepin, 1989). Petrovan *et al.* (2017) found that hares are able to exist and even thrive in miscanthus fields, even when they avoid it as a food source. Mixed silphie offers coverage for hares from the beginning of April. If the stands are harvested by mid-September, the rootstock will form new rosette leaves until snow falls. These offer a good cover in autumn (protection from wind, rain and predators).

C3 Results of sensitivity analysis

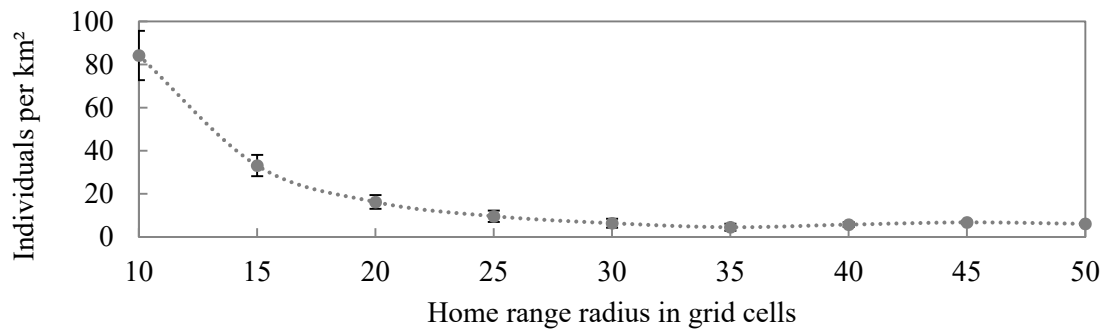


Figure C 2: Effect of the home range size on the mean population abundance in the base scenario *Uckermark*. Bars indicate the standard deviation of 100 replicates.

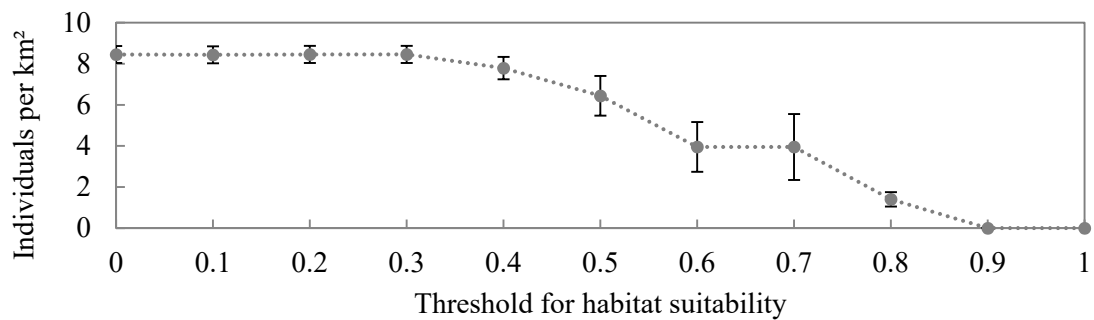


Figure C 3: Effect of the habitat suitability threshold on the mean population abundance in the base scenario *Uckermark*. Bars indicate the standard deviation of 100 replicates.

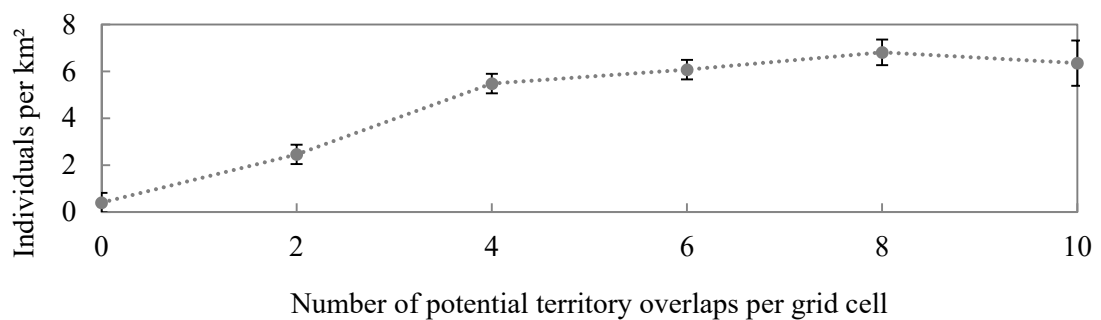


Figure C 4: Effect of the number of potential territory overlaps per grid cell on the mean population abundance in the base scenario *Uckermark*. Bars indicate the standard deviation of 100 replicates.

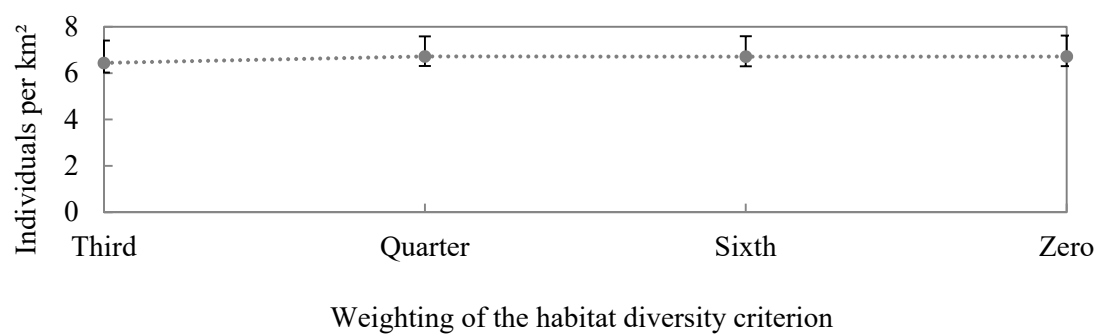


Figure C 5: Effect of the weighting percentage of the habitat diversity criterion on the mean population abundance in the base scenario *Uckermark*. Bars indicate the standard deviation of 100 replicates.

C4 Hare model code

```

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;
;;;GLOBALS;
;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

extensions
[
  profiler
  Rnd
  Table
]

globals
[
; thresholdSuitability    ;; [#]          ;; moved to interface; minimum threshold for habitat suitability
; totalcrops              ;; [#]          ;; number of crops in the landscape
; totalfields             ;; [#]          ;; number of fields in the landscape
; crop-list               ;; [number]     ;; list of all crops within the landscape
; fieldID-list            ;; [number]     ;; list of all field IDs within the landscape
; cropToSuit              ;; table        ;; table with foraging and breeding values for each crop
; diversity               ;; [number, 0-1] ;; diversity of crop types within the landscape
; fieldTable              ;; table        ;; table with fieldIDs and number of patches for each field
; fieldList               ;; list         ;; list of fieldIDs and number of patches for each field
; cropProbability         ;; list         ;; list of cultivation probabilities for each crop
; homeRangeRadius         ;; [cells]    ;; radius of the home range
; crowded-patches
; numJuvenilesDied
]

turtles-own
[
  status                ;; [string]    hare specification: juvenile, female, male
  age                   ;; [a]          age of the individuals
  longevity             ;; [a]          maximum age
  maturity              ;; [a]          sexual maturity
; mortalityAdult        ;; [%]         ;; moved to interface; mortality rate of adults
; mortalityJuvenile     ;; [%]         ;; moved to interface; mortality rate of juveniles
; suithomeRange          ;; [number, 0-1] mean habitat suitability of all grid cells within a homeRange
; homeRange             ;; [cells]     grid cells which belong to the homeRange
; homeRangeNumber       ;; [number]    number of cells which belong to the homeRange VV is the same for all
]

patches-own
[
  fieldID              ;; [#]          field ID number
  crop                 ;; [string]    crop type grown on the field
  breeding             ;; [number, 0-1] suitability as breeding habitat
  foraging             ;; [number, 0-1] suitability as forage habitat
  suitability           ;; [number, 0-1] habitat suitability of the cell
  numberOwners         ;; [#]          number of hares to whose homeRange the cell belongs to
  owner                ;; [turtle]    owner of the patch
]

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

```

APPENDICES

```
;;SETUP+GO;
;;;;;;;;;;;;;
;;;;;;;;;;;;;

;;SETUP;
;;;;;;;;;;;;;

to setup

    clear-all

    init-landscape          ;; imports the landscape from a text file
    init-cultivation        ;; crops are cultivated on the fields
    init-calculate-suitability ;; calculates habitat suitability for each cell
    init-hares              ;; ceates the initial population
    init-search-homeRange   ;; hares search for a suitable, occupyable homeRange
    init-calculate-suithomeRange ;; calculates habitat suitability of the homeRange
    init-update-view

    set crowded-patches no-patches

    reset-ticks
    reset-timer

    if View = "fields" or View = "crops" or View = "OFF" or View = "territories" or View = "habitat suitability" [ update-view ]      ;; update of world interface (see "to update-view")...

end

;;GO;
;;;;;;;;;;;;;
;;;;;;;;;;;;;

to go

    ask turtles [ set age age + 1 ]

    ask turtles with [status = "juvenile"] [ establish-homeRange ]

    ask turtles with [ age > longevity ][ die-of-longevity ]

    cultivate                ;; the crops on the fields are cultivated anew every year
    calculate-suitability     ;; calculates habitat suitability for each cell
    calculate-suithomeRange   ;; calculates habitat suitability of the homeRange
    search-homeRange         ;; adults and juveniles search for a suitable, occupyable homeRange
    reproduce               ;; females get offspring
    survive                  ;; specific mortality rates are applied to adults and juveniles
    update-view              ;; update of world interface
    tick                    ;; t = t + 1

end

;;;;;;;;;;;;;
;;;;;;;;;;;;;
;;INITIALISATION;
;;;;;;;;;;;;;
;;;;;;;;;;;;;

;;LANDSCAPE;
;;;;;;;;;;;;;
;;;;;;;;;;;;;

to init-landscape

    set fieldID-list []

    ifelse Landscape = "Germany" [ file-open "landscape_6.8ha.txt" ] [ file-open "landscape_27.5ha.txt" ]      ;; the landscape is imported
    while [not file-at-end?]
    [
        let next-x file-read
        let next-y file-read
        let next-fieldID file-read
```

```

        set fieldID-list fput next-fieldID fieldID-list
        ask patch next-x next-y
        [
            set fieldID next-fieldID
        ]
    ]

    file-close

    ask patches
    [
        set numberOwners 0
    ]
    ;; all cells are unoccupied at the beginning

end

;;Cultivation;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to init_cultivation

    set fieldTable table:group-agents patches [fieldID]
    set fieldList table:to-list fieldTable
    corresponding set of patches
    ;; creates a table with index/key "fieldID" and the agentset of patches as value
    ;; transforms the table into list of elements, which are lists with elements themselves: the fieldID, and the

    let no 0
    ;; counts entries in the fieldList

    foreach fieldList
    [
        [x] -> set fieldList replace-item no fieldList list (item 0 x) (count item 1 x)
        ;; element number "no" of the fieldList is replaced with a two-item list: [(fieldID) (number of patches with that
        set no no + 1
    ]

    if (Landscape = "Uckermark" and Scenario = "Basic")
    [
        set cropProbability [["wheat" 0.375] ["rape" 0.187] ["maize" 0.150] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
        ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
    ]
    ;; probability that a crop is selected for each scenario

    if (Landscape = "Uckermark" and Scenario = "Silphie")
    [
        set cropProbability [["wheat" 0.375] ["rape" 0.187] ["silphie" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
        ["maize" 0.050] ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
    ]

    if (Landscape = "Uckermark" and Scenario = "Miscanthus")
    [
        set cropProbability [["wheat" 0.375] ["maize" 0.150] ["miscanthus" 0.100] ["barley" 0.092] ["rape" 0.087] ["grassland" 0.053] ["pasture" 0.053]
        ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
    ]

    if (Landscape = "Uckermark" and Scenario = "Grass-clover ley")
    [
        set cropProbability [["wheat" 0.375] ["rape" 0.187] ["grass-clover ley" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
        ["maize" 0.050] ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
    ]

    if (Landscape = "Uckermark" and Scenario = "Alfalfa")
    [
        set cropProbability [["wheat" 0.375] ["maize" 0.150] ["rape" 0.102] ["alfalfa" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
        ["beets" 0.045] ["set-aside" 0.015] ["rye" 0.014]]
    ]

    if (Landscape = "Uckermark" and Scenario = "Set-aside")
    [
        set cropProbability [["wheat" 0.375] ["maize" 0.150] ["rape" 0.102] ["set-aside" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
        ["beets" 0.045] ["alfalfa" 0.015] ["rye" 0.014]]
    ]

    if (Landscape = "Uckermark" and Scenario = "Crop diversity")

```

APPENDICES

```
[
  set cropProbability [{"wheat" 0.232} {"rape" 0.116} {"maize" 0.093} {"barley" 0.059} {"grassland" 0.050} {"pasture" 0.050}
    {"beets" 0.050} {"alfalfa" 0.050} {"set-aside" 0.050} {"rye" 0.050} {"triticale" 0.050} {"silphie" 0.050}
    {"miscanthus" 0.050} {"grass-clover ley" 0.050}]
]

if (Landscape = "Germany" and Scenario = "Basic")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"maize" 0.178} {"grassland" 0.125} {"barley" 0.113} {"rape" 0.083}
    {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"set-aside" 0.024}]
]

if (Landscape = "Germany" and Scenario = "Silphie")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"grassland" 0.125} {"barley" 0.113} {"silphie" 0.100} {"rape" 0.083}
    {"maize" 0.078} {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"set-aside" 0.024}]
]

if (Landscape = "Germany" and Scenario = "Miscanthus")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"maize" 0.161} {"grassland" 0.125} {"barley" 0.113}
    {"miscanthus" 0.100} {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"set-aside" 0.024}]
]

if (Landscape = "Germany" and Scenario = "Grass-clover ley")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"grassland" 0.125} {"barley" 0.113} {"grass-clover ley" 0.100} {"rape" 0.083}
    {"maize" 0.078} {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"set-aside" 0.024}]
]

if (Landscape = "Germany" and Scenario = "Alfalfa")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"maize" 0.161} {"grassland" 0.125} {"barley" 0.113}
    {"alfalfa" 0.100} {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"set-aside" 0.024}]
]

if (Landscape = "Germany" and Scenario = "Set-aside")
[
  set cropProbability [{"wheat" 0.207} {"pasture" 0.181} {"maize" 0.178} {"grassland" 0.125} {"barley" 0.113} {"set-aside" 0.100}
    {"rye" 0.036} {"beets" 0.028} {"triticale" 0.024} {"rape" 0.007}]
]

if (Landscape = "Germany" and Scenario = "Crop diversity")
[
  set cropProbability [{"wheat" 0.140} {"pasture" 0.123} {"maize" 0.120} {"grassland" 0.085} {"barley" 0.077} {"rape" 0.056}
    {"beets" 0.050} {"alfalfa" 0.050} {"set-aside" 0.050} {"rye" 0.050} {"triticale" 0.050} {"silphie" 0.050}
    {"miscanthus" 0.050} {"grass-clover ley" 0.050}]
]

set cropProbability reverse cropProbability

foreach cropProbability                                     ;; go through the list of crop types and their proportions and add, for each croptype, fields
[
  [x] -> let proportion item 1 x
    let croptype item 0 x

  set proportion proportion * count patches
  let fieldSublist []
  foreach fieldList
  [
    [y] -> if item 1 y <= (proportion * 80 / 100) [ set fieldSublist fput y fieldSublist ]    ;; creates a sublist with fields whose area is (-20 %) smaller than the required crop proportion (proportion - 20
%, to avoid too large sums later)
  ]

  let summe 0
  let itemNumber 0
  let itemNumber2 0                                         ;; sums up field sizes
                                                           ;; item number in sublist
                                                           ;; item number in fieldList

  while [ (summe <= (proportion * 85 / 100)) and (length fieldList > 0) ]    ;; while the sum is (- 15 %) smaller than the required proportion, additional fields are selected from the sublist
  [
    let selectedField one-of fieldSublist
    set itemNumber position selectedField fieldSublist    ;; proportion - 15 %, to avoid too large sums later
                                                           ;; selects one of fieldSublist
  ]
]
```

```

        set itemNumber2 position selectedField fieldList
        let field item 0 selectedField
        set summe summe + item 1 selectedField

        ask table:get fieldTable field [ set crop croptype ]
        set fieldSublist remove-item itemNumber fieldSublist
        ifelse length fieldList > 0
        [ set fieldList remove-item itemNumber2 fieldList ]
        [ set summe 9999999 ]
    ]
]

let itemNumber2 0

while [ length fieldList > 0 ]
[
    let selectedField one-of fieldList
    set itemNumber2 position selectedField fieldList
    let field item 0 selectedField
    ask table:get fieldTable field [ set crop "wheat" ]
    set fieldList remove-item itemNumber2 fieldList
]

set fieldID-list remove-duplicates fieldID-list
set totalfields length fieldID-list

set crop-list []
ask patches [ set crop-list fput crop crop-list ]
set crop-list remove-duplicates crop-list
set totalcrops length crop-list

end

;;CALCULATESUITABILITY;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to init_calculate-suitability

    set cropToSuit table:make
    foraging and breeding

    table:put CropToSuit "wheat"      [ 0.75 0.75 ]
    table:put CropToSuit "rape"       [ 0.25 0.25 ]
    table:put CropToSuit "maize"      [ 0.50 0.25 ]
    table:put CropToSuit "barley"     [ 0.75 0.75 ]
    table:put CropToSuit "grassland"  [ 0.75 0.75 ]
    table:put CropToSuit "pasture"    [ 0.25 0.25 ]
    table:put CropToSuit "beets"      [ 0.75 0.50 ]
    table:put CropToSuit "alfalfa"    [ 0.75 0.25 ]
    table:put CropToSuit "set-aside"  [ 1.00 1.00 ]
    table:put CropToSuit "rye"        [ 0.50 0.50 ]
    table:put CropToSuit "triticale"  [ 0.50 0.50 ]
    table:put CropToSuit "silphie"    [ 0.50 0.75 ]
    table:put CropToSuit "miscanthus" [ 0.00 0.25 ]
    table:put CropToSuit "grass-clover ley" [ 0.75 0.50 ]

    if ( totalcrops >= 5 ) and ( totalcrops <= 10 ) [ set diversity 0.60 ]
    if ( totalcrops >= 11 ) and ( totalcrops <= 13 ) [ set diversity 0.80 ]
    if ( totalcrops >= 14 ) [ set diversity 1.00 ]

    ask patches
    [
        set foraging (item 0 table:get cropToSuit crop)
        set breeding (item 1 table:get cropToSuit crop)
        set suitability (foraging * breeding * diversity)
        set suitability suitability ^ (1 / 3)
        set suitability precision suitability 2
    ]
]

end

;; assign fieldID to "field"
;; assign field size of this field to "summe"

;; assign croptype to this field
;; remove selected field from the sublist

;; remove selected field from the main list
;; high value for summe to make the while loop stop

;; if fields are left, assign the most frequent crop "wheat" to them
;; assign fieldID to "field", item 0 is the smallest field

;; assign croptype to this field

;; the number of fields in the landscape is counted

;; the number of crops in the landscape is counted

;; crop is taken as the index of the table, each entry then has a list of two values, for the suitability of

;; the crop diversity is derived from the number of crops in the landscape

;; foraging * breeding * diversity
;; the geometric mean of foraging, breeding and diversity results in the general suitability of the cell

```


APPENDICES

```

;;Hares;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to init_hares

    crt initialPopulation                                ;; creates initial population
    ask patches [ set owner [] ]

    ask turtles
    [
        set size 10
        setxy random-pxcor random-pycor

        init_calculate-parameters                        ;; calculates all population parameters that are needed to setup the model

        set age random longevity + maturity              ;; minimum age 1, maximum age 13
        set status one-of ["female" "male"]              ;; random distribution of females and males
        if status = "female" [ set color red ]
        if status = "male" [ set color blue ]
        set homeRange patches in-radius homeRangeRadius
        ask homeRange
        [
            set owner fput myself owner
            set numberOwners numberOwners + 1
            if numberOwners > 1 [ set suitability (suitability - 0.02) ]    ;; if the cell belongs to two territories, the suitability is reduced by 0.02
        ]
    ]
end

;;CALCULATEHAREPARAMETERS;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to init_calculate-parameters

    set longevity 13
    set maturity 1
    ;; set mortalityAdult 0.3                                ;; moved to interface
    ;; set mortalityJuvenile 0.5                            ;; moved to interface
    ;; set thresholdSuitability 0.5                        ;; moved to interface
    ifelse (Landscape = "Uckermark") [set homeRangeNumber 5525] [set homeRangeNumber 2453]    ;; cells which belong to the homeRange
    ifelse (Landscape = "Uckermark") [set homeRangeRadius homeRangeRadiusUM] [set homeRangeRadius homeRangeRadiusGER]

end

;;SEARCHTERRITORY;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to init_search-homeRange

    ask turtles with [(suithomeRange < thresholdSuitability) or (any? homeRange with [numberOwners > 10])]
    [
        ask homeRange
        [
            set owner remove myself owner
            set numberOwners numberOwners - 1
            set owner remove nobody owner
            if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
        ]
        let searchPatches patches in-radius homeRangeRadius with [(numberOwners < 7) and (suitability >= thresholdSuitability)] ;; hares search for suitable patches
        ifelse any? searchPatches
        [
            move-to one-of searchPatches                    ;; 1st try: hares move to one of the suitable patches
            set homeRange patches in-radius homeRangeRadius
            ifelse any? homeRange with [numberOwners > 10]    ;; if there are too many hares within the home range, they search for another suitable patch
            [
                move-to one-of searchPatches                ;; 2nd try: hares move to one of the suitable patches
                set homeRange patches in-radius homeRangeRadius
                ifelse any? homeRange with [numberOwners > 10]    ;; if there are too many hares within the home range, they search for another suitable patch
            ]
        ]
    ]
end

```

```
[
    move-to one-of searchPatches
    set homeRange patches in-radius homeRangeRadius
    ifelse any? homeRange with [numberOwners > 10]
    [
        die
    ]
    [
        ask homeRange
        [
            set owner fput myself owner
            set numberOwners numberOwners + 1
            if numberOwners > 1 [ set suitability (suitability - 0.02) ]
        ]
    ]
]
[
    ask homeRange
    [
        set owner fput myself owner
        set numberOwners numberOwners + 1
        if numberOwners > 1 [ set suitability (suitability - 0.02) ]
    ]
]
]
[
    ask homeRange
    [
        set owner fput myself owner
        set numberOwners numberOwners + 1
        if numberOwners > 1 [ set suitability (suitability - 0.02) ]
    ]
]
]
[
    die
]
]
end

;; CALCULATE HABITAT SUITABILITY OF TERRITORIES
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
to init_calculate-suihomeRange
    ask turtles
    [
        set suihomeRange ((sum [suitability] of homeRange) / homeRangeNumber) ;; the suitability of the homeRange is calculated
        set suihomeRange precision suihomeRange 2
    ]
end

;; UPDATE VIEW
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
to init_update-view
    if View = "fields"
    [
        ask turtles [ show-turtle ]
        ask patches
        [
            set pcolor scale-color orange fieldID 2732 3493
        ]
    ]
    if View = "crops"
    [
```

APPENDICES

```
ask turtles [ show-turtle ]
ask patches
[
  if crop = "wheat" [set pcolor 26]
  if crop = "rape" [set pcolor 46]
  if crop = "maize" [set pcolor 126]
  if crop = "barley" [set pcolor 36]
  if crop = "grassland" [set pcolor 66]
  if crop = "pasture" [set pcolor 56]
  if crop = "beets" [set pcolor 136]
  if crop = "alfalfa" [set pcolor 126]
  if crop = "set-aside" [set pcolor 76]
  if crop = "rye" [set pcolor 16]
  if crop = "triticale" [set pcolor 6]
  if crop = "oats" [set pcolor 86]
  if crop = "grass-clover ley" [set pcolor 96]
  if crop = "ryegrass" [set pcolor 106]
  if crop = "peas" [set pcolor 62]
]
]

if View = "habitat suitability"
[
  let edge-patches []
  ask patches
  [
    if suitability >= thresholdSuitability [ set pcolor scale-color green suitability 1 0 ]
    if suitability < thresholdSuitability [ set pcolor scale-color grey suitability 0 0.5 ]
    if numberowners < 0 [set pcolor 0]
  ]

  ask turtles
  [
    show-turtle
    set edge-patches homeRange with [any? neighbors with [ owner != [owner] of myself ] ]
    ask edge-patches [ set pcolor [ color ] of myself - 2 ]
  ]
]

if View = "territories"
[
  ask patches
  [
    if suitability >= thresholdSuitability [ set pcolor scale-color green suitability 1 0 ]
    if suitability < thresholdSuitability [ set pcolor scale-color grey suitability 1 0 ]
  ]
  ask turtles
  [
    ask homeRange [ set pcolor [color] of myself + 2]
    let edge-patches homeRange with [any? neighbors with [ owner != [owner] of myself ] ]
    ask edge-patches [ set pcolor [ color ] of myself - 2 ]
    show-turtle
  ]
]

if View = "OFF"
[
  ask patches [ set pcolor black ]
  ask turtles [ hide-turtle ]
]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;
;;PROCEDURES;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;AGING;
;
```

```

to establish-homeRange
    set status one-of ["female" "male"]
    if status = "female" [ set color red ]
    if status = "male" [ set color blue ]

    let searchPatches patches in-radius 150 with [(numberOwners < 7) and (suitability >= thresholdSuitability)]
    ifelse any? searchPatches
    [
        move-to one-of searchPatches
        set homeRange patches in-radius homeRangeRadius
        ifelse any? homeRange with [numberOwners > 10]
        [
            move-to one-of searchPatches
            set homeRange patches in-radius homeRangeRadius
            ifelse any? homeRange with [numberOwners > 10]
            [
                move-to one-of searchPatches
                set homeRange patches in-radius homeRangeRadius
                ifelse any? homeRange with [numberOwners > 10]
                [
                    die
                ]
            ]
            [
                set homeRange patches in-radius homeRangeRadius
                ask homeRange
                [
                    set owner fput myself owner
                    set numberOwners numberOwners + 1
                    if numberOwners > 1 [ set suitability (suitability - 0.02) ]
                ]
            ]
        ]
    ]
    [
        set homeRange patches in-radius homeRangeRadius
        ask homeRange
        [
            set owner fput myself owner
            set numberOwners numberOwners + 1
            if numberOwners > 1 [ set suitability (suitability - 0.02) ]
        ]
    ]
    [
        set homeRange patches in-radius homeRangeRadius
        ask homeRange
        [
            set owner fput myself owner
            set numberOwners numberOwners + 1
            if numberOwners > 1 [ set suitability (suitability - 0.02) ]
        ]
    ]
    [
        die
    ]
end

to die-of-longevity
    ask homeRange
    [
        set owner remove myself owner
        set numberOwners numberOwners - 1
        set owner remove nobody owner
        if numberOwners >= 1
        [
            set suitability (suitability + 0.02)
            set suitability precision suitability 2
        ]
    ]
end

```

;; juveniles procedure: they become adults and search for homeRange

;; hares search for suitable patches

;; 1st try: hares move to one of the suitable patches

;; if there are too many hares within the home range, they search for another suitable patch

;; 2nd try: hares move to one of the suitable patches

;; if there are too many hares within the home range, they search for another suitable patch

;; 3rd try: hares move to one of the suitable patches

;; if there are still too many hares within the homeRange, it dies

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; if there are no suitable cells, die

;; hare which reached maximum age

APPENDICES

```
    ]
  ]
  die

end

;;CULTIVATION;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to cultivate

  set fieldTable table:group-agents patches [fieldID]                ;; creates a table with index/key "fieldID" and the agentset of patches as value
  set fieldList table:to-list fieldTable                            ;; transforms the table into list of elements, which are lists with elements themselves: the fieldID, and the
corresponding set of patches

  let no 0                                                           ;; counts entries in the fieldList

  foreach fieldList                                                  ;; convert patchsets (all fields with a given ID) to the size of the patchset
  [
    [x] -> set fieldList replace-item no fieldList list (item 0 x) (count item 1 x)    ;; element number "no" of the fieldList is replaced with a two-item list: [(fieldID) (number of patches with that
fieldID)]
    set no no + 1
  ]

  if (Landscape = "Uckermark" and Scenario = "Basic")              ;; probability that a crop is selected for each scenario
  [
    set cropProbability [["wheat" 0.375] ["rape" 0.187] ["maize" 0.150] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
                        ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Silphie")
  [
    set cropProbability [["wheat" 0.375] ["rape" 0.187] ["silphie" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
                        ["maize" 0.050] ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Miscanthus")
  [
    set cropProbability [["wheat" 0.375] ["maize" 0.150] ["miscanthus" 0.100] ["barley" 0.092] ["rape" 0.087] ["grassland" 0.053] ["pasture" 0.053]
                        ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Grass-clover ley")
  [
    set cropProbability [["wheat" 0.375] ["rape" 0.187] ["grass-clover ley" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
                        ["maize" 0.050] ["beets" 0.045] ["alfalfa" 0.015] ["set-aside" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Alfalfa")
  [
    set cropProbability [["wheat" 0.375] ["maize" 0.150] ["rape" 0.102] ["alfalfa" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
                        ["beets" 0.045] ["set-aside" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Set-aside")
  [
    set cropProbability [["wheat" 0.375] ["maize" 0.150] ["rape" 0.102] ["set-aside" 0.100] ["barley" 0.092] ["grassland" 0.053] ["pasture" 0.053]
                        ["beets" 0.045] ["alfalfa" 0.015] ["rye" 0.014]]
  ]

  if (Landscape = "Uckermark" and Scenario = "Crop diversity")
  [
    set cropProbability [["wheat" 0.232] ["rape" 0.116] ["maize" 0.093] ["barley" 0.059] ["grassland" 0.050] ["pasture" 0.050]
                        ["beets" 0.050] ["alfalfa" 0.050] ["set-aside" 0.050] ["rye" 0.050] ["triticale" 0.050] ["silphie" 0.050]
                        ["miscanthus" 0.050] ["grass-clover ley" 0.050]]
  ]

  if (Landscape = "Germany" and Scenario = "Basic")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["maize" 0.178] ["grassland" 0.125] ["barley" 0.113] ["rape" 0.083]
```

```

    ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["set-aside" 0.024]]
  ]

  if (Landscape = "Germany" and Scenario = "Silphie")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["grassland" 0.125] ["barley" 0.113] ["silphie" 0.100] ["rape" 0.083]
                        ["maize" 0.078] ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["set-aside" 0.024]]
  ]

  if (Landscape = "Germany" and Scenario = "Miscanthus")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["maize" 0.161] ["grassland" 0.125] ["barley" 0.113]
                        ["miscanthus" 0.100] ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["set-aside" 0.024]]
  ]

  if (Landscape = "Germany" and Scenario = "Grass-clover ley")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["grassland" 0.125] ["barley" 0.113] ["grass-clover ley" 0.100] ["rape" 0.083]
                        ["maize" 0.078] ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["set-aside" 0.024]]
  ]

  if (Landscape = "Germany" and Scenario = "Alfalfa")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["maize" 0.161] ["grassland" 0.125] ["barley" 0.113]
                        ["alfalfa" 0.100] ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["set-aside" 0.024]]
  ]

  if (Landscape = "Germany" and Scenario = "Set-aside")
  [
    set cropProbability [["wheat" 0.207] ["pasture" 0.181] ["maize" 0.178] ["grassland" 0.125] ["barley" 0.113] ["set-aside" 0.100]
                        ["rye" 0.036] ["beets" 0.028] ["triticale" 0.024] ["rape" 0.007]]
  ]

  if (Landscape = "Germany" and Scenario = "Crop diversity")
  [
    set cropProbability [["wheat" 0.140] ["pasture" 0.123] ["maize" 0.120] ["grassland" 0.085] ["barley" 0.077] ["rape" 0.056]
                        ["beets" 0.050] ["alfalfa" 0.050] ["set-aside" 0.050] ["rye" 0.050] ["triticale" 0.050] ["silphie" 0.050]
                        ["miscanthus" 0.050] ["grass-clover ley" 0.050]]
  ]

  set cropProbability reverse cropProbability

  foreach cropProbability
  [
    [x] -> let proportion item 1 x
          let croptype item 0 x

    set proportion proportion * count patches
    let fieldSublist []
    foreach fieldList
    [
      [y] -> if item 1 y <= (proportion * 80 / 100) [ set fieldSublist fput y fieldSublist ]
    ]
  ]
  % , to avoid too large sums later)

  let summe 0
  let itemNumber 0
  let itemNumber2 0

  while [ (summe <= (proportion * 85 / 100)) and (length fieldList > 0) ]
  [
    let selectedField one-of fieldSublist
    set itemNumber position selectedField fieldSublist
    set itemNumber2 position selectedField fieldList
    let field item 0 selectedField
    set summe summe + item 1 selectedField

    ask table:get fieldTable field [ set crop croptype ]
    set fieldSublist remove-item itemNumber fieldSublist
    ifelse length fieldList > 0
    [ set fieldList remove-item itemNumber2 fieldList ]
    [ set summe 99999999 ]
  ]

  ;; go through the list of crop types and their proportions and add, for each croptype, fields

  ;; sums up field sizes
  ;; item number in sublist
  ;; item number in fieldList

  ;; while the sum is (- 15 %) smaller than the required proportion, additional fields are selected from the sublist
  ;; proportion - 15 %, to avoid too large sums later
  ;; selects one of fieldSublist

  ;; assign fieldID to "field"
  ;; assign field size of this field to "summe"

  ;; assign croptype to this field
  ;; remove selected field from the sublist

  ;; remove selected field from the main list
  ;; high value for summe to make the while loop stop

```

APPENDICES

```

    ]
  ]

  let itemNumber2 0

  while [ length fieldList > 0 ]
  [
    let selectedField one-of fieldList
    set itemNumber2 position selectedField fieldList
    let field item 0 selectedField
    ask table:get fieldTable field [ set crop "wheat" ]
    set fieldList remove-item itemNumber2 fieldList
  ]

  set fieldID-list remove-duplicates fieldID-list
  set totalfields length fieldID-list

  set crop-list []
  ask patches [ set crop-list fput crop crop-list ]
  set crop-list remove-duplicates crop-list
  set totalcrops length crop-list

end

;;EVALUATION;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to calculate-suitability

  if ( totalcrops >= 5) and (totalcrops <= 10) [ set diversity 0.60 ]
  if ( totalcrops >= 11) and (totalcrops <= 13) [ set diversity 0.80 ]
  if ( totalcrops >= 14) [ set diversity 1.00 ]

  ask patches
  [
    set foraging (item 0 table:get cropToSuit crop)
    set breeding (item 1 table:get cropToSuit crop)
    set suitability (foraging * breeding * diversity)
    set suitability suitability ^ (1 / 3)
    set suitability precision suitability 2
    if numberOwners > 0
    [
      set suitability suitability - ((numberOwners - 1) * 0.02)
    ]
  ]

end

to calculate-suithomeRange

  ask turtles
  [
    set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)
    set suithomeRange precision suithomeRange 2
  ]

end

;;DISPERSAL;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;

to search-homeRange

  let matures turtles with [ status != "juvenile" ]

  ask matures
  [
    let searchPatches patches in-radius homeRangeRadius
  ]

```

```

set searchPatches searchPatches with [(numberOwners < 7) and (suitability >= thresholdSuitability)]
if any? searchPatches
[
  ask homeRange
  [
    set owner remove myself owner
    set numberOwners numberOwners - 1
    set owner remove nobody owner
    if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
  ]
  move-to one-of searchPatches with-max [suitability]
  set homeRange patches in-radius homeRangeRadius
  ask homeRange
  [
    set owner fput myself owner
    set numberOwners numberOwners + 1
    if numberOwners > 1 [ set suitability (suitability - 0.02) ]
  ]
  set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)
  set suithomeRange precision suithomeRange 2
]
]

ask matures with [(suithomeRange < thresholdSuitability) or (any? homeRange with [numberOwners > 10])]
[
  let searchPatches patches in-radius homeRangeRadius
  set searchPatches searchPatches with [(numberOwners < 7) and (suitability >= thresholdSuitability)]
  if any? searchPatches
  [
    ask homeRange
    [
      set owner remove myself owner
      set numberOwners numberOwners - 1
      set owner remove nobody owner
      if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
    ]
    move-to one-of searchPatches with-max [suitability]
    set homeRange patches in-radius homeRangeRadius
    ask homeRange
    [
      set owner fput myself owner
      set numberOwners numberOwners + 1
      if numberOwners > 1 [ set suitability (suitability - 0.02) ]
    ]
    set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)
    set suithomeRange precision suithomeRange 2
  ]
]

ask matures with [(suithomeRange < thresholdSuitability) or (any? homeRange with [numberOwners > 10])]
[
  let searchPatches patches in-radius homeRangeRadius
  set searchPatches searchPatches with [(numberOwners < 7) and (suitability >= thresholdSuitability)]
  if any? searchPatches
  [
    ask homeRange
    [
      set owner remove myself owner
      set numberOwners numberOwners - 1
      set owner remove nobody owner
      if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
    ]
    move-to one-of searchPatches with-max [suitability]
    set homeRange patches in-radius homeRangeRadius
    ask homeRange
    [
      set owner fput myself owner
      set numberOwners numberOwners + 1
      if numberOwners > 1 [ set suitability (suitability - 0.02) ]
    ]
    set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)
  ]
]

```

;; hares search for suitable patches

;; 1st try: hares move to one of the suitable patches

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; the suitability of the homeRange is calculated

;; hares search for suitable patches

;; 2nd try: hares move to one of the suitable patches

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; the suitability of the homeRange is calculated

;; hares search for suitable patches

;; 3rd try: hares move to one of the suitable patches

;; hares occupy their homeRange

;; if the cell belongs to two territories, the suitability is reduced by 0.02

;; the suitability of the homeRange is calculated

APPENDICES

```

        set suithomeRange precision suithomeRange 2
    ]
]

ask matures with [(suithomeRange < thresholdSuitability)]
[
    set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)           ;; the suitability of the homeRange is calculated
    set suithomeRange precision suithomeRange 2
    if suithomeRange < thresholdSuitability                                           ;; if there is no suitable home range, die
    [
        ask homeRange
        [
            set owner remove myself owner
            set numberOwners numberOwners - 1
            set owner remove nobody owner
            if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
        ]
        die
    ]
]

ask patches with [numberOwners > 10]                                                 ;; if there are still too many hares within the homeRange, it dies
[
    while [ length owner > 10 ]
    [
        let selectedHare one-of owner
        ask selectedHare
        [
            ask homeRange
            [
                set owner remove myself owner
                set numberOwners numberOwners - 1
                set owner remove nobody owner
                if numberOwners >= 1 [ set suitability (suitability + 0.02) ]
            ]
            die
        ]
    ]
]

ask turtles
[
    set suithomeRange ((sum [suitability] of homeRange) / homeRangeNumber)           ;; the suitability of the homeRange is calculated
    set suithomeRange precision suithomeRange 2
]

end

;;REPRODUCTION;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;

to reproduce

    ask turtles with [ status = "female" ]
    [
        hatch (12 + random 3)                                                         ;; females get 12-15 offspring each year
        [
            set status "juvenile"
            set color yellow
            set size 10
            set age 0
            set suithomeRange 0
            set homeRange []
        ]
    ]
]

end

;;SURVIVAL;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;

```

to survive

```

ask turtles with [(status = "female") or (status = "male")]
[
  if random-float 1 <= mortalityAdult          ;; the mortality rate for adults is applied
  [
    ask turtles-here with [status = "juvenile"] [ die ]      ;; juveniles die if their mother is dead
    ask homeRange
    [
      set owner remove myself owner
      set numberOwners numberOwners - 1
      set owner remove nobody owner
      if numberOwners >= 1
      [
        set suitability (suitability + 0.02)
        set suitability precision suitability 2
      ]
    ]
    die
  ]
]

ask turtles with [status = "juvenile"]
[
  if random-float 1 <= mortalityJuvenile        ;; the mortality rate for juveniles is applied
  [
    die
  ]
]

```

end

```

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;;;
;;VISUALPROCEDURES;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

```

to update-view

```

if View = "fields"
[
  ask turtles [ show-turtle ]
  ask patches
  [
    set pcolor scale-color orange fieldID 2732 3493
  ]
]

if View = "crops"
[
  ask turtles [ show-turtle ]
  ask patches
  [
    if crop = "wheat" [set pcolor 26]
    if crop = "rape" [set pcolor 46]
    if crop = "maize" [set pcolor 126]
    if crop = "barley" [set pcolor 36]
    if crop = "grassland" [set pcolor 66]
    if crop = "pasture" [set pcolor 56]
    if crop = "beets" [set pcolor 136]
    if crop = "alfalfa" [set pcolor 126]
    if crop = "set-aside" [set pcolor 76]
    if crop = "rye" [set pcolor 16]
    if crop = "triticale" [set pcolor 6]
    if crop = "oats" [set pcolor 86]
    if crop = "grass-clover ley" [set pcolor 96]
    if crop = "ryegrass" [set pcolor 106]
    if crop = "peas" [set pcolor 62]
  ]
]

```

APPENDICES

```

]
if View = "habitat suitability"
[
  ask patches
  [
    if suitability >= thresholdSuitability [ set pcolor scale-color green suitability 1 0 ]
    if suitability < thresholdSuitability [ set pcolor scale-color grey suitability 0 0.5 ]
    if numberowners < 0 [set pcolor 0]
  ]

  ask turtles with [age > 0]
  [
    show-turtle
    let edge-patches homeRange with [any? neighbors with [ owner != [owner] of myself ] ]
    ask edge-patches [ set pcolor black ]
  ]
]

if View = "territories"
[
  ask patches
  [
    if suitability >= thresholdSuitability [ set pcolor scale-color green suitability 1 0 ]
    if suitability < thresholdSuitability [ set pcolor scale-color grey suitability 1 0 ]
  ]

  ask turtles with [age > 0]
  [
    ask homeRange [ set pcolor [color] of myself + 2]
    let edge-patches homeRange with [any? neighbors with [ owner != [owner] of myself ] ]
    ask edge-patches [ set pcolor [ color ] of myself - 2 ]
    show-turtle
  ]
]

if View = "OFF"
[
  ask patches [ set pcolor black ]
  ask turtles [ hide-turtle ]
]

end

```

[illegible]

FIGURES

| | |
|---|----|
| Figure 1.1: Land cover of Denmark and Germany. The data are provided by Eurostat (2018) and Destatis (2018). | 3 |
| Figure 1.2: Cultivation of renewable resources in Germany (from Steinhausser <i>et al.</i> , 2015). | 6 |
| Figure 1.3: Changes in the abundance of 167 bird species in 26 European countries between 1990 and 2014, presented as an index. In addition, the index was calculated for 39 farmland bird species and 34 forest bird species (from Leopoldina <i>et al.</i> , 2018). | 9 |
| Figure 1.4: The European brown hare (<i>Lepus europaeus</i>). Photo by Shirui Cheng on Unsplash. | 10 |
| Figure 2.1: Visual overview of Mors, 10 x 10 km, mapping the basic elements of the landscape visible at this scale. | 24 |
| Figure 2.2: Effect of environmental conditions on hare simulation settings. Hares are categorised into five life stages that showing specific behavioural states. | 26 |
| Figure 2.3: Exemplary presentation of the scenario changes in Mors. The landscape section (1 x 1 km) shows the baseline conditions (A), the distribution of field related EFA types (B) and the widened field margins (C). | 28 |
| Figure 2.4: Female abundance and number of yearlings in the three model landscapes under the baseline scenario, observed on day 270 in each of 30 simulated years. The bars indicate the 95 % confidence interval calculated for the ten replicates. | 30 |
| Figure 2.5: Effect of the evaluated scenarios on female abundance in each landscape. Stars specify the level of significance, i.e., $**P \leq 0.001$, $*P \leq 0.01$, for each scenario relative to the baseline. | 31 |
| Figure 2.6: Percentage deviation from the long-term viability criterion of 10 females per km ² | 31 |
| Figure 2.7: The AOR (abundance-occupancy relationship)-index plotted for the evaluated scenarios in all three landscapes relative to the baseline. | 32 |
| Figure 2.8: Effect of a percentage increase of two EFA types on female abundance in Mors. The bars indicate the 95 % confidence interval calculated for the ten replicates. | 33 |
| Figure 3.1: Flowchart of literature search and selection process. | 45 |
| Figure 3.2: Evolution of the reviewed ALG approaches sorted by date of the first publication. DYPAL (Gaucherel <i>et al.</i> , 2006), G-RaFFe (Pe'er <i>et al.</i> , 2013), EFForTS-Lgraf (Dislich <i>et al.</i> , 2018), GenExP-LandSiTes software (Le Ber <i>et al.</i> , 2009, Le Ber & Mari, 2013), Landscape generator (Engel <i>et al.</i> , 2012, Everaars <i>et al.</i> , 2014), Landscape simulator (Papaix <i>et al.</i> , 2014), Landscape mosaic generator (Begg & Dye, 2015), Landscape generator (van Strien <i>et al.</i> , 2016), SG4GISAME structure generator (Inkoom <i>et al.</i> , 2017). | 47 |

| | |
|--|----|
| Figure 3.3: Overview of purposes of the reviewed ALGs. Numbers do not have to add up to the total number of reviewed papers, because multiple entries (e.g., multiple model purposes) are possible. | 47 |
| Figure 3.4: Example of a 4 km ² landscape generated by the software platform AgBioscape (Begg & Dye, 2015) with wheat crops (yellow), grass ley (light green), woodland (red), grass margins (orange), and hedgerow (dark green). | 50 |
| Figure 3.5: Visualization of different calculation steps in the model of Everaars <i>et al.</i> (2014). A given mean field size is used by a landscape generator to produce a natural-looking mosaic of agricultural fields (Layers 1 and 2; grey values chosen arbitrarily). A given cropping scenario determines which crops are present in the landscape and at what proportions (Layer 3; each crop represented by a shade of grey). | 51 |
| Figure 3.6: Landscape series generated by the landscape generator of van Strien <i>et al.</i> (2016). Landscapes in this series have three land use categories, various maximum edge lengths of land use 1 and different proportions of the adjacency between land uses 1 and 2. Note that for agricultural landscapes, “land use” would actually refer to “land cover”. | 52 |
| Figure 3.7: Two different tessellations based on sets of seeds generated by the GenExp-LandSiTes software (Le Ber <i>et al.</i> , 2009): the Voronoi tessellation (a) and the rectangular tessellation with only T-vertices (b). Infinite Voronoi cells were eliminated. | 53 |
| Figure 3.8: Application of a cellular automaton algorithm on a simulated landscape with 25 m resolution in SG4GISCAME (Inkoom <i>et al.</i> , 2017). | 54 |
| Figure 3.9: Example of simulated landscape structures generated by the <i>Ddal</i> landscape simulator (Papaix <i>et al.</i> , 2014) with two host types (light (50 %) and dark (50 %) grey) dispatched among a 155-field landscape. | 55 |
| Figure 3.10: Example of an agricultural landscape mosaic generated by the modeling platform DYPAL (Gaucherel <i>et al.</i> , 2006). | 56 |
| Figure 3.11: Virtual landscape generated by EFForTS-Lgraf (Dislich <i>et al.</i> , 2018), an extended version of <i>G-RaFFe</i> (Pe'er <i>et al.</i> , 2013). Roads are marked in white, household home bases in black, oil palm plantations in orange, rubber plantations in dark yellow. Dark green is the area which is not used for agriculture. | 57 |
| Figure 3.12: Example of Visual Dataflow Programming for generating a landscape based on Voronoi tessellation. Users compile programs by selecting and combining nodes that represent certain operations. Using Java, developers program further nodes. (See also Appendix B1) | 69 |
| Figure 4.1: Generated agricultural landscapes with an area of 4 × 4 km. (Left) <i>Uckermark</i> reference landscape with an average field size of 27.5 ha. (Right) <i>Germany</i> reference landscape with an average field size of 6.8 ha. The colours mark the fields and can be assigned to different crop types. | 83 |
| Figure 4.2: Habitat suitability of the base scenarios in <i>Uckermark</i> (left) und <i>Germany</i> (right) as a result of the geometric mean of suitability as forage habitat, suitability as breeding habitat and crop diversity. The green colours show habitats above the suitability threshold of 0.5. The grey colours show habitats below the suitability threshold of 0.5. Darker green indicates higher suitability, and lighter grey indicates lower suitability. | 84 |

| | |
|--|-----|
| Figure 4.3: Hare home ranges in the base scenarios in <i>Uckermark</i> (left) und <i>Germany</i> (right). Blue arrows mark males, red arrows indicate females and yellow arrows indicate females with juveniles. The home ranges are represented as circles surrounding the hares. The green colours show habitats above the suitability threshold of 0.5. The grey colours show habitats below the suitability threshold of 0.5. Darker green indicates higher, and lighter grey indicates lower suitability. Note the tracking of habitat suitability by the distribution of hare home ranges and the partly high overlap of home ranges. | 85 |
| Figure 4.4: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 7 <i>Sub-models</i> in Appendix C1. | 86 |
| Figure 4.5: Effect of the implemented mitigation scenarios on hare abundance. Stars specify the level of significance, $***P \leq 0.001$, for each scenario relative to the base scenario. | 93 |
| Figure 4.6: Relative changes in hare densities from the base scenario values. Bars indicate standard deviation of the replicates. | 93 |
| Figure 5.1: A 10 x 10 km landscape map with a resolution of 1 m ² in ALMaSS. The landscape is based on vector maps from a region in Denmark, Mors. | 104 |
| Figure 5.2: Generated agricultural landscapes with an area of 4 x 4 km. (Left) <i>Uckermark</i> reference landscape with an average field size of 27.5 ha. (Right) <i>Germany</i> reference landscape with an average field size of 6.8 ha. The colours mark the fields and can be assigned to different crop types. | 110 |
| Figure A 1: Visual overview of Naestved, 10 x 10 km, mapping the basic elements of the landscape visible at this scale. | 117 |
| Figure A 2: Visual overview of Odder, 10 x 10 km, mapping the basic elements of the landscape visible at this scale. | 118 |
| Figure A 3: Effect of increasing number of replicates on the mean female abundance for the baseline scenarios in Mors, Naestved and Odder. | 122 |
| Table B 1: List of publications in which the ALGs are described and / or applied. | 127 |
| Figure C 1: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 7 <i>Sub-models</i> | 136 |
| Figure C 2: Effect of the home range size on the mean population abundance in the base scenario <i>Uckermark</i> . Bars indicate the standard deviation of 100 replicates. | 145 |
| Figure C 3: Effect of the habitat suitability threshold on the mean population abundance in the base scenario <i>Uckermark</i> . Bars indicate the standard deviation of 100 replicates. | 145 |
| Figure C 4: Effect of the number of potential territory overlaps per grid cell on the mean population abundance in the base scenario <i>Uckermark</i> . Bars indicate the standard deviation of 100 replicates. | 145 |

FIGURES

Figure C 5: Effect of the weighting percentage of the habitat diversity criterion on the mean population abundance in the base scenario *Uckermark*. Bars indicate the standard deviation of 100 replicates..... 146

TABLES

| | |
|---|----|
| Table 2.1: The crop rotation scheme of a conventional arable farm. Eight crop types with different numbers of entries are included in the rotation list. Spring barley, for example, occurs 37 times out of 100, representing 37 % of the farm's crop type..... | 23 |
| Table 2.2: Percent cover of basic landscape elements in the three model landscapes. | 24 |
| Table 2.3: The most common farm types in the three model landscapes by area..... | 24 |
| Table 2.4: Percentages of EFA types in the three model landscapes. The baseline is the original unchanged landscape, where almost all of the measures are already included to some degree. The scenario percentages show small deviations from 5 % because the implementation could not be precisely achieved in the model in some cases. Where model code terms are, for historical reasons, different from scenario terms used here, these are specified..... | 27 |
| Table 2.5: Baseline hare densities predicted for each landscape. | 29 |
| Table 2.6: Factors by which female and yearling abundances increased relative to the baseline scenarios. Factors are averaged across the three landscapes considered. | 30 |
| Table 3.1: General information on existing agricultural landscape generators (ALGs), i.e., models or programs that have the option to automatically and systematically generate virtual agricultural landscapes with given features in terms of configuration and composition. | 46 |
| Table 3.2: Configurational and compositional details of existing agricultural landscape generators (ALGs). The scope of application of an ALG is demonstrated with specific case studies. Thus, the table shows only a selection of compositional details; usually, many more application types are feasible..... | 58 |
| Table 3.3: Availability of agricultural landscape generators (ALGs). | 64 |
| Table 3.4: Essential and optional features of agricultural landscape generated with a generic ALG. | 67 |
| Table 4.1: Habitat characteristics of the crop types considered in this study. The suitability values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on the literature. Values in italics have an intermediate value of 0.5 due to a lack of information to estimate them. Details can be found in the Appendix C2. | 87 |
| Table 4.2: Crop diversity in terms of the number of crop types in the model landscapes. The crop diversity value ranges from 0.0 (not suitable) to 1.0 (very well-suited)..... | 88 |
| Table 4.3: The simulated crop proportions for each of the 14 crops and for each scenario. The two base scenarios (UM, GER) match the crop distributions in the reference landscape Uckermark and the average distribution in Germany 2017 for the ten most common crops. For each base scenario, six mitigation strategies are explored: three alternative energy plant scenarios and three crop composition scenarios. For the alternative energy plant scenarios (AE1-AE3), the proportions of mixed silphie, miscanthus and grass-clover ley were increased by 10% in each case. For the first two crop composition scenarios (CC1, CC2), the proportions of alfalfa and set-aside were increased by 10% in each case. Crop composition scenario 3 (CC3) | |

| | |
|---|-----|
| integrates all 14 crops in the landscape. Key changes are displayed in bold. Further details on the scenarios are provided in the Methods section. | 90 |
| Table 4.4: Factors by which hare abundances changed relative to the base scenarios..... | 92 |
| Table A 1: The amount of all landscape elements in Mors. | 119 |
| Table A 2: The amount of all landscape elements in Naestved..... | 120 |
| Table A 3: The amount of all landscape elements in Odder. | 121 |
| Table A 4: Farm types in the three model landscapes. | 122 |
| Table A 5: Changes in the crop rotations of the conventional farm types for each scenario. | 123 |
| Table A 6: Changes in the crop rotations of the organic and other farm types for each scenario. | 124 |
| Table A 7: Changes in the polygon types for permanent set-asides and permanent extensive grasslands [%]..... | 125 |
| Table A 8: Changes in the polygon types for the field margin scenarios [%]..... | 125 |
| Table A 9: Absolute and relative changes in female abundances for all three landscapes..... | 125 |
| Table A 10: Absolute and relative changes in yearling abundances for all three landscapes. | 126 |
| Table A 11: Female abundances at percentage increase of the EFA types permanent set-asides and extensive grasslands in Mors..... | 126 |
| Table B 1: List of publications in which the ALGs are described and / or applied..... | 127 |
| Table C 1: Entities and state variables of the habitat-based hare model. | 133 |
| Table C 2: Hare parameters of the habitat-based hare model are listed with their value for the standard parameter set..... | 134 |
| Table C 3: The simulated crop proportions for each of the 14 crops and for each scenario. The two base scenarios (UM, GER) match the crop distributions in the reference landscape Uckermark and the average distribution in Germany 2017 for the ten most common crops. For each base scenario, six mitigation strategies are explored: three alternative energy plant scenarios and three crop composition scenarios. For the alternative energy plant scenarios (AE1-AE3), the proportions of mixed silphie, miscanthus and grass-clover ley were increased by 10% in each case. For the first two crop composition scenarios (CC1, CC2), the proportions of alfalfa and set-aside were increased by 10% in each case. Crop composition scenario 3 (CC3) integrates all 14 crops in the landscape. Key changes are displayed in bold. Further details on the scenarios are provided in the Methods section. | 140 |
| Table C 4: Habitat characteristics of the crop types considered in this study. The suitability values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on the literature. Values in italics have an intermediate value of 0.5 due to a lack of information to estimate them. Details can be found in the Appendix C2. | 141 |

| | |
|---|-----|
| Table C 5: Crop diversity in terms of the number of crop types in the model landscapes. The crop diversity value ranges from 0.0 (not suitable) to 1.0 (very well-suited)..... | 141 |
|---|-----|

ABBREVIATIONS

| | |
|----------|--|
| ABM | Agent-based model |
| AES | Agri-environment scheme |
| ALG | Agricultural Landscape Generator |
| ALMaSS | Animal, Landscape and Man Simulation System |
| AOR | Abundance-Occupancy Relationship |
| | |
| BfN | Bundesamt für Naturschutz |
| BnatSchG | Bundesnaturschutzgesetz |
| | |
| CA | Cellular Automata |
| CAP | Common Agricultural Policy |
| | |
| EEG | Erneuerbare-Energien-Gesetz |
| EFA | Ecological Focus Area |
| EU | European Union |
| | |
| FSPM | Functional-structural plant modelling |
| | |
| GIS | Geographic Information Systems |
| | |
| ha | Hectar |
| | |
| IBA | Integrated biodiversity area |
| iLUC | Indirect land use change |
| IUCN | International Union for Conservation of Nature |
| | |
| LAI | Leaf-Area Index |
| LUCC | Land-use and cover change models |
| | |
| VDP | Visual Dataflow Programming |

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