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Mitigating bioenergy-driven biodiversity decline: a modelling approach with the European brown hare

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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 and differed in average field size and crop composition. The crops grown annually are evaluated in terms of forage suitability, breeding suitability and crop richness 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 richness. 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 richness led to distinct increases in hare abundance in both landscapes (> 0.3). 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.

1. Introduction

The increased cultivation of energy crops in 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, Steinhausser *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 (Edwards *et al.*, 2000, Smith *et al.*, 2005, Zellweger-Fischer *et al.*, 2011). 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, Pepin & 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 (Smith *et al.*, 2005). 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 (Rühe & Hohmann, 2004, Strauß *et al.*, 2008).

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 area under energy crop cultivation in Germany has increased considerably in the last 20 years (Destatis, 2018). Energy crops are mainly used for biogas and biofuel production, with maize being the most important crop for use in biogas plants and oilseed rape for the production of biofuels. 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.

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 (O'Sullivan & Perry, 2013). 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 richness. 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.

2. 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 is implemented in NetLogo 6.0.3 (Wilensky, 1999) and available in the CoMSES Computational

Model Library (Langhammer & Grimm, 2019)[1]. 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).

2.1 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 the first part of the workflow, the landscape mosaic generation, was used 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 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 km × 4 km with a resolution of 100 m² (400 × 400 grid cells).

2.1.1 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

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

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 proportional correlation between field size and farm size. In 2016, the average farm size in Germany was 61 ha of agricultural land and in the Uckermark 247 ha (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 1).

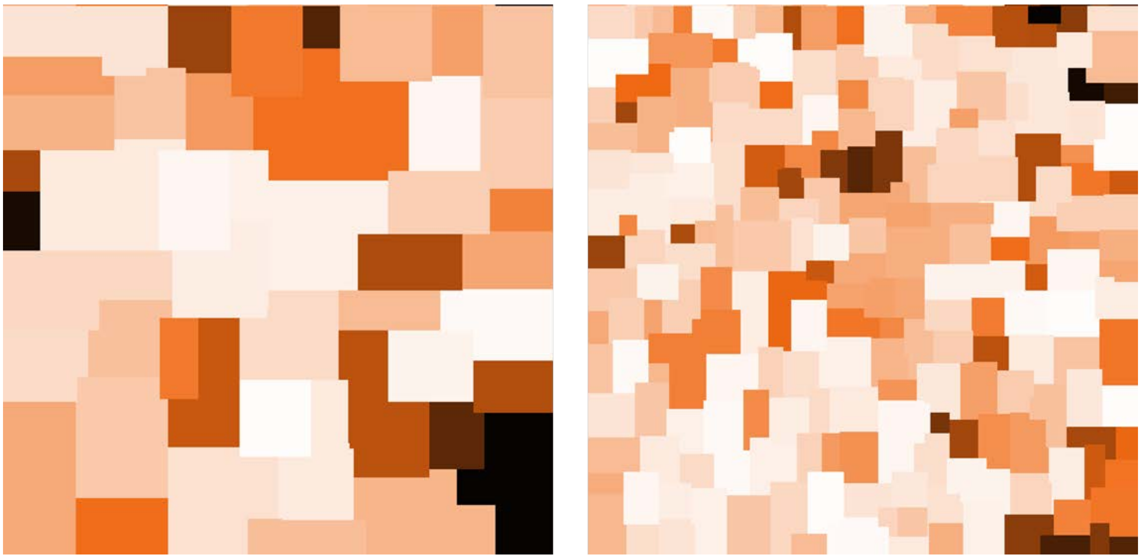

Figure 1: Generated agricultural landscapes with an area of 4 km × 4 km. (Left) *Uckermark* reference landscape with an average field size of 27.5 ha. (Right) *Germany* reference landscape with an average field size of 6.8 ha. The colours mark the fields and can be assigned to different crop species.

2.2 Hare model description

This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010).

2.2.1 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.

2.2.2 Entities, state variables and scales

The model includes two types of entities: square grid cells and individuals (hares). Table 1 gives an overview of these entities and their state variables. Hares are characterised by the following key variables and parameters: identity number (*owner*), 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 1, Table 2).

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

Entity	Variable	Description	Scale
Landscape	*richness*	Crop richness of the landscape (R_C)	0 – 1
Patches	*pxcor, pycor*	Spatial unit on the landscape grid	0 – 399
	crop	Crop species of a patch	1 – 14
	foraging	Suitability as forage habitat (F_H)	0 – 1
	breeding	Suitability as breeding habitat (B_H)	0 – 1
	suitability	General habitat quality for the hare (S_H)	0 – 1
	numberOwners	Number of hares to whose home range the cell belongs to	0 – 10
	owner	Hare ID, which is assigned to a grid cell	0 – ∞ (theoretically)

Entity	Variable	Description	Scale
Hares	*xcor*, *ycor*	Spatial location of the hare on the landscape grid	0 – 399
	age	Age of the hare	1 – 13
	home range	Set of grid cells defined by homeRangeRadius	2453 ≙ 25 ha (GER), 5525 ≙ 55 ha (UM)
	suithomeRange	Habitat suitability of the home range	0 – 1

171 Table 2: Hare parameters of the model with their value or range for the standard parameter set.

Parameter	Description	Default value or range	Sources for parameterization
status	Hare specification	juvenile / female / male	
longevity	Maximum age	13	Broekhuizen (1979)
maturity	Sexual maturity	1	Broekhuizen & Maaskamp (1981)
offspring	Number of offspring per year and female	12-15	Marboutin *et al.* (2003)
mortalityAdult	Mortality rate of adults	0.3	Marboutin & Peroux (1995)
mortalityJuvenile	Mortality rate of juveniles	0.5	Marboutin & Peroux (1995)
thresholdSuitability	Threshold below which survival is not possible	0.5	Manual calibration
weightingSuitability	Weighting of the three suitability criteria foraging, breeding and crop richness	1/3	Manual calibration [a]
homeRangeRadiusUM	Radius of the home range in *Uckermark*	42	Ullmann *et al.* (2018)
homeRangeRadiusGER	Radius of the home range in *Germany*	28	Interpolated [b]
maximumOwners	Max. number of owners assigned to a search cell	7	Manual calibration
maximumOverlap	Max. number of home ranges overlapping	10	Manual calibration
suitabilityReduction	Reduction of the habitat suitability value when home ranges overlap	0.02	Manual calibration
attempts	Max. number of attempts to find a new home range	3	Manual calibration [c]

[a] 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 Rühe & 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*).

[b,c] Hard-coded via algorithm.

Grid cells represent 100 m² and are characterised by their coordinates and the variables assigned to them. To avoid edge effects, the grid is wrapped to a torus. Each grid cell is covered by one of 14 crop species 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 richness ($richness\ R_C$) are derived. The foraging and breeding values range from 0.0 (not suitable) to 1.0 (very well-suited) and are based on expert knowledge drawn from the literature (Figure 2, Table 3). 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. 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 Supplementary Material.

Suitability as forage habitat, F_H, specifies the suitability of each crop species as a food source. Suitability as breeding habitat, B_H, indicates the suitability of the crop species for getting offspring. The value depends on crop density, crop height and management activities. Crop richness, R_C, indicates the distribution and quantity of crops within the landscape. Many studies show that habitat diversity, in general, including crop richness, has a clear positive effect on hare populations (Tapper & Barnes, 1986, Lewandowski & Nowakowski, 1993, Reichlin *et al.*, 2006, Santilli & Galardi, 2016). Following this, we related the crop richness value to the number of crops in three levels (Table 4). The values were chosen to implement a relationship between overall crop richness in the landscape and habitat suitability. They represent the fact that habitat suitability does not only depend on local features within a habitat, but also on the features of the surrounding landscape. Note that in our simulations, only three values of R_C were possible: 0.6 for base landscapes with 10 crop species, 0.8 for landscapes with one additional crop for mitigation, and 1.0 when all 14 crop species listed in Table 5 were present.

The geometric mean of all three variables (F_H, B_H, R_C) results in the habitat suitability value (S_H) for each individual grid cell (Figure 2):

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

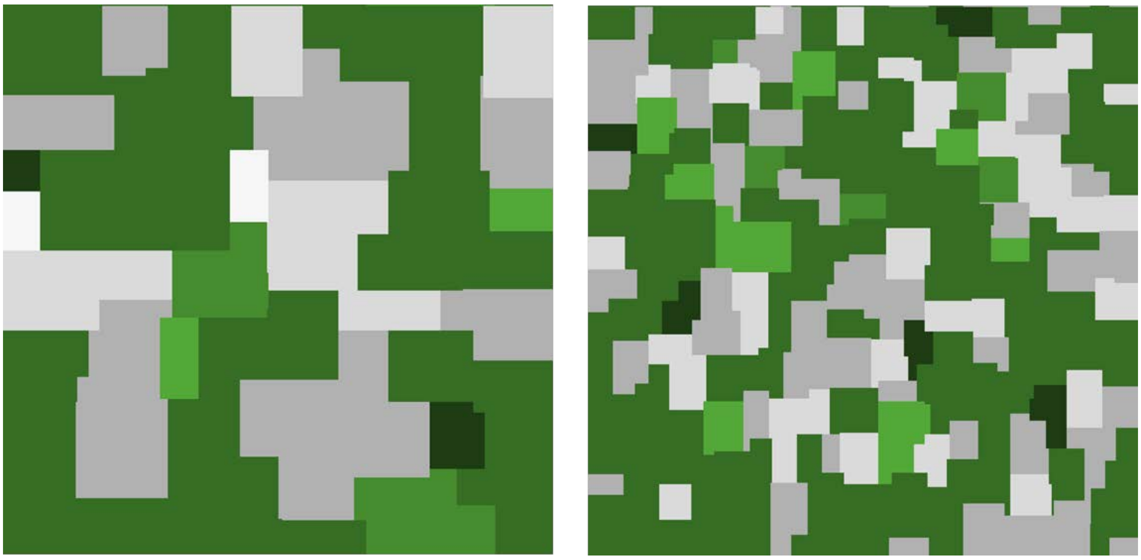

Figure 2: Habitat suitability of the base scenarios in *Uckermark* (left) und *Germany* (right) as a result of the geometric mean of suitability as forage habitat, suitability as breeding habitat and crop richness. The green colours show habitats above the suitability threshold of 0.5. The grey colours show habitats below the suitability threshold of 0.5. Darker green indicates higher suitability, and lighter grey indicates lower suitability.

Table 3: Habitat characteristics of the crop species 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 A2.

Crop species	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	*0.50*
Grassland (ext.)	0.75	0.75
Grass-clover ley	0.75	0.50
Maize	0.50	0.25
Miscanthus	0.00	0.25
Oats	*0.50*	*0.50*
Oilseed rape	0.25	0.25
Pasture (int.)	0.25	0.25
Rye	*0.50*	*0.50*
Set-aside	1.00	1.00
Silphie	*0.50*	0.75
Triticale	*0.50*	*0.50*
Wheat	0.75	0.75

Table 4: Crop richness in terms of the number of crop species in the model landscapes.

Landscape	Scenario	Number of crop species	Crop richness of the landscape (R_C)
Uckermark, Germany	Base	10	0.6
	AE1, AE2, AE3, CC1, CC2	11	0.8
	CC3	14	1.0

AE Alternative energy plant scenarios
CC Crop composition scenarios

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 (Figure 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. Both parameters, *homeRangeOverlap* and *suitabilityReduction*, as well as other unknown parameters (Table 2) were estimated by calibrating the model with the hare counts in the reference landscape in the Uckermark of 5 individuals per 100 ha (data provided by the BioMove Research Training Group DFG GRK 2118/1). They indirectly simulate competition for habitat and avoid unnatural clumping of too many individuals per area.

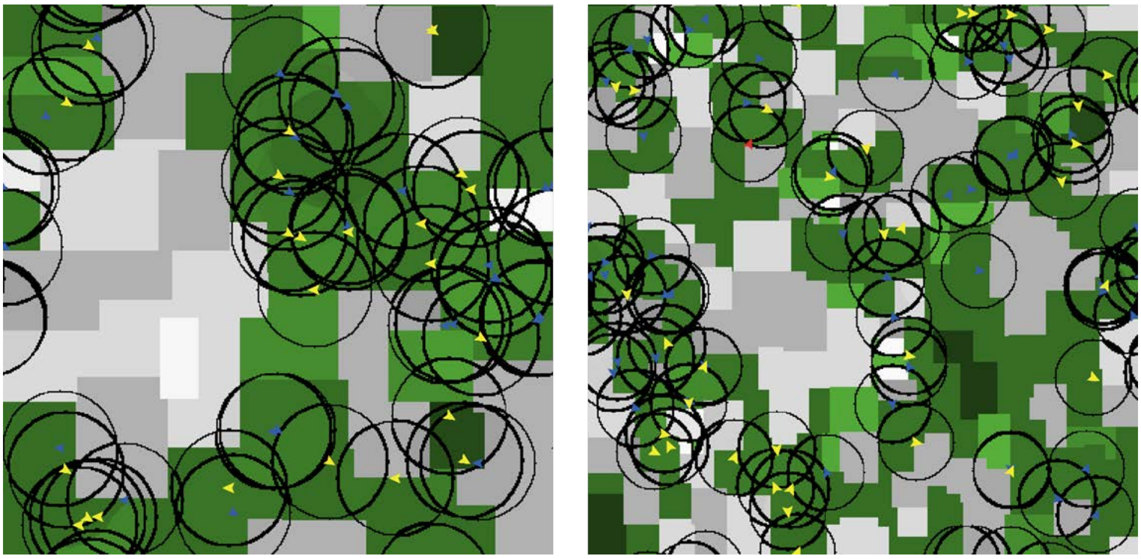

Figure 3: Hare home ranges in the base scenarios in *Uckermark* (left) und *Germany* (right). Blue arrows mark males, red arrows indicate females and yellow arrows indicate females with juveniles. The home ranges are represented as circles surrounding the hares. The green colours show habitats above 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.

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 Rühe & 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 (*Germany*), i.e., a home range of 55 ha to 42 grid cells (420 m) in *Uckermark*.

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

2.2.3 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 program used. A flowchart of the model process is depicted in Figure 4.

First, all hares become one year older, and juveniles become young 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 species are reassigned to all fields each year (*cultivation*). The selection of the crop species 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 species 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 species, the variables foraging, breeding and richness 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. 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.

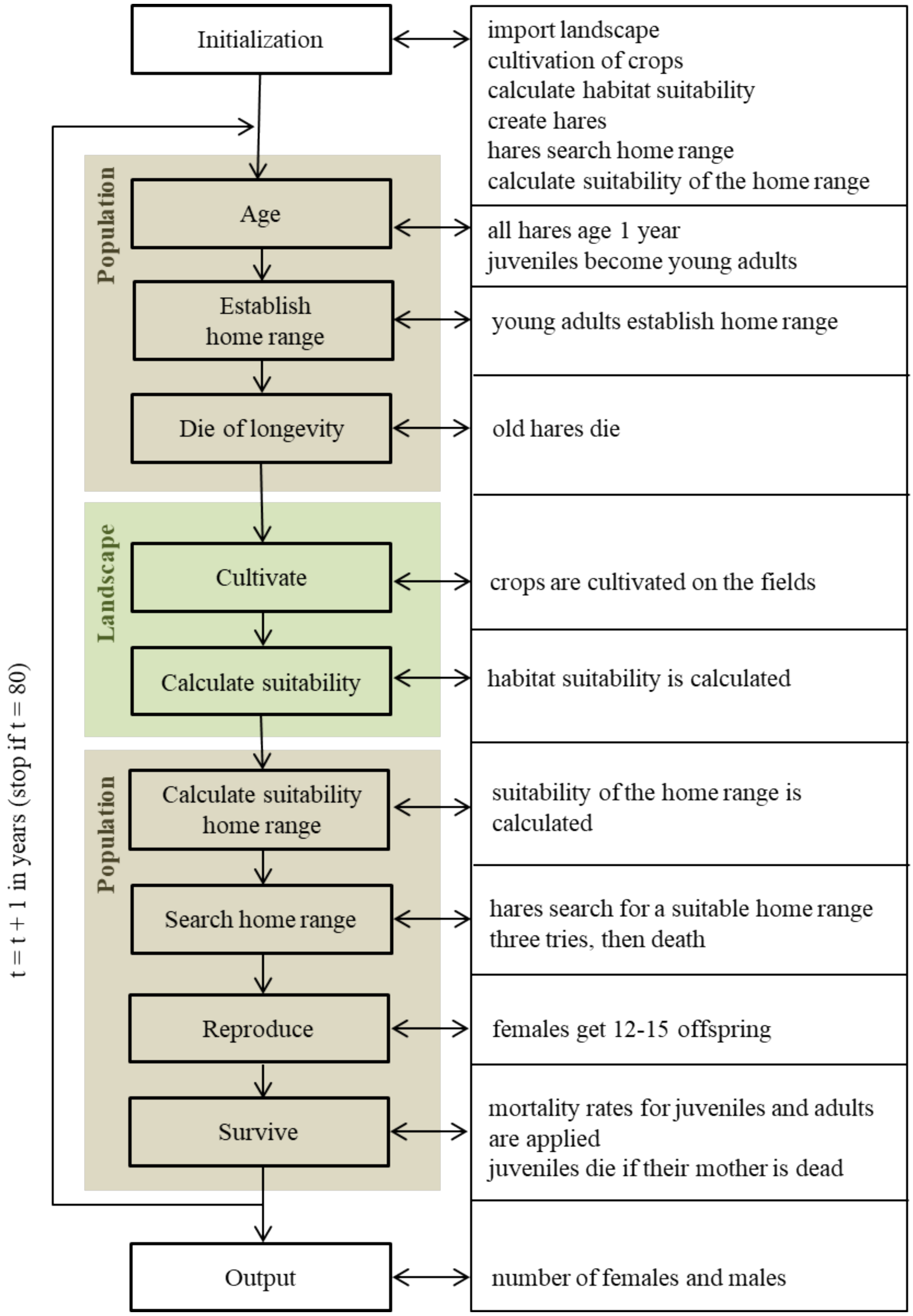

Figure 4: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 2.2.7 *Submodels.*

2.2.4 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.

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 young adults or their habitat quality is not sufficient, they must disperse to find a more suitable habitat. Therewith, the hares respond to changes in landscape structure and overall hare abundance in an adaptive way.

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 richness within the model landscape.

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 staring 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 species 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 within the search radius. (6) Females obtain a random number between 12 and 15 offspring. (7) Hare age is random between 1 and 13 in the first time step. 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. The first 30 years are discarded to avoid transient effects.

2.2.5 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).

Crop species are then distributed to the fields according to the chosen scenario. From each crop species or rather the whole number of crops, the variables (1) suitability as forage habitat, (2) suitability as breeding habitat and (3) crop richness 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.

2.2.6 Input data

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

2.2.7 Submodels

Ageing

Because the model follows an annual rhythm, all individuals get one year older in each time step. Juveniles become young 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 species. Fourteen different crop species 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 species in the landscape is defined by a cultivation probability, with the selection of the crop species per field remaining the same throughout each simulation run for each mitigation scenario. Thus, as in reality, crops are assigned to the fields each year, and an evaluation for the hare population takes place. Table 5 shows the cultivation probabilities of all crop species for each scenario.

Table 5: 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.

	Crop proportion [%]													
Scenario	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

Evaluation

First, the variables (1) suitability as forage habitat (*foraging* F_H), (2) suitability as breeding habitat ($breeding\ B_H$) and (3) crop richness ($richness\ R_C$) are derived from each crop species or rather the whole number of crops. Table 3 and Table 4 give an overview of the assessment criteria. The geometric mean of all three variables (F_H, B_H, R_C) results in the habitat suitability value (S_H) for each individual grid cell:

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

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

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.

Juveniles that mature are searching for a home range within a radius of 150 cells (1.5 km) prior to the assignment of new crop species. Their search radius is larger than that of the adults in order to find suitable grid cells outside the mother's home range. The other 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 species, field configurations, and the density of conspecifics. These factors affect hare distribution and abundance two times per year, for establishing young adults, and, after new assignments of crops, for established adults.

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).

2.3 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 5). 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.

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 richness CC3).

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 (Semere & Slater, 2007, Dauber & Miyake, 2016, Schorpp & Schrader, 2016). 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 (Gansberger *et al.*, 2015). 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 (Kocar & Civas, 2013). 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 (Destatis, 2018). 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 (Stinner *et al.*, 2008).

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).

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 5. For the crop richness 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.

Sensitivity analysis

We conducted sensitivity experiments and spot checks (data not shown), i.e. varied key parameters over their full range and performed specific tests for single parameters while keeping all other parameters constant to understand how the variation affects model predictions. During calibration it turned out that some parameters, the radius of the home range (*homeRangeRadius*), the threshold for habitat suitability (*thresholdSuitability*) and the home range overlap (*homeRangeOverlap*) were most sensitive. To test the sensitivity, we varied the values of the two parameters in the base scenario *Uckermark* and the base scenario *Germany* and calculated the resulting hare population abundance. The *thresholdSuitability* parameter was varied from 0 to 1 in 0.1-interval steps. The parameter *homeRangeRadius* varied from 10 to 50 grid cells in steps of five. To test the influence of hare home range overlap, we varied the number of possible overlaps from 0 to 20 hares in steps of two. Furthermore, we performed sensitivity analysis by reducing the weighting of the crop richness criterion. Instead of weighting one-third compared to forage and breeding suitability, we tested one-quarter, one-sixth and zero. The sensitivity analyses were based on 100 replicates with the same input parameters as that of field size and number of crops.

2.4 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).

3. Results

Due to model calibration, 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 6, Figure 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 6: Factors by which hare abundances changed relative to the base scenarios within 50 years.

Landscape	Scenario	Individuals per km²	Abs. change	Rel. change
Uckermark	Base	3.9		
	AE1	5.5	1.60	0.41
	AE2	4.5	0.53	0.14
	AE3	5.5	1.60	0.41
	CC1	4.2	0.30	0.08
	CC2	4.7	0.75	0.19
	CC3	4.9	1.01	0.26
Germany	Base	8.2		
	AE1	12.7	4.57	0.56

Landscape	Scenario	Individuals per km²	Abs. change	Rel. change
	AE2	6.9	-1.32	-0.16
	AE3	12.8	4.60	0.56
	CC1	9.1	0.97	0.12
	CC2	10.3	2.12	0.26
	CC3	12.5	4.29	0.53

Impact of alternative energy crops

The relative effect of the alternative energy crops was significantly different in both landscapes (Figure 6). 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) (Figure 6). The most positive effect in both landscapes included the crop richness 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*.

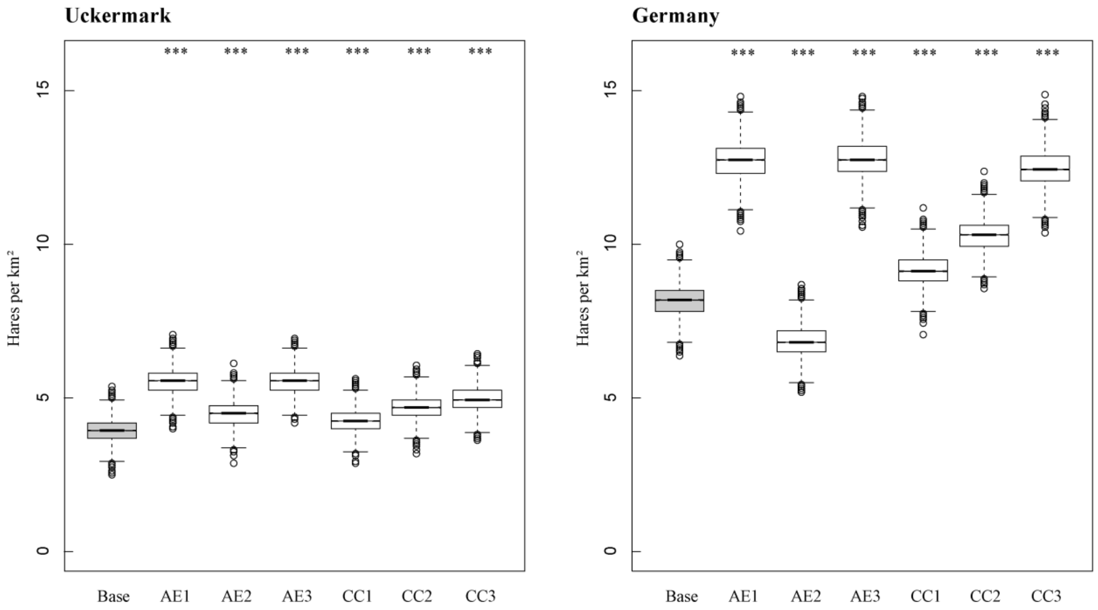

Figure 4: Effect of the implemented mitigation scenarios on hare abundance. Stars specify the level of significance, ***$P \leq 0.001$, for each scenario relative to the base scenario.

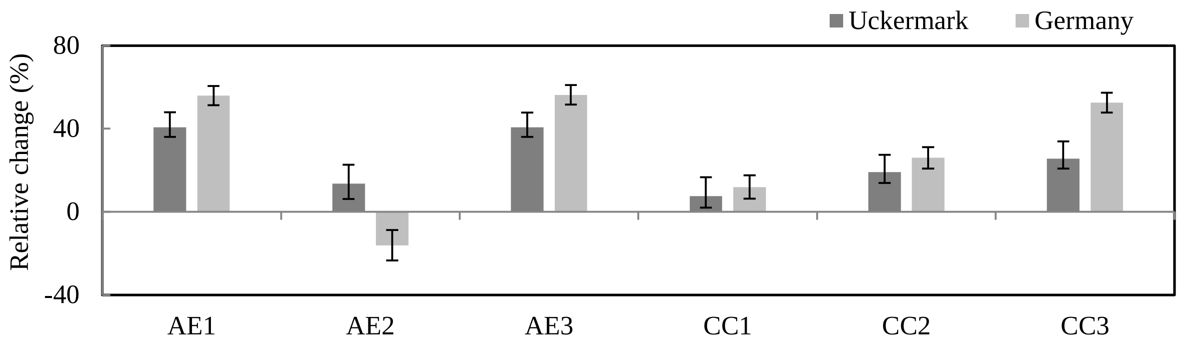

Figure 5: Relative changes in hare densities from the base scenario values. Bars indicate standard deviation of the replicates.

Overall, the mitigation measures of mixed silphie, grass-clover ley and increased crop richness led to distinct increases in hare abundances in both landscapes (> 0.3).

Sensitivity analyses

Figure A 1 in the Appendix shows that a reduction of the hare home range radius in the model correlates with an increase in population abundance. 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 56.8 individuals per 100 ha in *Uckermark* and 63.3 individuals per 100 ha in *Germany*. 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 2.7 individuals per 100 ha in *Uckermark* and 2.3 individuals per 100 ha in *Germany*.

The threshold for habitat suitability strongly influences hare population development. At a threshold higher than 0.4, the population abundances decrease rapidly until it dies out at a threshold of 0.7 in both landscapes(Figure A 2). Below a threshold of 0.5, the hare population stabilises at a density of 6.5 individuals per 100 ha in *Uckermark* and 15.4 individuals per 100 ha in *Germany*.

Furthermore, there is a strong correlation between the number of potential home range overlaps per grid cell in the model and the hare abundance. A huge maximal overlap of 20 hare home ranges per grid cell leads to a population density of 4.4 individuals per 100 ha in *Uckermark* and 8.9 individuals per 100 ha in *Germany* (Figure A 3). On the other hand, when no overlap was allowed, it led to a population density of 0.0 individuals per 100 ha in *Uckermark* and 0.6 individuals per 100 ha in *Germany*.

A reduction in the weighting of the crop richness criterion from less than 25% led to a strong decrease in the hare population abundances in both landscapes (Figure A 4). 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 zero led to the extinction of the hare populations in both landscapes.

4. 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, Rühe & 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 species 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 species 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 species. 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 species 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 richness 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 richness 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 m^2. 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 because this is the period in which most breeding takes place (Tapper, 1987, Flux & Angermann, 1990). In reality, crops are mainly used on a seasonal basis, so that general statements regarding a crop species can be made only to a limited extent. 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. To assess the suitability of crops as breeding habitats, we considered conditions such as crop height and management activities in spring and summer.

We could not parameterize the weighting of the three criteria for forage, breeding and crop richness because there are no data available for them. However, the sensitivity analysis shows that a reduction in the weighting of the crop richness criterion had a strong effect on hare population abundance. This result underlines the importance of crop richness for population development. However, our assumptions on how crop richness in the entire model landscape affects local habitat suitability were largely imposed, but do not affect the comparative assessment of different 10 or 11 crop species scenarios. Currently there seem to be no data available which would allow to replace these assumptions with more realistic and emergent ones. 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). 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. The number of attempts is a compromise between the probability of success to find a new place and the computing time it takes to perform this process for all hares and grid cells. 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 (Broekhuizen & Maaskamp, 1981, Tapper & Barnes, 1986, Rühe & Hohmann, 2004, Smith *et al.*, 2004, Bertolino *et al.*, 2013). Following this, the home ranges in *Uckermark* are much larger than those in *Germany*.

The overlap of home ranges of individual hares fluctuates strongly in reality; in densely populated areas, there is a strong overlap (Rühe & Hohmann, 2004). In the model, the maximum overlap of ten home ranges was assumed to match the real population densities in the Uckermark. This indirectly controls the intraspecific competition, which of course also affects the results. Population growth can only take place within the framework of this rule and is therefore limited. Nevertheless, we assume that direct intraspecific competition in nature is also subject to similar, though much more complex, limiting factors.

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.

5. 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.

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7. References

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