Hare model: ODD

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This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm *et al.*, 2006, Grimm *et al.*, 2010). The model is implemented in NetLogo 6.0.3 (Wilensky, 1999) and used to simulate brown hare population dynamics in bioenergy-driven landscapes.

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).

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 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)
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),

Entity	Variable	Description	Scale
			5525 ≙ 55 ha (UM)
	suithomeRange	Habitat suitability of the home range	0 – 1

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 [b]

[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] 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 1, 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 1):

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

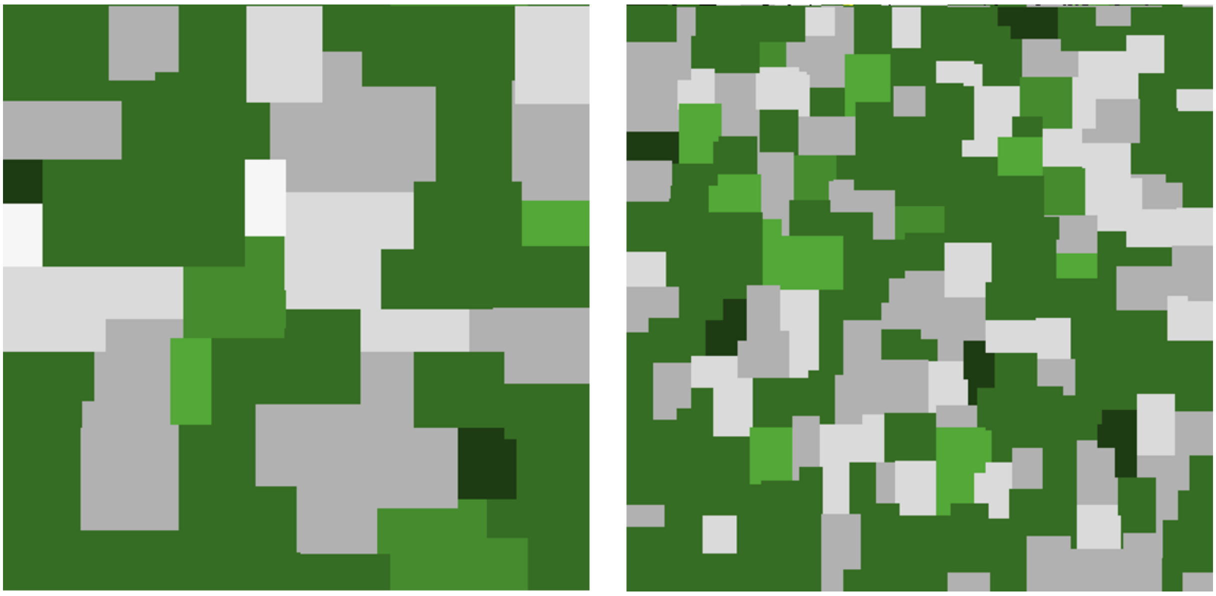

Figure 1: Habitat suitability of the base scenarios in *Uckermark* (left) und *Germany* (right) as a result of the geometric mean of suitability as forage habitat, suitability as breeding habitat and crop richness. The green colours show habitats above the suitability threshold of 0.5. The grey colours 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 2). 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.

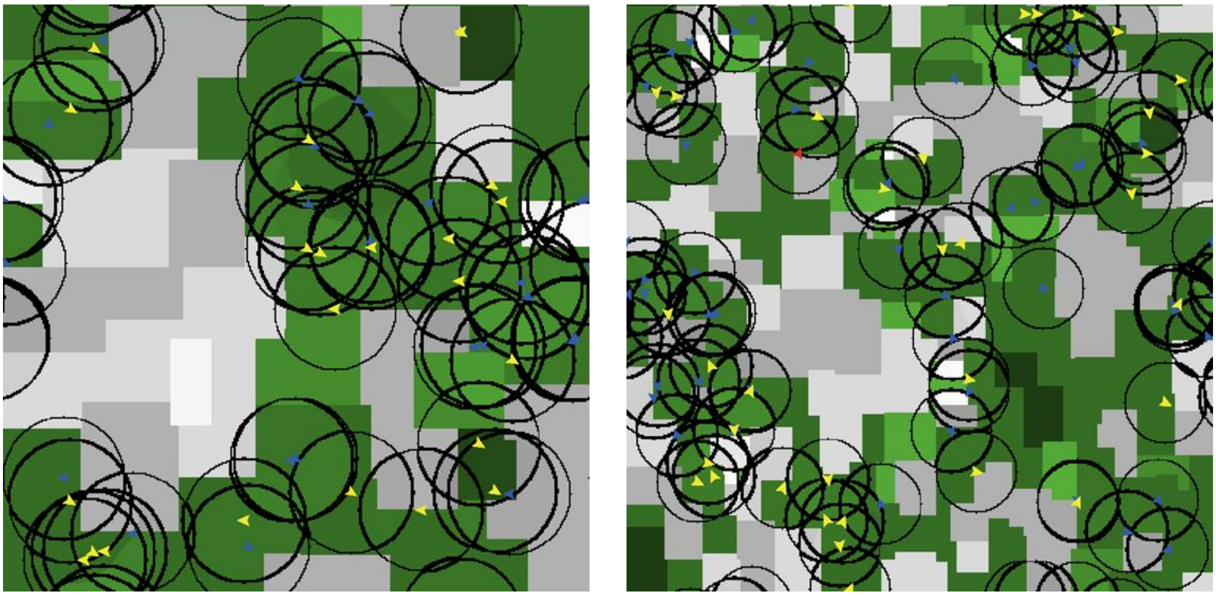

Figure 2: Hare home ranges in the base scenarios in *Uckermark* (left) und *Germany* (right). Blue arrows mark males, red arrows indicate females and yellow arrows indicate females with juveniles. The home ranges are represented as circles surrounding the hares. The green colours show habitats above 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.

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 3.

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.

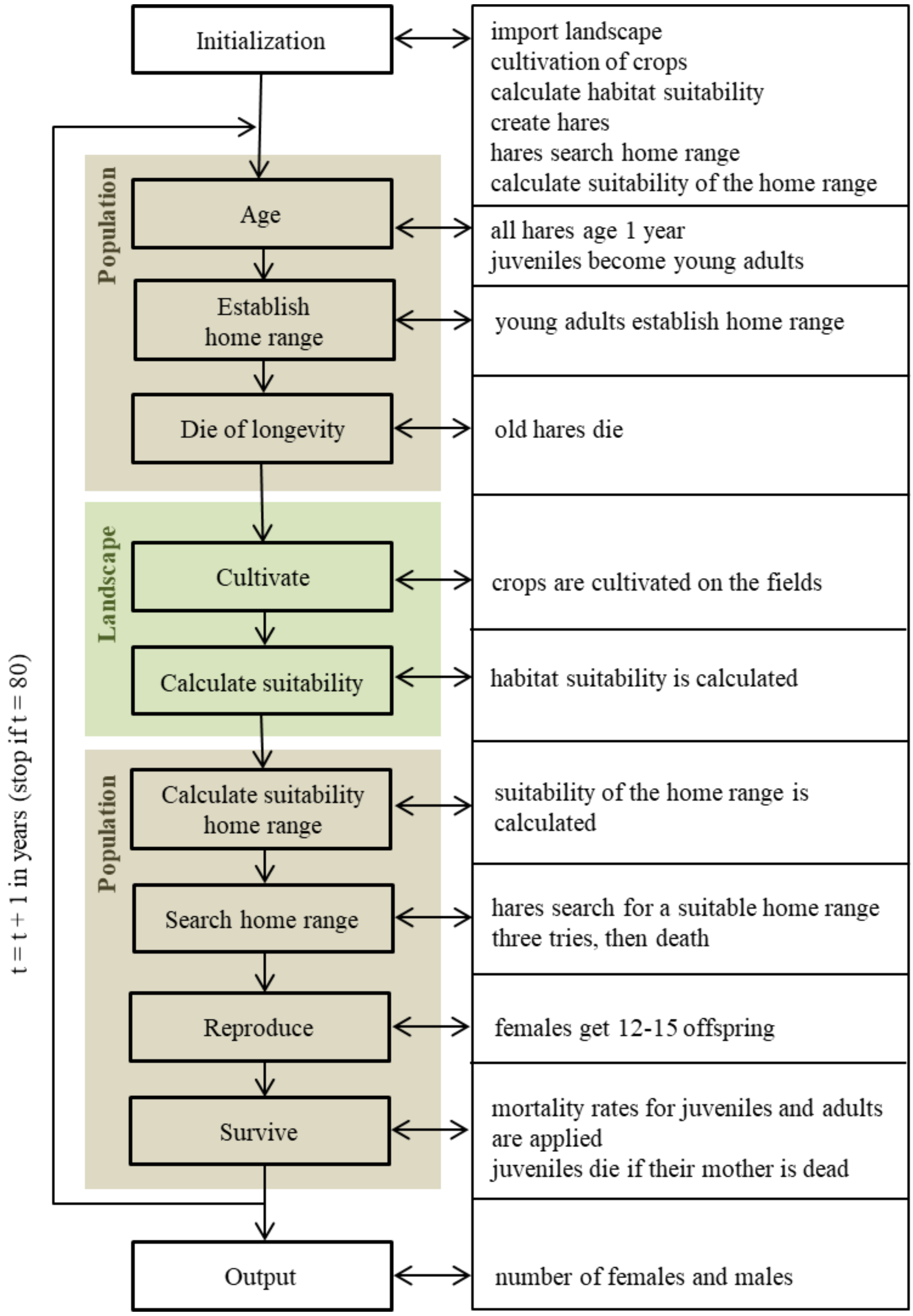

Figure 3: Flowchart of the habitat-based hare model including initialization and sub-models. For a detailed description of each process, see Section 7 *Submodels.*

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.

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.

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 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).

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