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Modelling the cost-effective spatio-temporal allocation of conservation measures in agricultural landscapes facing climate change

Abstract

In agricultural landscapes, climate change has profound impacts on species that society aims to conserve. In response to climate change, species may adapt spatially (with range shifts) and temporally (with phenological adaptations), which may make formerly effective conservation sites and measures less effective. As climate change also has an impact on yields, opportunity costs of land use-based conservation measures may also change spatially and with respect to the timing of conservation measures. Due to these spatio-temporal modifications of the costs of conservation measures and their impacts on species, formerly cost-effective conservation sites and measures may no longer be so in a changing climate. We combine ecological-economic modelling with climate science to investigate climate change-induced modifications of the timing and spatial allocation of cost-effective conservation measures. We apply our model to the case study of conserving the large marsh grasshopper on agricultural grasslands in the German federal state of Schleswig-Holstein. Comparing the periods 2020-2039 and 2060-2079, our model indeed indicates that climate change induces modifications in the cost-effective spatial allocation of conservation measures and that measures which are adapted to phenological changes remain cost-effective under climate change.

Keywords: *climate-ecological-economic model; conservation planning; large marsh grasshopper; cultural landscapes; biodiversity conservation*

1. Introduction

Climate change has profound effects on biodiversity and is considered one of the main threats behind what conservation biologists call the “sixth mass extinction” (Heller & Zavaleta 2009, Cafaro 2015). Generally, species have three ways of responding to climate change: (1) Species may adapt spatially through range shifts reaching from micro-habitat shifts to large-scale dispersal (Bellard et al. 2012). However, to enable a species’ migration, the location of habitat sites needs to be adapted to create suitable habitat in the species’ new range (Oliver et al. 2016). (2) Species may adapt temporally through phenological adaptations. Phenological adaptations refer to changes in the timing of life cycle events. These changes have been observed in many species and occur in both agricultural crops and wild plants and animals (Wätzold et al. 2020). Phenological adaptations allow species to maintain synchrony with abiotic conditions, but may lead to asynchrony of predator-prey systems, insect-plant systems (Bellard et al. 2012) or with agricultural land use (Santangeli et al. 2018). Asynchronies may thus reduce a species’ population viability when climatic conditions in the species’ range change. (3) Species may adapt physiologically through behavioral modifications (Bellard et al. 2012). Especially spatial and temporal adaptations are well-documented (Bellard et al. 2012) and considered in this article. Current conservation efforts tend to implicitly assume stable climatic conditions and

are thus insufficient to protect species under changing climatic conditions (Triviño et al. 2018). Therefore, conservation measures that take into account the impact of climate change are needed urgently (Ando & Mallory 2012, Pecl et al. 2017, Reside et al. 2018).

In the last two decades or so, a substantial amount of research from ecologists has been conducted on how to most effectively conserve species under climate change (see for example the reviews by Heller & Zavaleta (2009) and Jones et al. (2016)). From an economic point of view, it is important that species are not only conserved effectively, but also in a cost-effective manner. In the context of this paper, we refer to cost-effectiveness as the ability of conservation measures to maximize a species' population viability for given costs in a region that experiences climate change (Gerling & Wätzold 2020). In agricultural landscapes, designing cost-effective conservation measures under climate change provides specific challenges:

(1) The impact of conservation measures on species differs spatially (Ansell et al. 2016). Under climate change, species' ranges shift, so that conservation measures become more effective on some sites, and less effective on others (Triviño et al. 2018).

(2) The timing of conservation measures may have to take into account a species' life cycle (Johst et al. 2015). As the timing of life cycle stages may change under climate change, a fixed timing of agricultural land use may render a conservation measure less effective over time. For example, ground nesting meadow birds may adapt their breeding behavior to phenological changes resulting from climate change (Santangeli et al. 2018), and if so, a mowing date chosen to conserve their nests may have to be adapted to remain effective.

(3) Costs of species conservation in agricultural landscapes differ spatially (Lewis et al. 2011, Lewis & Polasky 2018), and climate change may impact yields in a spatially differentiated manner (Rashford et al. 2016, Ray et al. 2019). This implies that opportunity costs of conservation measures may increase on some sites and decrease on others, resulting in a changed cost pattern in a landscape.

(4) The costs of conservation measures may also depend on their timing, e.g. on mowing dates or grazing periods (Mewes et al. 2015). Under climate change, a specific timing of a conservation measure may become relatively more (or less) costly in comparison with an earlier (or later) timing.

In summary, designing cost-effective conservation measures in agricultural landscapes has to take into account the spatio-temporal heterogeneity of both the measures' costs and their impact on species in the dynamic context of climate change. It has been demonstrated that ecological-economic modelling is an appropriate approach to integrate ecological and economic data and information for cost-effective conservation (Polasky et al. 2008, Gerling et al. 2019, Drechsler 2020), also in agricultural landscapes (Armsworth et al. 2012, Wätzold et al. 2016). However, in order to investigate cost-effective conservation measures in a changing climate, ecological-economic models have to integrate climate data and information and thus move from ecological-economic modelling to climate-ecological-economic (CEE) modelling.

We present a CEE model that takes up the above-mentioned challenges by integrating data from different disciplinary models in an optimization procedure to analyze the cost-effective

spatio-temporal allocation of conservation measures under climate change. The basis of the CEE model are high resolution climate projections from a regional climate model. The data generated by this model allow us to later examine both temporal and spatial changes in costs and benefits of conservation measures. Additionally, we consider spatially heterogeneous data on the productivity of the land to integrate further spatial differences. Based on the climate and land productivity data, we model vegetation growth. This enables us to determine the timing and frequency of land use for both the business-as-usual (BAU) land use and conservation measures. This process is based on daily climate data and includes the impact of extreme events such as flooding, as well as the quantity and quality of harvest at the time of land use. This information allows us to determine the opportunity costs of conservation measures in a spatially and temporally explicit manner. An ecological model assesses the impact of the conservation measures on a species, explicitly considering their timing and the climatic influence. The final result is a set of conservation measures and their spatial allocation to reach the highest ecological benefit given a cost constraint under current and future climatic conditions.

We apply the CEE model to investigate the cost-effectiveness of different mowing regimes as conservation measures for the large marsh grasshopper (LMG) (*Stethophyma grossum*) in Schleswig-Holstein, Germany, in the years 2020-2039 and 2060-2079. Our governance setting is that a conservation agency owns grassland areas in Schleswig-Holstein and aims to cost-effectively conserve the LMG. The species and the case study region were chosen due to a combination of data and expert knowledge availability, conservation relevance and the sensitivity of the species to temporal changes of grassland use.

Our research is at the intersection of two strands of the literature. The first strand is the design of cost-effective conservation measures in agricultural landscapes (Armsworth et al. 2012, Wu & Yu 2017), with a particular focus on the spatial heterogeneity of costs and conservation benefits (Wu & Bogess 1999, Lewis et al. 2011, Duke et al. 2014) and on their spatio-temporal heterogeneity (Wätzold et al. 2016). The second strand is the small but growing economic literature on biodiversity conservation in a changing climate. A substantial part of this literature focusses on the application of portfolio theory to address the issue of uncertainty in the context of the spatial allocation of conservation activities under climate change (Ando & Hannah 2011, Ando & Mallory 2012, Mallory & Ando 2014, Shah et al. 2016). An example for further research is Lewis and Polasky (2018), who examined the provision of wildlife habitat and other ecosystem services under climate change using auctions.

Only few authors address the topic of cost-effective conservation in a changing climate. Hily et al. (2017) and Schöttker and Wätzold (2020) developed conceptual models to investigate the cost-effectiveness of different types of conservation payments respectively governance structures. Other research focuses on real landscapes with changing ecological conditions and spatially differentiated costs (but ignores their changes over time) (Alagador 2015, Zwiener et al. 2017, Alagador & Cerdeira 2019). However, none of this research considers all the specific challenges of cost-effective conservation under climate change in agricultural landscapes mentioned above.

2. The conservation problem

2.1. Case study region

Schleswig-Holstein is a Federal state located in Northern Germany, its western maritime part has a coastline at the North Sea, the eastern continental part has a coastline at the Baltic Sea. Between 1961 and 1990, the annual average temperature was 8.3°C with relatively few hot days in summer and few cold days in winter in comparison to the rest of Germany. In the same period, the annual average precipitation was 789mm, but has been increasing since and shows a large variability between years (DWD 2017). Schleswig-Holstein covers an area of approximately 15,800 km² (Business Development and Technology Transfer Corporation of Schleswig-Holstein n.d.). Approximately 9,900 km² are used agriculturally (Statistisches Amt für Hamburg und Schleswig-Holstein n.d.), of which approximately 3,200km² are permanent grassland (Statistisches Amt für Hamburg und Schleswig-Holstein 2019).

Regarding nature conservation, the foundation “Stiftung Naturschutz Schleswig-Holstein” is a key player in the area. It has purchased 360km² of land throughout Schleswig-Holstein (Stiftung Naturschutz Schleswig-Holstein n.d.), and manages it in order to maintain or create suitable conditions for species conservation. The conservation of grassland habitats for the LMG is of high interest to the “Stiftung Naturschutz Schleswig-Holstein” because the species is an indicator species for a certain grassland habitat type. The foundation was a partner in the project in which the CEE model was developed and contributed to its development by providing species-specific expertise. In our modelling procedure, we do not restrict possible conservation areas to areas currently owned by the foundation. The reasons for this are that we want to obtain more general results for Schleswig-Holstein and not only for the areas currently owned by the foundation. Moreover, a general analysis allows recommendation on future land purchase of the foundation.

2.2. The large marsh grasshopper

The LMG is a grasshopper species widely distributed in Central Europe (Heydenreich 1999). It prefers wet meadows and marshes as habitat (Koschuh 2004) and can be considered an indicator for the quality of grasslands (Heydenreich 1999), especially extensive wet meadows (Keller et al. 2012). In the case study region, the LMG used to be considered “endangered” (Winkler 2000) but was recently categorised as “least concern” (Winkler & Haacks 2019).

Populations of the LMG have declined in many regions because of the intensification of grassland use (Miller & Gardiner 2018). While more intensive grassland use has detrimental effects due to trampling and a homogenization of the vegetation structure (Miller & Gardiner 2018, Poniatowski et al. 2018), extensive grazing or mowing are beneficial for the species (Miller & Gardiner 2018). The timing of grassland use is also important as the species is particularly susceptible to disturbances during the larval and imago phases (Miller & Gardiner 2018).

Climate change has ambiguous impacts on the species. On the one hand, higher temperatures have shown to benefit the species due to increasingly rapid larval development, which in turn decreases larval mortality, and due to higher flight activity of the LMG, which contributed to an expansion of many populations (Trautner & Hermann 2008, Poniatowski et al. 2018, Löffler

et al. 2019). On the other hand, the species is dependent on very wet soils during its pre-imaginal stages, which means that possible dryer conditions during parts of the year may have negative effects on the species (Trautner & Hermann 2008, Poniatowski et al. 2018).

2.3. Conservation problem and possible conservation measures

Having the “Stiftung Naturschutz Schleswig-Holstein” in mind, we assume that a conservation agency owns grassland areas in the case study region. We also assume that the agency leases its land to farmers who may use it agriculturally but with certain restrictions to conserve some target species or habitat (Schöttker & Wätzold 2020). As the restrictions cause opportunity costs (i.e. foregone profits) to the farmers, the agency has to compensate them for these restrictions, which is done indirectly through rent reduction. Given limited financial resources, the agency aims to select conservation measures which maximize a conservation benefit subject to a cost constraint. Specifically, this means that the foundation is not able to implement conservation measures at all sites, but has to choose which sites to manage according to which conservation measure, and which sites to manage with the BAU mowing regime. We assume that the agency knows the conservation benefit of the measures and the opportunity costs of farmers and compensates farmers according to their costs.

For this study, we consider different mowing regimes as potential conservation measures. The measures were selected based on information from species experts on the species’ requirements during the different life cycle stages, while considering that the measures should not be too costly. As the timing of these stages may change under climate change, conservation measures are defined phenologically in relation to the beginning of the vegetation period, rather than setting a fixed date. In the following, we refer to “mowing regime” as a generic term that includes the BAU mowing regime and the conservation measures. Table 1 summarizes the potential conservation measures.

Table 1: Potential conservation measures for the large marsh grasshopper

Measure name	General description	Specific requirements
M1a	Early mowing	Mowing until 7 weeks after the beginning of the vegetation period, maximum 1 cut
M1b		Mowing until 9 weeks after the beginning of the vegetation period, maximum 1 cut
M2a	Late mowing	Mowing after 21 weeks after the beginning of the vegetation period, maximum 1 cut
M2b		Mowing after 23 weeks after the beginning of the vegetation period, maximum 1 cut
M3	2-cut meadow	Mowing until 7 and after 23 weeks after the beginning of the vegetation period, maximum 2 cuts

3. CEE model

3.1. Overview of the CEE model

The CEE model consists of various sub-models. Figure 1 gives an overview of how they are related, and the following subchapters 3.2-3.7 describe the sub-models in detail. For modelling purposes we divide the case study region into grid cells. The spatial scale of the grid consists of two layers. Climate data is generated for climate cells of 12km x 12km. Additionally, grassland cells contain information on grassland productivity at a resolution of 250m x 250m. Each of these grassland cells is assigned to the corresponding climate cell. The grassland productivity value is assigned according to the German system of “grassland numbers” (Grünlandzahl), which is an overall productivity index taking into consideration factors such as water availability, soil characteristics and others (BMEL n.d.). The value can range from 1 to 100 (Reguvis n.d.), where 100 represents highest productivity. In our case study region, values range from 8 to 78. In the CEE model, we ignore a possible impact of climate change on grassland numbers, as we include the impact of climate change on grass growth directly through a “vegetation model”. The grassland numbers should therefore be only seen as an indicator for productivity classes in the landscape.

The basis of the CEE model is a “climate model”, which provides detailed climate data (e.g. precipitation, temperature etc.) for a period between 2015 and 2080. The “vegetation model” estimates grassland growth depending on local conditions and the climatic conditions of a specific year. Based on information from the “climate model” and “vegetation model”, the “timing of mowing module” provides information on the yield-maximizing timing of cuts for all mowing regimes for each grassland cell and year.

The “agri-economic cost assessment” uses information from the “timing of mowing module”, and the “vegetation” and “climate models”. It determines the profit-maximizing number of cuts of each mowing regime for each grassland cell and year and estimates the costs of the conservation measures for each grassland cell and year. The “ecological model” uses input from the “climate model” and receives the profit-maximizing mowing schedule from the “agri-economic cost assessment”. It generates information about the impact of each of the possible mowing regimes on the LMG for each grassland cell and year.

Finally, based on the information from the “ecological model” and “agri-economic cost assessment”, the “optimization” determines the type and spatial allocation of conservation measures. We assume that the mowing regimes are chosen for a period of 20 years and compare the results of two periods: 2020-2039 and 2060-2079. The final result is a set of conservation measures to be implemented in each period to reach the highest ecological benefit, given the cost constraint.

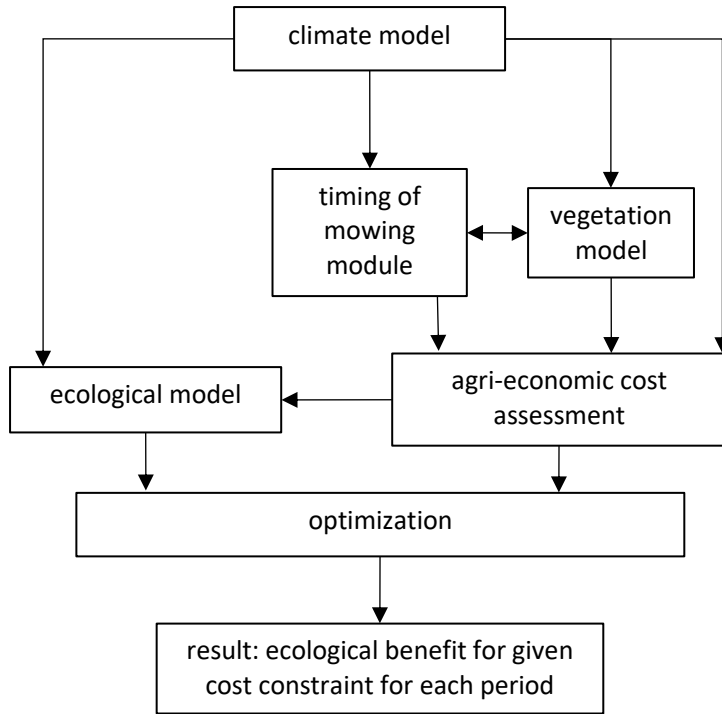


Figure 1: Overview of the climate-ecological-economic model

3.2. Climate model and data

The meteorological data required by the “ecological model”, “vegetation model”, “timing of mowing module” and “agri-economic cost assessment” are derived from high resolution climate projections with the regional climate model COSMO-CLM (Rockel et al. 2008, Fröh et al. 2016). COSMO-CLM is a non-hydrostatic model based on the weather prediction model COSMO of the German Weather Service (cosmo n.d.) with specific extensions by the Climate Limited-area Modelling-Community (CLM-Community n.d.) required to perform transient, long-term climate simulations. The simulations were originally created for the EURO-CORDEX initiative (eurocordex n.d., Jacob et al. 2014) and were extended and extensively analyzed within the German research project ReKliEs-DE (Huebener et al. 2017, HLNUG 2019). The model domain covers the entire European continent with the adjacent Mediterranean Sea as far as North Africa. The horizontal resolution of the model grid is approximately 12 km. The atmospheric processes are resolved by 40 layers of up to 22.7 km height. Soil moisture and temperature are simulated in 10 layers down to 15 m. All simulations start in 1950 and last until 2100. In this paper we only use data from 2015-2044 and 2055-2080 to sample 20-year time series from 2020-2039 and 2060-2079 (Leins et al. 2021).

The execution of regional simulations on a limited domain always requires the specification of spatially and temporally variable lateral boundary values. These lateral boundary data are interpolated in space and time from the results of global climate simulations with a much coarser spatial resolution. The COMSO-CLM simulation used here is driven by results of the global Earth-System model EC-EARTH operated by the Irish Centre for High-End Computing, ICHEC. The model is part of the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor et al. 2012) which has provided substantial information about possible 21st century

global climate developments for different greenhouse gas (GHG) scenarios to the IPCC Assessment Report 5 (AR5) (IPCC 2013). The scenario RCP4.5 (van Vuuren et al. 2011) is regionalized by COSMO-CLM for Europe and is used in this study.

This regional climate simulation used in this study provides a basic impression of the influence of a GHG scenario on the potential development of future climate. The scenario RCP 4.5 was selected because it represents an intermediate temperature increase and a moderate modification of precipitation. The principal influence of different scenarios on European climate has been investigated in detail by Keuler et al. (2016) and in the ReKliEs-De project. Different scenario simulations (RCP 2.6, RCP 4.5 and RCP 8.5) show a significant temperature increase over Germany that is about three and a half times stronger in the RCP8.5 scenario than in the RCP2.6 scenario and more than one and a half times stronger than in the RCP4.5 scenario. However, in the case study region, the expected temperature increase is more moderate than in other areas of Germany. The annual precipitation amounts show only a slight but not significant increase especially over northern Germany. A common feature of all simulations is a shift of precipitation from summer to winter and spring so that winter precipitation increases and summer precipitation decreases.

The data required for this study have been extracted from the RCP 4.5 simulation on a small subdomain of 36 x 36 climate cells covering northwest Germany. The parameters currently used by the CEE model are daily values of the mean temperature at the ground (soil surface), the accumulated precipitation, the total sink for soil water (sum of evapotranspiration and groundwater-runoff) and the total soil moisture content over the first 8 soil layers (about 4m deep).

3.3. Vegetation model

The “vegetation model” is a simplified and modified version of the model by Schippers and Kropff (2001) and simulates the dynamics of individual plants considering annual growth cycles. The main processes in a cycle are plant mortality, biomass assimilation, allocation of biomass, and mowing. The daily mortality is modelled as a function of the daily temperature, explicitly considering frost days. Biomass assimilation is modelled by a growth factor which depends on the N concentration in the plant, the humidity in the soil, absorbed radiation, temperature and a number of plant species-specific parameters. N concentration in the plant is modelled as a function of the grassland productivity. Soil humidity is considered for the top 50 cm layer which is about the typical depth of the grass roots. The soil humidity in this layer is determined from the soil moisture content of the “climate model” (section 3.2) assuming that the soil humidity increases linearly from top to bottom. Absorbed radiation depends on incoming global radiation and the plant’s leaf area index, which depends on the active biomass in the shoots and the shape of the plant. The assimilated biomass is allocated between roots and shoots, depending on the current ratio of shoot and root biomass and the plant’s N concentration. Assimilated shoot biomass is distributed between active and reserve shoot biomass.

Mowing is modelled by reducing the shoot biomass and a subsequent temporary change of the allocation of assimilated shoot biomass between active and reserve (Schippers and Kropff (2001) provide further details). We assume that the vegetation is cut down to 5cm of height

(Oomes 1992). When providing information on the biomass to be cut to subsequent sub-models, the “vegetation model” automatically subtracts these 5cm from the grass height.

3.4. Timing of mowing module

The “timing of mowing module” determines the yield-maximizing timing of the different cuts of each mowing regime for each climate cell. We consider three factors to influence the timing of mowing, which we briefly explain in the following; Gerling et al. (2020) provide further details.

The first factor is climate-dependent vegetation growth, which may differ between climate cells. We assume that the grassland productivity has no impact on the timing of harvest, and take a typical grassland productivity value of 65 (note that the impact of grassland productivity on the yield is considered below in the “agri-economic cost assessment”). The timing of the first cut is approached when a meadow reaches 85% of the expected biomass or 36cm of grass height. The timing of any subsequent cut is determined in relation to the timing of the first cut and occurs when 85% of the expected biomass or, in this case only 25cm of grass height, are reached. This is approximately six weeks after the previous cut but may change depending on climatic conditions.

As a second factor, the timing may have to be adapted due to restrictions from conservation measures. In this case, we select the timing that is as close as possible to the timing determined previously, as this leads to the lowest yield loss.

Finally, the timing may have to be adapted due to flooding and/ or high levels of precipitation. Due to data limitations we ignore differences in drainage conditions within climate cells. We assume that the agency respectively farmers consider the weather forecast in order to postpone or bring forward any cuts in case of unsuitable weather conditions, and that the weather forecast predicts the weather of the next seven days accurately. The agency respectively farmers may therefore bring the cutting date forward by up to one week, or delay it as long as necessary. Long floods of seven days or more lead to a severe decrease in quality of the biomass, which makes it necessary to dispose of the harvest. Overall, the “timing of mowing module” provides the yield-maximizing, climate cell-specific timing of the BAU mowing regime and of all conservation measures.

3.5. Agri-economic cost assessment

The “agri-economic cost assessment” serves two purposes: 1) to determine how many cuts are profit-maximizing for each mowing regime on each grassland cell in a certain year, and 2) to assess the (opportunity) costs of all conservation measures on each grassland cell and year. The “agri-economic cost assessment” is described briefly below; Gerling et al. (2020) provide a more detailed description.

First, the “agri-economic cost assessment” determines the yield that is harvested at the timing determined by the “timing of mowing module”. For the yield, we consider its quantity (amount of biomass harvested) and quality (digestibility and energy concentration) measured in MJ NEL/dt (Mega Joule Net Energy Lactation per dt of biomass). Generally, the quality of a harvest increases in spring until it peaks between June and mid-August and decreases

afterwards until autumn (Mewes et al. 2015). Inundations may have a negative impact on yield quality.

Next, the monetary value of the yield (henceforth: yield value) and the variable costs of implementing a mowing regime are calculated. The yield value is calculated by multiplying the yield with the price of concentrated feed. In Germany, the price of concentrated feed typically serves as a proxy for the price of the energy contained in the yield as the harvest of grasslands is often not sold directly on the market but is used as fodder for on-farm livestock (Mewes et al. 2015). Variable costs of a mowing regime are calculated by considering the machinery use, working hours, fuel consumption and the use of other material necessary to implement a specific mowing regime. For conservation measures and the BAU mowing regime, costs may exceed the yield value for the second, third or fourth cut on low productivity grassland cells or if weather events or measure restrictions lead to unsuitable timings. We assume that the grassland is only cut if the yield value exceeds the costs. Thus, we get the profit-maximizing number of cuts for each mowing regime on each grassland cell in a certain year.

Finally, the opportunity costs of a conservation measure are calculated by determining the difference in profit between the BAU grassland use and the conservation measure.

3.6. Ecological model

The “ecological model” *HiLEG* (*High-resolution Large Environmental Gradient*) is a spatially differentiated population dynamics model, which we use to simulate the life cycle of the LMG. It considers the impacts of a mowing regime and climate change on the population viability of the species. We only summarize its main features and refer the interested reader to Leins et al. (2021) for a detailed description of the entities, processes and equations of the “ecological model”.

The model applies a stage- and cohort-based approach to represent the different processes of the LMG’s three life stages: (1) egg/embryo (July to June of the following year), (2) larval (May-October), and (3) imago (July-October) (Heydenreich 1999, Kleukers et al. 1997, Marshall & Haes 1988). These stages are distinguished into a below-ground (egg/ embryo) and an above-ground (larval, imago) phase (Ingrisch 1983, Heydenreich 1999). The timing of each stage indicated here is an approximation and differs between cohorts. Depending on the external drivers – such as weather conditions – different timings may be observed.

In the model application, the first stage is split into a pre-diapause (1a) (roughly July-October), a diapause (1b) (roughly October-April), and an embryo phase (1c) (roughly April-June), yielding five life stages in total. Stages 1b and 2 are subdivided into cohorts to account for egg survival in case of unsuitable winter conditions and varying larva development speed depending on the hatching time. Moreover, it is considered that a certain time must pass to complete a stage’s development and evolve into the consecutive life stage. Each of the life stages and cohorts in every grassland cell has a distinct density summing up to the total population density in the considered area.

Changes in life stage or cohort density happen either due to mortality or because individuals evolve from one life cycle stage into the next (“transition”). The transition or mortality rates

are recalculated continuously depending on the current values of external drivers while including stochasticity. External drivers considered by the model are three climatic variables (temperature, precipitation, soil moisture) and the impact of mowing. The described population dynamics are simulated independently for each grassland cell in the study region using daily time steps.

The starting date, the run time in years, the climate scenario and a mowing regime typically define a single simulation run. Furthermore, several replicates are created by initially changing the random seed that influences the stochastic processes. The output of a simulation is the ecological benefit, here measured by the mean population density, averaged over the simulated time frame and 50 random replicates.

3.7. Optimization

The output of the “agri-economic cost assessment” and the “ecological model” are used as inputs to a simple “optimization” procedure in order to determine the cost-effective set and allocation of conservation measures. First, the mowing regime yielding the highest benefit-cost ratio of each 20-year period is determined for each grassland cell. Next, the grassland cells are ranked according to decreasing benefit-cost ratios. Then, the mowing regime of the grassland cell with the highest benefit-cost ratio is implemented (Duke et al. 2014), afterwards the mowing regime of the cell with the second highest benefit-cost ratio and so on until the cost constraint is reached. The cost constraint is set to 19.69 million euro per annum, which allows for the conservation of approximately 5% of the grassland in the study area. We selected a relatively large cost constraint for didactical purposes as the size of the cost constraint only affects the number of conservation sites but has little impact on their spatial allocation (results not shown), and the spatial allocation of conservation areas is more visible with a larger cost constraint. On all other grassland cells, the BAU mowing regime is implemented. For the next 20-year period, the optimization process is repeated. As a result we receive a set of conservation measures and their spatial allocation that maximizes the ecological benefit – the mean population density of the LMG – for given cost constraints for the two considered periods.

4. Results and analysis

4.1. Cost-effective conservation measures and their timing

We find that measure M1a (the measure with the very early mowing date) is the cost-effective measure on all grassland cells for both periods. The reason for the dominance of this temporal restriction lies in the interplay of ecological and economic conditions: Postponing the early cut of M1a leads to a rapid decrease of the population viability as a large proportion of the LMG is in the highly susceptible above-ground phase. From the cost perspective, the early cutting date of measure M1a is not far from the profit-maximizing timing, resulting in rather low opportunity costs.

Measures M2a and M2b have cuts in late summer and thus larger opportunity costs as the harvest quality decreases with later harvest dates and hence the yield value decreases, too. The combination of these two characteristics – the rapidly decreasing ecological benefit and the

increasing opportunity costs of measures with later timings of cuts – make the very early cutting date the most cost-effective measure.

The measure that allows a second cut (measure M3) is not cost-effective. The reason is that mowing 23 weeks after the beginning of the vegetation period (and 16 weeks after the first cut) results in very low harvest quality. This implies a small – in some areas even negative – economic benefit that cannot outweigh the associated decrease in the ecological benefit.

Despite changing climatic conditions, the same conservation measure (M1a) is cost-effective in both periods. This does not mean, however, that the timing of grassland use does not change. As the measures have been defined phenologically in relation to the beginning of the vegetation period rather than by setting a fixed date, they are automatically somewhat adapted to climate change. This potential for temporal adaptations maintains the ranking of the measures as both costs and ecological benefits of conservation measures depend largely on the timing of grassland use relative to the beginning of the vegetation period.

4.2. Cost-effective spatial allocation of conservation measures

Regarding the spatial allocation of conserved sites, we observe a spatial shift of cost-effective sites with climate change (Figure 2).

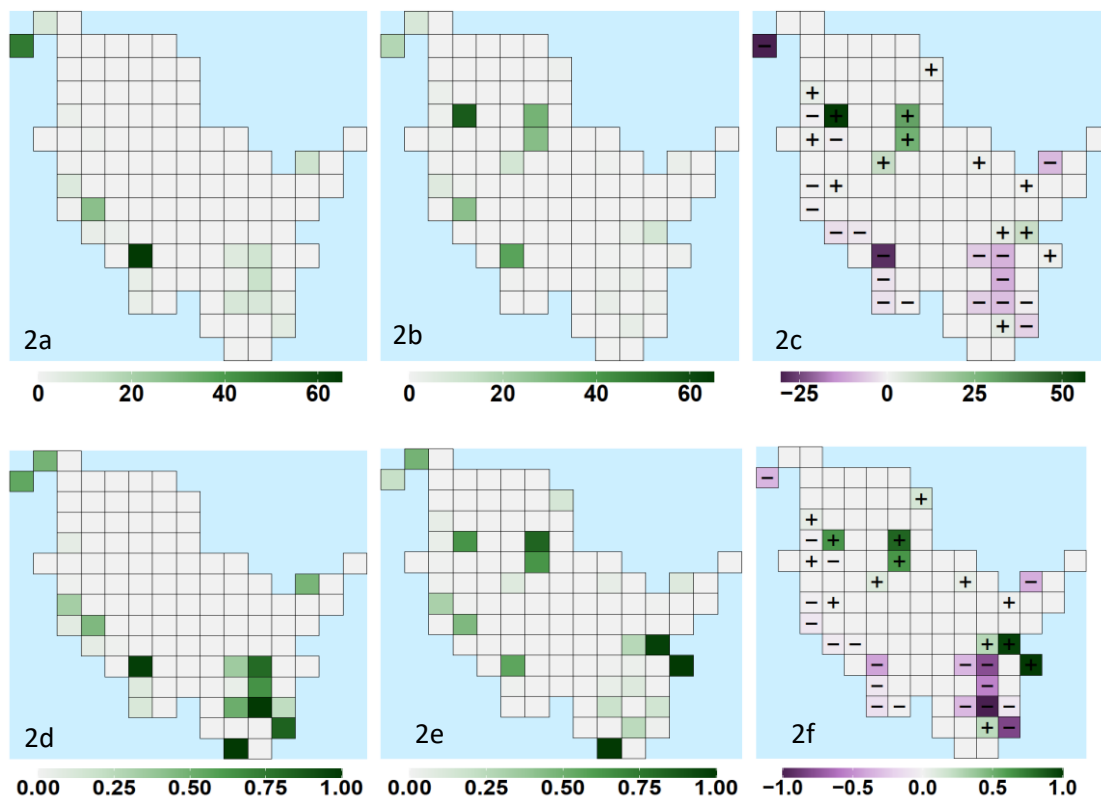


Figure 2: Grassland area with cost-effective conservation measures in each 12x12km climate cell: the first row (2a-2c) shows a representation of the absolute area in km² in the first period 2020-2039 (Fig. 2a), the second period 2060-2079 (Fig. 2b), and differences between the two periods (Fig. 2c); the bottom row (2d-2f) shows the proportion of grassland managed with conservation measures out of all grassland in the first period (Fig. 2d), the second period 2060-2079 (Fig. 2e), and the difference in the proportion of grassland with conservation measures between the two periods (Fig. 2f).

Regarding the absolute size of conserved areas in km², we observe a shift from the first period, with conservation measures being mainly implemented along the Western edge of Schleswig-Holstein, to the second period, with conservation measures being allocated more evenly between the west and the center of the Federal State (Figure 2a-c). However, the amount of grassland differs between climate cells. This implies that cells with a small grassland share but substantial changes in the conserved areas are not adequately represented by changes in the absolute area of grassland. We therefore also consider changes in the proportion of grassland. Figure 2d-f shows changes in areas in the south-east of the case study region, where a large part of the grassland is conserved in the first period (Figure 2d). In the second period, these areas lose importance relative to areas slightly further north (i.e., in the east of the Federal State) and in the center of the case study region.

To understand whether the changes in the cost-effective spatial allocation of conservation measures are mainly driven by changes in ecological benefits or costs, we consider the conservation potential according to climatic conditions (excluding the impact of grassland use) (Figure 3a-b) and the changes in average costs under climate change (Figure 3c-d).

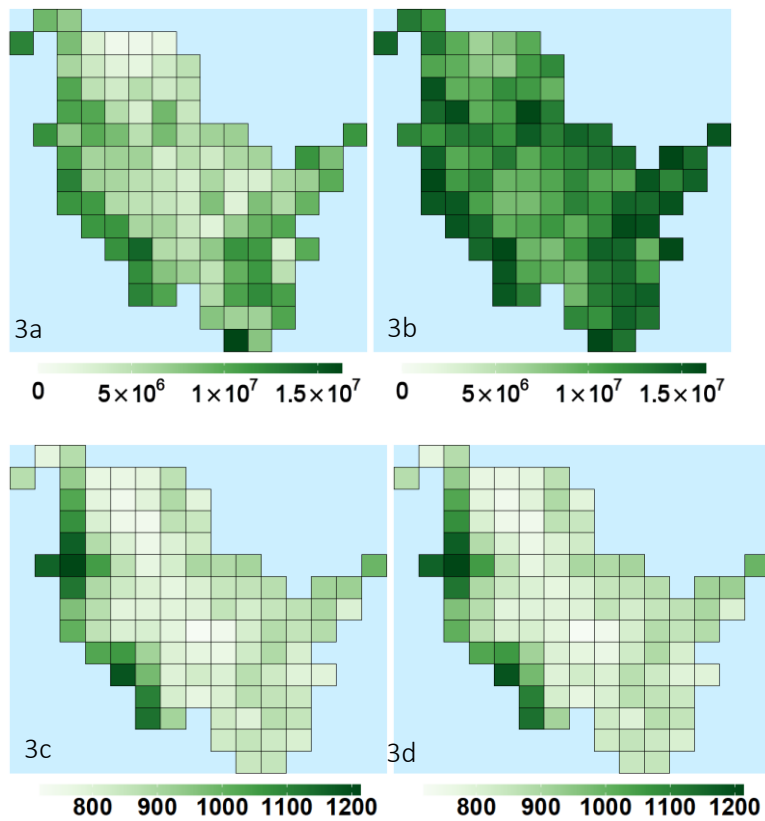


Figure 3: Conservation potential (= modelled number of grasshoppers per km² in the climate cell in the absence of any land-use induced mortality) for the first period 2020-2039 (Fig. 3a), and the second period 2060-2079 (Fig. 3b), and the average annual costs in euro of measure M1a of a climate cell for the first period 2020-2039 (Fig. 3c) and the second period 2060-2079 (Fig. 3d). Each grid cell represents a 12x12km climate cell.

Figure 3a-b shows that climatic changes generally improve the conditions for the LMG while the conservation costs remain relatively stable (Figure 3c-d). Regarding spatial differences of

costs and conservation benefits, the following observations are noteworthy: (1) the areas in the south-east combine both relatively low costs and high benefit. These areas contain only little grassland, but a very large proportion of this grassland is managed with conservation measures, especially in the first period (cp. Figure 2). In the second period, the conservation potential of the center and east improves more than the conservation potential in the south-east (Figure 3b). As the sites in the center and east have even lower costs than the south-east (Figure 3c-d), the importance of the center and east as sites for cost-effective conservation increases. (2) The second area selected for conservation, especially in the first period, is the area along the western edge of the case study region (cp. Figure 2). While this area has a high conservation potential, it is also a high-cost area. Given that the center of the case study region has a low conservation potential in the first period (Figure 3a), the cost-effective solution in the first period is therefore driven more by the conservation potential of the western areas than the availability of low-cost sites in the center. However, in the second period, the conservation potential of the center improves (Figure 3b), and some sites are chosen there instead of the more costly sites at the western edge.

5. Discussion and Conclusion

We developed a climate-ecological-economic model (CEE model) to investigate cost-effective conservation measures under climate change and applied it to examine the case of the large marsh grasshopper (LMG) on agricultural grassland in Schleswig-Holstein, Germany. We specifically address four challenges that are relevant in agricultural landscapes and which, to our knowledge, have so far not been addressed jointly. Climate change may influence (1) the spatial distribution of ecological benefits of conservation measures, (2) the ecological benefits of conservation measures with a specific timing relative to measures with other timings, (3) the spatial distribution of costs of conservation measures, and (4) the costs of conservation measures with a specific timing relative to measures with other timings.

In the CEE model, climate data and information on vegetation growth determine the timing of the different cuts of a mowing regime. Based on the timing of the different cuts, and the resulting quality and quantity of harvest, the costs of different conservation measures and their ecological benefits are modelled. Finally, an “optimization” module determines which mowing regime (a conservation measure or the BAU mowing regime) is implemented on each grassland cell. The results show the choice of cost-effective conservation measures including their timing and their locations for the periods 2020-2039 and 2060-2079.

On a methodological level, our results demonstrate the importance of developing CEE models that combine ecological-economic modelling with climate science. Only by integrating knowledge from different disciplines were we able to identify the necessary spatial and temporal changes to maintain the cost-effectiveness of conservation measures under climate change. Moreover, our results show the importance of considering both spatial and temporal variabilities in ecological benefits and costs when developing conservation measures in a changing climate. Regarding the choice of conservation measures, out of the five measures available, only the measure with the very early mowing date (M1a) is selected in both periods. The sustained cost-effectiveness of measure M1a is caused by the phenological definition of the measures, which sets the mowing dates relative to the beginning of the vegetation period

(rather than setting a fixed date). As costs and conservation benefits of a measure depend largely on the timing of mowing relative to the beginning of the vegetation period, the same measure is cost-effective under all modelled climatic conditions. However, the timing of many existing conservation measures is defined by a fixed date rather than phenologically (see Keenleyside et al. (2011), Perkins et al. (2011), Russi et al. (2014) for examples of different European agri-environment schemes with fixed dates). Setting a fixed date for conservation measures is a simple and relevant criterion if the climatic conditions are stable, as the date can be set by taking into account the typical timings of a target species' life cycle stages (Johst et al. 2015). However, if climatic conditions change and the species' development is increasingly early, keeping fixed dates may lead to a disjunction between the species' life cycle and the timing of measures (Schroeder et al. 2012, Santangeli et al. 2018, Gerling & Wätzold 2020). Additionally, harvesting at a fixed date (when the beginning of the vegetation period is increasingly early) may also influence the costs of the measure over time. While a fixed date may be adapted by regular policy interventions, bureaucratic inertia may delay or even prevent such adaptations (Dobusch & Kapeller 2013). A general policy recommendation derived from these insights is that linking the timing of a conservation measure to a phenological event rather than setting a fixed date seems favorable under changing climatic conditions.

In our case study, climate change induces a modification of the cost-effective spatial allocation of conservation efforts. This result has important implications for conservation in agricultural landscapes. In order to make use of newly cost-effective sites, species migration has to be ensured. However, habitat fragmentation is a key problem that inhibits species' successful migration, especially in agricultural landscapes (Collingham & Huntley 2000). Under climate change, strategies to enable species to keep track with their new climatically suitable zone – such as corridors and stepping stones – are commonly discussed (Alagador et al. 2015, Jones et al. 2016, Gerling & Wätzold 2020). However, this is usually considered when the former range becomes increasingly less suitable. Our research has shown that enabling migration may also be important for cost-effectiveness reasons. However, in this case a new trade-off emerges: while new regions may be more cost-effective, enabling a species' migration towards these sites generates additional costs as new migration pathways may need to be created (Vos et al. 2008) and the probability of extinction along the way increases (Early & Sax 2011, Xu et al. 2019). The extent to which the cost-effectiveness gains of the new sites then outweigh the additional risks and costs associated with migration will depend on the species concerned and its dispersal abilities. While the LMG considered in our case study has a low dispersal ability, other species may be able to migrate to new sites more easily (Vos et al. 2008).

Our CEE model is subject to limitations. The results depend on projected climate data, which can only represent approximations. Future climate change depends on greenhouse gas emission reductions and thus largely on political decisions. Similarly, the “vegetation model”, the “agri-economic cost assessment”, the “ecological model” and the determination of the timing of mowing rely on assumptions and simplify complex processes. Given these limitations, we do not aim to predict exact and small-scale changes with our model, but rather aim to understand system interactions between agricultural land use and the ecological and climate systems. By combining relatively detailed sub-models we aim for a mechanistic understanding of these complex interactions with no claim for numerical accuracy (cp. Grimm et al. 2020). Enhancing

the understanding of system interactions by way of modeling is valuable for further discussions on how to ensure cost-effectiveness for conservation when facing changing climatic conditions.

The purpose of the presented research was to develop a CEE model for the analysis of cost-effective conservation measures when costs and benefits change in a spatio-temporally heterogeneous manner with a changing climate. Further research could analyze the robustness of model results and the role of uncertainty in greater depth (Ando & Hannah 2011, Mallory & Ando 2014, Ando et al. 2018). It may also consider additional complexities of the real world to further advance the understanding of the impact of climate change on cost-effective conservation. Examples include the consideration of metapopulation dynamics in the ecological model (Hanski 1998) and the analysis of incentive-based policy instruments such as agri-environment schemes, where land users' behavior plays an important role (Wätzold et al. 2016, Gerling & Wätzold 2020).

Generally, we conclude that the high threat of climate change to biodiversity and the current dearth of economic analysis of biodiversity conservation under climate change make the benefits of further research in this field likely to be very high.

6. Literature

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