Large scale PVA modelling of insects in cultivated grasslands: the role of dispersal in mitigating the effects of management schedules under climate change

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Abstract

In many species, dispersal is decisive for survival in a changing climate. Simulation models for population dynamics under climate change thus need to account for this factor. Moreover, large numbers of species inhabiting agricultural landscapes are subject to disturbances induced by human land use. We included dispersal in the HiLEG model that we previously developed to study the interaction between climate change and agricultural land use in single populations. Here, the model was parameterized for the large marsh grasshopper (LMG) in cultivated grasslands of North Germany to analyze (1) the species development and dispersal success depending on severity of climate change in sub regions, (2) the additional effect of grassland cover on dispersal success, and (3) the role of dispersal in compensating for detrimental grassland mowing. Our model simulated population dynamics in 60-year periods (2020-2079) on a fine temporal (daily) and high spatial (250 x 250 m^2) scale in 107 sub regions, altogether encompassing a range of different grassland cover, climate change projections and mowing schedules. We show that climate change alone would allow the LMG to thrive and expand, while grassland cover played a minor role. Some mowing schedules that were harmful to the LMG nevertheless allowed the species to moderately expand its range. Especially under minor climate change, in many sub regions dispersal allowed for mowing early in the year, which is economically beneficial for farmers. More severe climate change could facilitate LMG expansion to uninhabited regions, but would require suitable mowing schedules along the path. These insights can be transferred to other species, given that the LMG is considered a representative of grassland communities. For more specific predictions on the dynamics of other species affected by climate change and land use, the publicly available HiLEG model can be easily adapted to the characteristics of their life cycle.

KEYWORDS: bilinear interpolation, climate change, dispersal success, land use, large marsh grasshopper, spatially explicit model

1 Introduction

The recent IPCC 2021 assessment report (Masson-Delmotte et al., in press) confirms that climate change poses a great threat to global biodiversity. In response to these developments, the distribution of species is expected to change (Van der Putten et al., 2010), potentially leading to increased extinction risk as ranges shrink or species must persist in new communities. Species distribution models (SDMs) are therefore widely used to predict future distributions based on climate, habitat, and occurrence data (Srivastava et al., 2019). However, in fragmented and agricultural landscapes, extinction risk is at the same time severely affected by land use practices (Oliver and Morecroft, 2014). Accounting for these effects with SDMs, which are correlative by definition, is particularly difficult for insects that require a representation of their life cycle on a fine temporal scale. Here, the timing of anthropogenic processes such as management schedules relative to the species life stage can be critical for population viability (Leins et al. 2021).

Population Viability Analyses (PVA) using mechanistic models are an important complement to SDMs for estimating the risk of species loss in changing and disturbed environments (Naujokaitis-Lewis et al., 2013). PVA models describe a species' viability as a function of its life cycle, environmental conditions such as forage supply, and anthropogenic influences such as mechanical disruption of habitats (Beissinger and McCullough, 2002; Coulson et al., 2001).

Incorporating a dispersal process into such model analysis is considered another important factor for predicting both population viability (Driscoll et al., 2014) and species distribution (Bateman et al., 2013). According to metapopulation theory (Hanski, 1999; Levins, 1969), dispersal between habitats in a fragmented landscape can prevent extinction. Moreover, it is critical to the interpretation of SDMs whether and how quickly species can actually reach regions that have been projected to be suitable (Bateman et al., 2013).

In this study, we explore the combined effect of climate change and disturbance through land use on a dispersing species by conducting a PVA of the large marsh grasshopper (LMG, Figure 1) in cultivated grasslands of North Germany. The LMG, a well-studied species inhabiting wet meadows and marshes, is considered an indicator for the quality of grassland communities, similar to other grasshopper species (Báldi and Kisbenedek, 1997; Keßler et al., 2012; Sörens, 1996). It is a slow, yet fair disperser due to its flight ability (Sörens, 1996) and – as a likely profiteer of climate change – believed to extend its range (Leins et al., 2021; Poniatowski et al., 2020; Trautner and Hermann, 2008). Anthropogenic disturbances, in particular the timing of mowing events, affect the species differently depending on the current stage of the LMG's life cycle. In terms of the LMG's environment, the German federal state of Schleswig-Holstein (SH) serves as study region, for which we extracted a highly resolved map of its grasslands (72,969 plots of roughly 6.25 ha each) using the software DSS-Ecopay (Mewes et al., 2012; Sturm et al., 2018). Furthermore, three climate change projections of increasing severity up to the year 2080 function as environmental conditions, while mechanical grassland mowing applies as anthropogenic disturbance.

Figure 1: A male adult of the large marsh grasshopper, *Stethophyma grossum* (photo: Daniel Konn-Vetterlein)

With the described setting, we address the following three research questions regarding the LMG: (1) Are there (regional) differences in dispersal success depending on climate change scenario? (2) Is the success of dispersal additionally affected by spatial patterns such as grassland cover? (3) Can dispersal compensate for otherwise detrimental grassland mowing?

We used the PVA model HiLEG (*Hi*gh-resolution *L*arge *E*nvironmental *G*radient) introduced in Leins et al. (2021) and extended it by two features for the analysis of this study: the actual dispersal process within a predefined neighborhood of species habitats; and bilinear interpolation of the available, spatially coarse climate projections to achieve heterogeneous, gradual values of high spatial resolution throughout the study region. HiLEG is originally a spatially differentiated stage- and cohort-based simulation model that can be parameterized to adapt the life cycle of terrestrial animal species, in particular insects. The new features together with the high-resolution grassland map render HiLEG from a spatially *differentiated* to a spatially *explicit* simulation model.

In our preceding study (Leins et al. 2021) of the LMG, we explored the effects of climate change at a rather low spatial (12 x 12 km^2) but high temporal resolution (daily time steps) while the 22 predefined management schedules were timed on a weekly basis. We found that although the LMG mostly benefits from climate change, the timing of land use, i.e., the mowing schedule, is the most critical factor for the species' survival. This is particularly relevant, because the intensification of anthropogenic grassland use in Germany is advancing (Bundesamt für Naturschutz, 2017). Moreover we could show that the high temporal resolution we chose was indeed critical to detect the often large long-term effects of management schedules in combination with climate change.

The original model, however, represented isolated local effects on the LMG and ignored dispersal between habitats. Due to the described relevance of dispersal effects, it is convenient to include at least general assumptions about dispersal distances, rates and timing. Thus, we extended HiLEG by the features described above to analyze the implications of external drivers on dispersal success of the LMG. Together with the realistic distribution of the grassland map we can additionally consider spatial landscape patterns that possibly play a role once dispersal is included.

The result of the analysis depends on the relative timing of dispersal and mowing events, but local effects of climate change and management may still dominate. Since high-resolution maps of species occurrence are often not available, a more general question is therefore, what the additive value of introducing higher spatial resolution and dispersal to a large-scale PVA model might be.

2 Material and methods

There are four main elements to our analysis: the study region (German federal state SH), the target species (LMG), climate data (projections from 2020 to 2080) and land use (grassland mowing). The following subsections include a description of these elements. Simulations for the present study are performed using an extension of the HiLEG model introduced in Leins et al. (2021). Section 2.5 includes a description of the model along with the relevant changes made to it for this study.

2.1 North German grasslands

The most northern German federal state SH serves as study region. More precisely, the state's grassland areas, i.e., 72,969 cells of roughly 6.25 ha in size each, were extracted using the Software DSS-Ecopay (Mewes et al., 2012; Sturm et al., 2018) and mapped to 107 climate cells (Figure 2) of available climate projections (Section 2.3). The mapping of all cells including their further specifications are described in Supplement S4. Compared to the agricultural area of Germany as a whole (50.6 %), SH is the most intensively farmed federal state with 68.5 % (Statistisches Bundesamt, 2021).

2.2 The large marsh grasshopper

The well-studied LMG (*Stethophyma grossum*, Linné 1758) is widely distributed in Central European grass- and wetlands (Heydenreich, 1999). Due to the high water requirements of its eggs, the species is bound to wet habitats such as meadows and marshes, although the grasshopper itself tolerates a wide range of temperatures and humidity (Ingrisch and Köhler, 1998; Koschuh, 2004). It used to be considered threatened in SH state (Winkler, 2000) but was recently given the status of "least concern" (Winkler and Haacks, 2019). Still, the LMG is regarded an indicator for the quality of grassland biotopes (Keßler et al., 2012; Sörens, 1996), similar to other grasshopper species (Báldi and Kisbenedek, 1997). The annual life cycle of the LMG (Figure 3) can be divided into the following five life stages, beginning with the stage after oviposition: (1) prediapause development inside egg, roughly occurring between July and November, below ground; (2) diapause (preventing too early development during mild winter months), November-March, below ground; (3) embryo development before egg hatching, March-June, below ground; (4) larva maturation, May-October, above ground; (5) imago (including oviposition), July-October, above ground; (Heydenreich, 1999; Ingrisch and Köhler, 1998; Kleukers et al., 1997; Köhler and Weipert, 1991; Malkus, 1997; Marshall and Haes, 1988; Oschmann, 1969). Although the majority of a LMG population usually stays within a close range of its hatching location (Malkus, 1997), it was shown that new populations could establish in habitats several hundred meters from their origin within two years (Marzelli, 1994) while some offspring even reached distances of three or more kilometers (Keller, 2012; Van Strien, 2013). The latter is likely to be facilitated by the LMG's flight ability (Sörens, 1996).

Population development is affected differently by the climate conditions in a LMG habitat. Embryo hatching in spring (Wingerden et al., 1991) and larval development during summer (Ingrisch and Köhler, 1998; Uvarov, 1977) is accelerated by warm temperatures. Eggs/embryos experience stress in the event of a sustained dry soil before and after winter (Ingrisch, 1983). In the face of climate change, increasing temperatures might benefit the species by accelerating its development and expansion (Poniatowski et al., 2018; Trautner and Hermann, 2008) while extended droughts might prove detrimental for hygrophilous species like the LMG (Löffler et al., 2019).

2.3 High-resolution climate projections

We obtain climate data from high-resolution scenario simulations of the COSMO-CLM[1] regional climate model (CCLM4-8-17) published by Keuler et al. (2016). In our analysis, the lateral boundaries of COSMO-CLM were controlled by simulation results from the global model ICHEC[2]-EC-EARTH and three Representative Concentration Pathways (RCPs) distinguished by action taken towards reducing CO_2 emissions (in parenthesis): RCP2.6 (full force, FF), RCP4.5 (moderate, MOD) and RCP8.5 (business as usual, BAU). Time series of daily climate data (mean or sum) are provided by the regional model, spatially resolved to grid cells of size 12 x 12 km^2. We used the years 2015-2080 of these time series and resampled them without losing long-term trends by randomly rearranging years within a 20-year time window (see Supplements S1, Section 5). This was necessary because the stochastic model

[1] Consortium for Small-scale Modeling in Climate Mode
[2] Irish Centre for High-End Computing

processes (section 2.5) would otherwise have been limited by the fact that only a single, deterministic climate projection was available per global model, RCP and grid cell. Three climate parameters were relevant for the LMG population dynamics as implemented in our model: *surface temperature* [°C], *contact water* [kg m^{-2}] and *relative humidity upper ground* [%].

We applied bilinear interpolation to the climate values of the four adjacent climate cells of each grassland cell to achieve heterogeneous, gradual climate data values of high spatial resolution throughout the grassland of the study region. This was done by weighing the distances from the center of the adjacent climate cells to a grassland cell of interest, multiplying their climate values by the resulting weights and summing up the results (Section 2.5). Figure 4 illustrates the calculation of the directional weights for a single grassland cell using a simplified geometric example. The calculated values of the weights per grassland cell are referenced in Supplement S4.

2.4 Grassland mowing

Anthropogenic disturbances to the LMG are represented by mechanical grassland mowing that occurs two to three times per year depending on the applied of 18 mowing schedules (Table 1). In terms of our model, the impact of mowing on the model species is exclusively negative, though of different magnitude with respect to the above- and belowground life stages. Indirect effects of mowing, e.g. the observation that an early and/or late cut could be beneficial for the species (Malkus, 1997; Miller and Gardiner, 2018; Sonneck et al., 2008), are not included in the model. However, such extensive maintenance cuts with only a minor mortality effect on the LMG are accounted for by the base mowing schedule named *M20+00+44* (acronym: *M00*) that stands for an undisturbed environment and always takes effect where no other schedules apply. The first number of the schedule's name stands for early mowing calendar week 20 (day 133) and the last number for late mowing week 44 (day 301). The middle number defines the (additional) mowing weeks 22-38 of more intensive grassland mowing schedules (acronyms: M22-M38). If either of the numbers in the schedule name is a double zero, the respective mowing time is omitted, so there are only two mowing events rather than three.

Gerling et al. (2021) gave the main lead for the implementation of these two-cut schedules: on the one hand, they apply for the intensive schedules of mowing weeks 22-25 which omit early mowing in week 20, because grassland cuts are usually at least six weeks apart. On the other hand, it is the case for the schedules of mowing weeks 35-38 that omit mowing in week 44. Here, such an additional late maintenance cut is neither necessary, because of slowed grassland growth in autumn, nor economically beneficial for farmers.

2.5 Extended HiLEG model

A comprehensive description of the HiLEG model following the delta-ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2020, 2006) is provided in Supplement S1. Here, we give a 'Summary ODD' (Grimm et al., 2020), which includes a digest of HiLEG's main model description as introduced in Leins et al. (2021) and an overview of the extensions applied to the model for the present study. Unaffected mechanisms and parameters are either briefly described for general understanding or omitted in the main text. ODD keywords are in italics and capital letters hereafter.

We apply the HiLEG model to the LMG's life cycle, with its life stages influenced by climate and land use. Both, the species' development and mortality are affected by climate conditions, while the latter additionally increases during mowing events, especially in the species' aboveground phase

(Section 2.2). The model extension adds a dispersal module rendering HiLEG spatially explicit, thus allowing dispersal between populations within a predefined radius. Essential climate variables are spatially differentiated on a large scale (12 x 12 km^2) and resolved to a higher scale of 6.25 ha in the model extension through bilinear interpolation (Figure 4) to achieve relevant spatial gradients within the grasslands of the North German federal state SH (Figure 2B). We ignore other spatial heterogeneity in land use and biotic variables such as vegetation height or habitat size. Hereafter, all descriptions that neither concern the dispersal process nor bilinear interpolation of the climate data were already included in the original model version.

While the ultimate *PURPOSE* of the HiLEG model is to analyze the regional effects of different climate change scenarios (CCS) and mowing schedules on the population viability of species such as the LMG (Leins et al., 2021), we here focus on exploring the potential role of dispersal, which was ignored in the original version of HiLEG. The *PURPOSE* of the extended model is to answer the following questions:

(1) Are there (regional) differences in dispersal success depending on CCS?
(2) Is the success of dispersal additionally affected by spatial patterns such as grassland cover?
(3) Can dispersal compensate for otherwise detrimental grassland mowing?

We have drawn from literature the empirical *PATTERNS* that ensure the model is sufficiently realistic for its purpose, namely the observed characteristics of the species' dispersal metrics and life cycle with its sensitivity to environmental conditions. The model design is aligned with these patterns. In terms of population structure, density, persistence and dispersal, the model output was not compared to other data, since they are scarce. All model predictions are, thus, relative, not absolute. However, 251 known LMG habitats (Figure 2B, orange circles) adapted from survey data[3] recorded in the years 2000 to 2016 are used to analyze some implications of regional effects. We used C++ for the implementation of the model's source code. It is available for both, the original model and extensions, via a GitLab repository[4] along with the executable program and the input files used for the simulations runs.

The following *ENTITIES* build the model's core: *Climate Cells* (defining large scale climate conditions in a 12 x 12 km^2 region), *Grassland Cells* (defining environmental conditions, e.g. interpolated climate values, on a scale of 250 x 250 m^2), and per *Grassland Cell* a *Population* comprised of *Life Stages*, which are comprised of age-distinguished *Cohorts*. The most relevant *STATE VARIABLE* for the interpretation of the simulation results is the *density* [in individuals/eggs m^{-2}] of a *Cohort*, *Life Stage* or *Population*. During a year, the LMG develops through five consecutive *Life Stages* (Figure 3): (1) prediapause, (2) diapause, (3) embryo, (4) larva, and (5) imago. *Density* is transferred to the next *Life Stage* (life cycle) or neighboring *Populations* (imago dispersal), and lost through mortality. The auxiliary *ENTITY Flow* controls the *density* transfer and in this function connects both the stages of the life cycle and habitats within a neighborhood. Environmental conditions such as climate, disturbances and grassland cover (stochastically) influence the amount of transferred/lost *density*. See Supplement S1, Section 2 for details on *ENTITIES* and *STATE VARIABLES*.

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[3] provided by *Landesamt für Landwirtschaft, Umwelt und ländliche Räume* via our project partner *Stiftung Naturschutz Schleswig-Holstein*
[4] HiLEG GitLab repository: git.ufz.de/leins/hileg

The model runs on basis of daily time steps where the *SCALE* corresponds to the sampling of the climate data. By definition, a year has 364 days (52 full calendar weeks) to account for the weekly mowing schedules. A simulation run takes 21,840 time steps (60 years) starting in the beginning of 2020 and terminating by the end of 2079. In the case of premature extinction of all *Populations*, simulations stop earlier. Each *Grassland Cell* in the study region (Section 2.1) represents a potential species habitat and is connected to cells within a predefined radius to allow dispersal between habitats.

To be able to better observe dispersal effects and explore its potential role for population viability, we chose an artificial *INITIAL* setting for each simulation run in terms of species distribution: a single *Population* is placed at the center of one of the 107 *Climate Cells* (i.e., the *Grassland Cell* closest to the geometric center of the *Climate Cell,* cf. black crosses in Figure 2B). In that way, we distinguished between 107 populated starting and the remaining unpopulated non-starting locations. Furthermore, a simulation run is *INITIALIZED* with one out of three CCS (section 2.3) and one of 18 mowing schedules (Table 1). The artificial setup with a single starting location per simulation run, thus no initial populations at other locations of the study region, allows us studying regional dispersal effects independent of potential immigration from other starting locations.

The *Population* at a starting location receives an initial density per *Life Stage* (i.e., 0.725 eggs m^{-2} in the diapause stage, zero density for all other *Life Stages*). Independent of the defined mowing schedule, a starting location is only exposed to the extensive mowing schedule M20+00+44 by default to serve as rather undisturbed source of dispersal to their close vicinity. *Populations* at non-starting locations are initialized empty and receive their density through potential immigration. All non-starting locations are subject to the initially defined mowing schedule.

For comparability with the original model setup of spatially stationary populations, we additionally ran the simulations with extensive mowing schedule M20+00+44 while the dispersal process was disabled. Thereby, the starting population remains confined to its source habitat and is predominantly affected by climate. Comparison with the other mowing schedules is not practical because, as described above, they are not applied to the source habitats in the simulations with dispersal.

Distinct climate data time series were employed as *INPUT DATA* per *Climate Cell* to drive the model dynamics. To have heterogeneous, gradual values at the location of each *Grassland Cell* as well, bilinear interpolation was applied using the climate data of the (up to) four closest adjacent neighbors. This is achieved by weighing the distances from a *Grassland Cell* G_a to the center of the (up to) four *Climate Cells* $\{\Omega_{a,NE}, \Omega_{a,SE}, \Omega_{a,SW}, \Omega_{a,NW}\}$ into secondary cardinal directions of G_a. The resulting bilinear weights $w_{bilin}^{a,dir}$ are multiplied with their respective climate values $\omega_{clim}^{a,dir}$ and then summed to achieve the interpolated value ω_{clim}^{a} at G_a.

$$\omega_{clim}^{a} = \sum_{dir \in DIR_{sec}} w_{bilin}^{a,dir} \cdot \omega_{clim}^{a,dir} \tag{1}$$

$$w_{bilin}^{a,dir} = 1 - \frac{\left(size_{clim} - dist_{a,dir}^{x}\right) \cdot \left(size_{clim} - dist_{a,dir}^{y}\right)}{[size_{clim}]^2} \tag{2}$$

$$dist_{a,dir}^{xy} = \left|coord_{xy}^{a} - center_{xy}^{a,dir}\right| \cdot size_{hab} \tag{3}$$

Here, $DIR_{sec} \subset DIR = \{N, NE, E, SE, S, SW, W, NW\}$ are the secondary cardinal directions NE, SE, SW and NW of the cardinal directions North (N), Northeast (NE), East (E), Southeast (SE), South

(S), Southwest (SW), West (W) and Northwest (NW) and $\omega_{clim}^{a,dir}$ is the projected value in the *Climate Cell* $\Omega_{a,dir}$ into direction dir of G_a. Size of *Climate Cell* and *Grassland Cell* are given by $size_{clim}$ and $size_{hab}$ (Table 2). The value $dist_{a,dir}^{xy}$ for the distances in x- and y-direction are calculated using the geometric center of a *Climate Cell* ($center_{xy}^{a,dir}$).

Six main *PROCESSES* are included in the model: 'Update environmental drivers', 'Flow update', 'Life Stage update', 'Cohort update', 'Bilinear climate interpolation' and 'Dispersal setup'. The first three are *SCHEDULED* for every inhabited Grassland *Cell* and during each time step of a simulation run. 'Cohort update' and 'Bilinear climate interpolation' are submodels of 'Life Stage update' and 'Update environmental drivers', respectively, and thus *SCHEDULED* every time step, as well. 'Dispersal setup' is only *SCHEDULED* in the event of an empty *Grassland Cell* becoming inhabited. Additionally, five types of sub *PROCESSES* can be associated with a *Life Stage* that apply depending on parametrization: (1) mortality (all stages), (2) development (prediapause, diapause), (3) transfer (all except imago), (4) reproduction (imago only), and (5) dispersal (imago only). For all sub processes, a daily *base rate* representing benign or observed average environmental conditions is assumed. Environmental drivers can modify ('influence') these base rates of the processes using predefined functions called *Influences* (Supplement S1, Section 7.1)

While the first four above sub processes are already part of the original model, bilinear climate interpolation (see above) and the dispersal process are introduced in the present version. Figure 2C depicts the relevant grassland cells included for calculating the dispersal from an exemplary source population inside the climate cell with ID 34 to the neighborhood in reach as it was applied for the LMG. Cells belonging to this neighborhood are either within a predefined radius $\mathrm{rad_{disp}}$ (Table 2) from the source population in question; or the closest (if any) grassland cells in each of the eight cardinal directions DIR (see above) that have no neighbors within the predefined radius. The latter is called long distance dispersal (LDD, see Supplement S1, Sections 7.1.7 and 7.5) and is included to account for the LMG's flight ability (Sörens, 1996) that is especially relevant in otherwise isolated habitats. Figure 5 illustrates how and in which cases grassland cells are selected for the LDD process.

The dispersal rate (Eq. 4) between any population P_a and a neighbor P_b within the neighborhood N_a is stochastically determined each time step using the *base dispersal rate* defined for the *Life Stage* of interest (here, $rate_{disp}^{ima}$ for the LMG's imago stage) and a dispersal probability $p_{a,b}^{disp}$ (Eq. 5):

$$rate_{disp}^{ima}(a,b) = rate_{disp}^{ima} \cdot p_{a,b}^{disp} \tag{4}$$

$$p_{a,b}^{disp} = pref_{a,b} \cdot p_{a,b}^{find} \cdot p_{a,b}^{surv} \tag{5}$$

The dispersal probability itself is calculated using a preference factor ($pref_{a,b}$) to select nearby target populations depending on the distance to all neighbors, a probability ($p_{a,b}^{find}$) to find the selected neighbor during the dispersal process and a probability ($p_{a,b}^{surv}$) to survive the dispersal, where both latter probabilities depend on grassland cover. Parameters applied to adjust the three factors/probabilities are given in Table 2. Furthermore, the dispersers are subject to dispersal mortality which is calculated using the inverse of all the dispersal probabilities multiplied by the *base dispersal rate*:

$$mort_{disp}^{ima} = \left(1 - \sum_{P_n \in \mathrm{N}_a} p_{a,n}^{disp}\right) \cdot rate_{disp}^{ima} \tag{6}$$

Table 2 gives an overview of the simulation parameters additionally defined model extension. We followed the maximum covered distance of 1,500m described by Griffioen (1996) for the LMG's dispersal radius and defined the individuals that travelled the largest distance during one day (1 out of 168) in a 'mark and recapture' study by Malkus (1997) as dispersers to determine the daily base dispersal rate. The remaining dispersal parameters were approximated using initial test simulations and their usage is explained in more detail in Supplement S1, Section 7.5.

The model output is *DESIGNED* in such a way that different aspects of a population development and dispersal success can be *OBSERVED* or rather analyzed with respect to the study's *PURPOSE*. This data is distinguished into direct parameters produced for each inhabited cell during the simulation runs of the model itself, and indirect parameters calculated for a region's whole population in the post-processing of the direct output. Relevant evaluation parameters of the first category are the daily *life stage densities* given in individuals/eggs m^{-2} depending on the respective stage. They allow *OBSERVING* the actual dispersal process over time. The indirect evaluation parameters, used to facilitate the *OBSERVATION* of a population's dispersal success, are the following four: (1) the *dispersal distance* in meters from a source habitat to an occupied habitat, (2) the *established distance* in meters from a source habitat to a habitat with imago density ≥ 0.002 individuals m^{-2} during a year, (3) the *population size* in total number of individuals/eggs in all established habitats, and (4) the *population density* in individuals/eggs m^{-2} for all established habitats. For the analysis, it was convenient to consider parameters (1) and (2) on the basis of their maximum value, i.e., the habitat farthest from the source, to compare dispersal success. All parameters were determined only using inhabited cells at the end of a simulation year to match values in the same life stage (typically diapause) and after mowing schedules have been fulfilled. In the following, *population size* and *density* are thus given in *eggs*, because populations are usually in the diapause life stage by the end of the year.

3 Results

The dispersal success of the LMG differed depending on region, climate change scenario (CCS) and mowing schedule.

Figure 6 depicts different outcomes of the dispersal process exemplary for an initial population in the center of climate cell 34 (black arrow in top left subplot). The first two rows of Figure 6 show the distribution of LMG populations chronologically in 15-year-steps in an undisturbed (first row) and disturbed environment (second row) using the MOD scenario: Under ideal conditions with extensive mowing (Table 1, M20+00+44), the LMG continuously spread out until it occupied grasslands in a distance > 20,500 meters and established in grasslands in a distance > 12,500 meters in the year 2079 (Figure 6, first row). The dispersal process became significantly slowed down (10,250 / 8,000 m) when a mowing schedule with a deviating early cut in calendar week 23 (M00+23+44) was applied (Figure 6, second row). The three bottom columns of Figure 6 compare the final dispersal success in the year 2079 between simulation scenarios. It became evident that the mowing schedule had a different impact on the dispersal success depending on which CCS occurred: Deviating early mowing in, for instance, week 23 (Figure 6, third row, M00+23+44) still allowed substantial dispersal success for the LMG in the event of the less severe FF scenario (Figure 6, first bottom column), while it already became quite inhibited for both other scenarios (Figure 6, second/third bottom column), especially MOD. Mowing just one week later (Figure 6, M00+24+44) already had a great negative impact on the dispersal success in all three CCS, allowing population establishment only in close vicinity of < 5,000 m for the FF scenario while restricting it to grassland roughly within the dispersal radius of 1,500 m from the source habitat for MOD and BAU. The strong negative impact in climate cell 34 continued for several weeks and the dispersal success afterwards became more inhibited for the FF scenario, shown on the example of additional mowing in calendar week 34 (Figure 6, M20+34+44). Later schedules starting with additional mowing in calendar week 35 (Figure 6, M20+35+00) allowed for gradual improvement in dispersal success. In these cases, the dispersal process became slightly more successful in the MOD than in the BAU scenario and remained restricted the most for the FF scenario.

Figure 7 provides a good overall view of the dispersal success in terms of *maximum established distance* at the end of a simulation run depending on CCS, mowing schedule and source habitat. In an undisturbed environment (M00), established populations on average reached distances of roughly 14,000 m and at most up to 40,000 m. More importantly the figure highlights, in which simulations population establishment basically remained restricted to the dispersal radius of the source habitat (Figure 7, dots below black horizontal dashed line). This was the case for virtually all of the regions (or rather source habitats) when mowing schedules M20+26+44 (M26) to M20+31+44 (M31) were applied. Only outside of this time window, i.e., early mowing before calendar week 26 or late mowing after week 31, dispersal could be successful to some extent, depending on region and CCS. As described above on the example of climate cell 34, early mowing schedules were in favor of the FF scenario while late mowing was in favor of MOD and especially BAU.

We could find some interrelations (Figures 8), when comparing the evaluation parameters to simulations without dispersal (Figure 8A) or to grassland cover (Figure 8B). Note that Figure 8 only shows the spatial distribution of parameters stemming from simulations of the FF scenario, because spatial patterns were similar for all three CCS. For the benefit of simplicity, we therefore only illustrate one CCS. Please refer to Supplement S2 for comprehensive illustrations of the spatial distribution and yearly development of all evaluation parameters.

The *population density* of stationary populations without dispersal (Figure 8A) – though roughly being a factor 2.5 larger than in simulations with dispersal (Figure 8F) – showed a positive correlation of different extent with *population size* (Figure 8C), *population density* (Figure 8F) and *maximum established distance* (Figure 8I). Generally speaking, the correlation was always higher for less severe CCS (cf. ρ-values in Figures 8D, G, J). The *population size* could only moderately be derived from simulations without dispersal (Figure 8D) while there was a high correlation to the *population density* (Figure 8G). Even the *maximum established distance* could be fairly estimated from simulations without dispersal (Figure 8J).

Regarding the effect of spatial patterns on the dispersal success, there were only correlations expectable within the domain of the HiLEG model: independent of the CCS and mowing schedule, grassland cover within the dispersal radius of a source habitat (Figure 8B) positively correlated with *population size* (Figure 8E) but did not correlate with *population density* (Figure 8H); due to the LDD process, a large *dispersal distance* was achieved in regions with low grassland cover, resulting in a moderate negative correlation with this evaluation parameter (Figure 8K).

Though the correlation with grassland cover was similar for all CCS, Figure 9 shows that there are regional patterns in SH that only became apparent when looking at the difference (delta) of dispersal success between CCS depending on the considered mowing schedule. Values shown in Figure 9 are the yearly absolute delta in *established distance* of the three CCS pairs (FF vs. MOD, FF vs. BAU, MOD vs. BAU) averaged over the whole simulation run. The most prominent of the regional patterns occurring in many of the deltas was a division of SH into two parts by a virtual diagonal line running from the Northwest to the Southeast (e.g. Figure 9D). Regions in the Northeast of this diagonal usually allowed a greater dispersal success for more severe CCS (Figures 9B-I) with occasional exceptions in the eastern part (Figures 9C-F). Though the tendency in the Southwest of the diagonal was a more successful dispersal for less severe CCS, there were more exceptions to this pattern and a more heterogeneous outcome. Most importantly, without substantial disturbances (Figure 9A) or when mowing late (Figure 9G), dispersal was more successful throughout all regions for the MOD scenario when comparing it to FF. Only with early mowing schedules, the diagonal pattern still applied (Figure 9D). Another notable pattern was the reduced dispersal success of the BAU scenario in the central western interior, which was most prominent when looking at the delta for late mowing of FF vs. BAU (Figure 9H) and MOD vs. BAU (Figure 9I). This pattern occurred because the dispersal success for the BAU scenario was strongly inhibited in the beginning and especially during the last decades of the simulation run, though it was not limited during mid-simulation (data not shown, see Supplement S3, e.g. pages 88 and 106). Overall the largest deltas in dispersal success occurred in the upper Northeast, along most of the west coast and in the southeastern regions.

Please note again that the regional deltas depicted in Figure 9 represent the mean deltas over the full simulation runs. In some regions it was, in fact, not consistently the same CCS over time that allowed for more successful dispersal (cf. above remarks). This can occasionally lead to three mistakable outcomes in Figure 9: (1) a low delta (light color) is illustrated though in most simulation years either one of the CCS allowed a clearly higher dispersal success, (2) the color indicates a lower delta than it actually occurred by the end of the simulations, (3) the color points to the opposite scenario than the one that shows the better dispersal success by the end of the simulations. In most of the cases, however, the color is a good indicator for the CCS allowing better dispersal success. We chose it deliberately to avoid focusing only on the final dispersal success and instead have a condensed overview of the delta in dispersal success that includes its chronology as well. We refer the interested reader to Supplement S3, where the deltas of all scenarios are provided including a detailed illustration of the discussed chronological changes in the delta of dispersal success.

4 Discussion

We extended the HiLEG model by a dispersal process and thereby obtained the following insights: (1) qualitative patterns of dispersal success are similar in the study region independent of CCS, but there are regions that allow more successful dispersal depending on severity of climate change; (2) spatial patterns have an effect on foremost population size (high grassland cover) and dispersal distance (low grassland cover), but only in a way that was to expect within the model domain; and (3) mowing schedules that might seem problematic when looking at an isolated habitat could still allow (slowed) dispersal outside of a population's home range. The implications of these findings will be discussed below in more detail.

4.1 LMG is a fair but slow disperser

We used a study by Marzelli (1994) to validate our results for a realistic implementation of the dispersal process and thus allow a reasonable comparison of the dispersal success. The author found that in a natural and anthropogenically undisturbed grassland environment new LMG populations could establish in a distance of 400 m from an existing population within two years. Considering the defined measure for *established distance* (Section 2.5) our model confirmed these findings that the LMG is in fact a fair but slow disperser. Within an environment of extensive grassland mowing (Table 1, M20+00+44) the LMG on average established in distances of about 14,000 m in 60 years (i.e., roughly 467 m every two years).

This distance, though being a fair share larger than in the field study, is a good result for several reasons: The conditions in our simulations were considered ideal other than in the natural environment of the field study. The simulated grassland plots had a fixed size thus dispersal steps were restricted to a minimum distance of 250 m explaining the results > 400 m. Regarding the applied dispersal radius, a 'mark and recapture' study by Malkus (1997) only found specimens in a maximum distance of 624 m. Other studies using genetic markers, however, estimated maximum dispersal distances of 3,000 m (Van Strien, 2013) or calculated a connection distance between two populations of up to 3,264 m (Keller, 2012). The value of 1,500 m we adapted from Griffioen (1996) thus appears to be plausibly middle ground, at least in an environment of high grassland cover.

In a more fragmented landscape, mobility of the LMG must be considered in a different light. Bönsel and Sonneck (2011) conducted a triannual 'mark and recapture' study for an isolated, yet stable habitat and found that none of the LMG specimens migrated to either one of the four suitable 1,500 to 9,000 m distant study sites, concluding a low dispersal activity in a highly fragmented environment. Marzelli (1994) observed, on the other hand, that the LMG is able to cross unsuitable areas of 300 m, allowing dispersal at least in a slightly fragmented landscape. Regarding the LDD process there is no quantification of its parameters but evidence that it occurs at least occasionally: individuals of the LMG were found on an island 10 km offshore with the next known onshore population about 16 km away (Oppel, 2005) while flight was observed where individuals ascended more than 20 meters into the air and out of sight (Trautner and Hermann, 2008).

With this knowledge we implemented LDD to allow expansion in fragmented landscapes where the distance between grassland plots is larger than 1,500 m (see Section 2.5). The effects on LMG dispersal by potentially unbridgeable barriers such as highways or forests and climate conditions such as wind direction were ignored in our simulations, as we focused on studying the interplay of climate change relevant parameters and mowing schedules. However, we increased dispersal mortality with decreasing grassland cover (Section 2.5) to account for unsuitable conditions in fragmented landscapes.

The fact that the dispersal success remained within reasonable bounds despite the applied simplifications and estimations provides the confidence to consider our simulation results of applied mowing schedules valid as well. More importantly, the projected rather short dispersal distances, especially in a disturbed environment, reinforce the choice for our approach to study the development of individual populations at regional or even local level.

4.2 Climate change facilitates the expansion in North SH state

Looking at the regional patterns of dispersal success in an undisturbed environment for each CCS separately, they are qualitatively very similar to the results for scenario FF in Figures 8C, F, I. Some of the patterns even follow climatic conditions already largely found in simulations without dispersal that will be discussed later. Comparing the deltas between evaluation parameters of the three CCS pairs (FF vs. MOD, FF vs. BAU, MOD vs. BAU) revealed, however, regional differences (Figure 9) with possible implications for climate dependent management strategies.

With some exceptions in the Southwest, the LMG widely benefits from climate change in SH. This again confirms our previous findings (Leins et al., 2021) as well as the results from similar studies (Poniatowski et al., 2018; Trautner and Hermann, 2008). A moderate climate change (MOD) would be beneficial for the LMG in the whole study region. In case of severe climate change (BAU) only the western coastal regions would be worse off but the conditions running from North to East of the study region would improve the most in this scenario. The latter is relevant for two reasons.

First, the northeastern interior of SH is the region where currently most of the inhabited LMG habitats are located (Figure 2B, orange circles). With climate change in mind, conditions would thus improve the most particularly for these existing populations. Second, the northern regions are currently the most difficult terrain for the LMG, where hardly any populations are found. Although it is going to remain the least suitable region climatically (Figure 8F), it would improve the most in the more severe CCS (Figures 9B-F) and as a result could facilitate LMG expansion to the North. Poniatowski et al. (2020) already found that many grasshopper species including the LMG expand their range due to global warming. Especially a climate change driven northern range shift is often discussed for – among other species (Van der Putten, 2012) – insects as well (Stange and Ayres, 2010) and was particularly shown for several grasshopper species (Poniatowski et al., 2018).

4.3 Higher grassland cover allows larger population size

The second region currently scarcely populated by the LMG is the west coast of SH and its interior. Only in the southern and central parts along the coast, a few populations are found. This is despite the fact of it having a high grassland cover (Figure 2B) and that our simulations showed suitable conditions of potentially high *population density* throughout the region (Figure 8F) even with mild climate change (FF). Especially on the central west coast with highest grassland cover (Figure 8B) that is notably correlated with high *population size* (Figure 8E, ρ between 0.63 and 0.68) there are currently no known LMG populations (Figure 2B, missing orange circles).

Even though it is reasonable that the higher availability of grassland allows a larger number of populations – and thus higher overall *population size*, the reason for the LMG to be spread thin apparently is neither the climatic nor the biotic conditions but likely the fact that the northwestern region of SH has the state's highest percentage of agricultural land, with more than 74% (Statistisches Amt für Hamburg und Schleswig-Holstein, 2021).

The negative correlation of grassland cover with *established distance* (Figure 8K, ρ=-0.45 to -0.52), on the other hand, can be ignored within the domain of the model. It is due to the fact that especially in fragmented landscapes the LDD process applies, allowing for above-average dispersal distances.

The main problem for all of the currently (mostly) uninhabited regions, especially in the Northwest of the study region, is the relatively large distance to the closest established LMG populations (Figure 2B, orange circles). Measures to assist the LMG to migrate by itself to these regions are likely to depend on local constraints and can only be partly derived from the results of the present study. We will nevertheless address potential management strategies later in the discussion.

4.4 Mowing slows down dispersal but still allows it up to a threshold

The key to all above considerations is the right timing of grassland mowing because it is one of the critical factors for the dispersal success (Figure 7) and survival of LMG populations. In our preceding study, it was unclear how to interpret the diminishing effect of mowing on the LMG's lifetime during summer and early autumn (Leins et al., 2021, Figure 9). From the results of the present study we learn that, while population development might become increasingly restricted when mowing up to calendar week 25 and down to calendar week 32 (Figure 7), it still allows (slower) dispersal and establishment outside of a source habitat's dispersal radius (Figure 6).

It is important to bear in mind that there is a spillover effect within the dispersal radius due to the unrealistically undisturbed source habitats and that the mowing dates should be interpreted in relative, not absolute terms (Section 2.5). Yet, the resulting dates provide valuable insight for potential management strategies in agricultural grasslands, because it means that there are ways of supporting LMG establishment and dispersal while allowing economically beneficial land use. Especially the early mowing weeks of late spring and early summer are of relevance here, because they produce the best yields for farmers (Gerling et al., 2021).

Furthermore, with a minor climate change (FF) mowing is even less problematic for a longer period of time before summer in most parts of SH than it would be with the more severe scenarios MOD and BAU (Figures 9D-E). Assuming that begin and duration of vegetation growth do not shift in the same way as the life cycle development of the LMG, the longer period of unproblematic mowing with the FF scenario is highly relevant when considering the implications of climate change for the species:

We discussed above that from climate change alone the LMG would benefit in all (MOD) or most (BAU) parts of the study region. However, SH is with an agricultural area of 68.5% (Statistisches Bundesamt, 2021) the most intensively farmed state in Germany (50.6%). In such an environment, the LMG would thus be better off in case of minor climate change or none at all. It would still require measures reducing intensive grassland use to allow the LMG to thrive and expand, but they ought to be implemented easier and more cost-efficient.

4.5 Spatially stationary simulations as fair indicator for suitable regions

As pointed out above, simulations without dispersal could already help identifying regions that in principle support LMG development and highlight the general implications of disturbances such as mowing on LMG populations. Depending on the evaluation parameter of simulations with dispersal, we found correlations of different extent with the *population density* stemming from the spatially stationary simulations (Figure 8, second column): Less surprisingly, the *population density* of established habitats within a region highly correlated (Figure 8G, ρ=0.74-0.87), because it is mainly driven by regional climate conditions. Furthermore, there is only little correlation (Figure 8D, ρ=0.24-0.4) with the *population size* as it depends more on grassland cover (see above).

Interestingly, however, there is a noticeable positive correlation (Figure 8J, ρ=0.56-0.71) with the *established distance*, especially for the less severe CCS. Therefore, results from simulations of stationary populations could already be a good indicator for the development – and even the general ability to disperse – of species such as the LMG in a regional context. Within the domain of our model, high spatial resolution thus is not the key factor for broadly identifying (climatically) suitable regions. This is a useful insight, especially because simulations without dispersal require less information about a target species and have a much shorter runtime.

The actual development and distribution of a dispersing population could, however, change both qualitatively and quantitatively depending on the spatial patterns and climatic gradients within a region. Particularly in combination with disturbances, the introduction of the dispersal process delivered valuable information: First, mowing schedules that seemed highly problematic in spatially stationary simulations could still allow (reduced) dispersal success. Second, the grassland cover could change the implications of a region's general suitability, because it might either hinder dispersal in fragmented landscapes of otherwise suitable conditions (Bönsel and Sonneck, 2011) or improve population establishment with high cover (Figure 8E) and thus a larger number of refuges.

The relevance of a dispersal process and spatial patterns might increase further if other factors are additionally considered. A mechanistic dispersal process (Vinatier et al., 2011) instead of the present statistical approach could, for instance, result in a more directed preference for neighboring habitats. This effect would especially apply, if (micro) climate was more heterogeneous or less gradually distributed in a study region. Similarly, a more realistic distribution of varying land use (timing) or other detrimental/beneficial environmental conditions could hinder/promote regional dispersal attempts. Furthermore, considering the effects of spatial patterns such as fragmentation on, for example, dispersal and mortality rates or extinction events might further change species distribution. Ways of including some of these mechanisms into the model to analyze the dispersal success in more detail are addressed at the end of the discussion.

4.6 Management decisions require expertise on a regional level

Overall our results showed that there is no universal formula for protecting and supporting LMG populations in cultivated grasslands of North Germany, just a tendency in the implications of (future) climate change and a coarse window of unsuitable mowing schedules. Though a broad approach of quite extensive land use could be applied using our results, it would probably not be feasible on a large spatial scale, because such measures of poor spatial targeting have proven to be less effective (Meyer et al., 2015). At the same time, the uncertainty of climate change makes robust and cost-effective conservation policies necessary (Drechsler et al., 2021). Therefore, management decisions require expertise on a regional or even local level and should remain flexible, especially in grasslands (Joyce et al., 2016), to be able to react to the severity of climate change (Hulme, 2005).

Heller and Zavaleta (2009) compiled a ranked list of recommendations for management strategies and conservation planning in the face of climate change, some of which could be applied to the scenario in our analysis as well. Using their study in the following, we discuss approaches that could be derived from our results, i.e., strategies incorporating the (right) timing of mowing events.

At the top of their list in this regard, unsurprisingly, is the integration of climate change monitoring into conservation planning, particularly in terms of management schedules. Another apparent approach is to increase the number and size of refuges. Such refuges could in general be achieved by applying mowing schedules reasonably far outside the unsuitable time window and nearby known LMG habitats (Figure 2B, orange circles).

Depending on management goal and occurring climate change (cf. flexible management), different parts of SH (Figure 9) should be prioritized for these measures: the northeastern regions, if the goal is reinforcing beneficiary populations under *more* severe climate change or preserving vulnerable ones under a *less* severe climate change; and the southwestern regions, to reinforce beneficiary populations under *less* severe climate change or preserve vulnerable ones under a *more* severe climate change.

In terms of dispersal, increasing connectivity by locating habitats close to each other and creating migration corridors or stepping stones is named as a key factor. Buffered zones around protected habitats are discussed as well, because they could compensate for unforeseen population shifts due to changing conditions. These measures are of different relevance inside our study region, as both grassland cover and species occurrence vary depending on region. The most inhabited eastern interior of SH is quite distant from the widely uninhabited Northwest, having large patches of low or no grassland cover in between. Here as well as in other inhabited regions of substantial grassland cover, the more practical approach may be to support existing populations by focusing on more extensive mowing schedules while allowing undirected dispersal through the creation of buffered zones or nearby habitats of less intensive mowing.

Regarding directed dispersal, there are only a few populated habitats on the edge of the uninhabited region, which likely require reinforcement and/or buffered zones first, before they can serve as origin for a northwestwards dispersal path along smartly distributed stepping stones of extensively mown grassland plots. Given our results, autonomous establishment of a LMG population in the Northwest would nonetheless take several decades.

Inhabited regions of low grassland cover as they are mostly found in the Southeast of the study region might, however, need another approach for assisting survival and/or dispersal of the LMG: since suitable habitats are rather scarce, it is highly relevant to leave existing populations as undisturbed as possible. Creating similarly undisturbed satellite habitats in terms of metapopulation theory (Hanski, 1999; Levins, 1969) could additionally promote occasional (long distance) dispersal and compensate for local extinction, e.g., due to unsuitable climate events.

Yet, not only because the benefits of metapopulation dynamics in fragmented landscapes for slowly dispersing species like the LMG are controversial (Bönsel and Sonneck, 2011) as discussed above, it would require an additional study to assess the above hypotheses. Simulations within such a study should include the analysis of more diverse management schedules in the neighborhood of an established population or along a migration path, and possibly more mechanistic consideration of small-scale LMG dispersal behavior. Furthermore, it would have to reduce the unrealistic positive effect within the dispersal radius of a source habitat (Section 4.4) to obtain robust results regarding local dispersal success.

Such simulations could easily be conducted with only minor modifications to the HiLEG model and deliver valuable insights to conservation agencies in SH for the protection of local LMG populations. With the right set of parameters, the model could additionally be adjusted for the life cycle of other species to achieve a broader picture of the implications for disturbed grassland communities in the face of climate change. However, as grasshopper species like the LMG are considered indicators for the quality of grassland biotopes (Báldi and Kisbenedek, 1997; Keßler et al., 2012; Sörens, 1996), the analysis of single species already gives a good idea of the implications for such a community.

5 Conclusion

The introduction of dispersal into the highly resolved, yet formerly non-spatially-explicit HiLEG model provided valuable insights regarding the implications of anthropogenic disturbances for the large marsh grasshopper (LMG) under different climate change scenarios. Our study reconfirmed that the LMG in principle benefits from a moderate climate change in temperate regions and was also helpful in unraveling the impact of grassland mowing schedules that were previously unclear. Namely that some of the schedules, despite inhibiting population development, could still allow species dispersal to some extent. It depends on the regional conditions and severity of climate change which mowing schedules this mainly involves.

A milder climate change permits a longer mowing period in the beginning of the season and is more beneficial in the southwestern parts of Schleswig-Holstein (SH). This is an important observation, because early mowing provides the highest yields for farmers. More severe climate change, on the other hand, allows for earlier resumption of mowing after summer, especially outside the western interior of the state. Grassland cover only plays a minor role in the development of the LMG, though a high cover facilitates population establishment within a region.

However, many of the regions that might either improve the most under climate change (North SH) or offer high grassland cover (West SH) are currently scarcely populated by the LMG. Assisting the grasshopper in migrating to those regions will require flexible management decisions on a local level, especially because the key factors hindering the LMG from thriving are anthropogenic (thus controllable) disturbances such as grassland mowing. Improving these practices likely benefits other (insect) species as well, because of the LMG's role as indicator for the quality of grasslands.

In the above discussion, we identified five factors that we recommend to consider for such regional management decisions: (1) the development of climate conditions (when and in which region to apply measures); (2) the grassland cover (size, number and distribution of refuges); (3) the existence of LMG populations (habitats prioritized for protection); (4) in uninhabited regions, the distance to and direction of established populations (size, number and distribution of stepping stones); and (5) the local land use custom (opportunities and economical acceptance for measures of protection).

The results from both the present and previous study, with and without consideration of dispersal, provided a number of key indicators for potential management strategies in cultivated landscapes. With their input alone, a reasonable protection of grassland (insect) species such as the LMG can be achieved. To further assist stakeholders on a regional level in their decision for viable management strategies, a more realistic or rather heterogeneous integration of disturbances could be of relevance. Such a follow up study can easily be performed with only minor modifications to the HiLEG model along with the matching set of parameters – eligible for other target species as well.

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7 Competing Interests Statement

There is no known competing interest that could have influenced the present work.

8 Author Contributions section

JL: concept, design and implementation of the model; acquisition and processing of input data; analysis and interpretation of the simulation output; drafting and visualization of the article. MD: model concept; data interpretation; review and editing of the article.

9 Data Accessibility Statement

Open access model code, executables and required input data are available via GitLab (git.ufz.de/leins/hileg). Output data generated by the HiLEG simulation runs for this study can be found at ufz.de/record/dmp/archive/11898/en/ and the aggregated data used for analysis and illustration at ufz.de/record/dmp/archive/11896/en/ (with dispersal) and ufz.de/record/dmp/archive/11899 (without dispersal). A representation of the data used for mapping and weighing climate and grassland cells for bilinear interpolation can be found at ufz.de/record/dmp/archive/11900. A GitLab link to the exact model version along with detailed descriptions of the input data and simulation parameters will follow upon publication.

10 References

Báldi, A., Kisbenedek, T., 1997. Orthopteran assemblages as indicators of grassland naturalness in Hungary. Agric. Ecosyst. Environ. 66, 121–129. https://doi.org/10.1016/S0167-8809(97)00068-6

Bateman, B.L., Murphy, H.T., Reside, A.E., Mokany, K., VanDerWal, J., 2013. Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling. Divers. Distrib. 19, 1224–1234. https://doi.org/10.1111/ddi.12107

Beissinger, S.R., McCullough, D.R., 2002. Population Viability Analysis. University of Chicago Press.

Bönsel, A.B., Sonneck, A.-G., 2011. Habitat use and dispersal characteristic by <Emphasis Type="Italic">Stethophyma grossum</Emphasis>: the role of habitat isolation and stable habitat conditions towards low dispersal. J. Insect Conserv. 15, 455–463. https://doi.org/10.1007/s10841-010-9320-4

Bundesamt für Naturschutz, 2017. Agrar-Report 2017 - Biologische Vielfalt in der Agrarlandschaft. BfN / Bundesamt für Naturschutz (Hrsg.), Bonn.

Coulson, T., Mace, G.M., Hudson, E., Possingham, H., 2001. The use and abuse of population viability analysis. Trends Ecol. Evol. 16, 219–221. https://doi.org/10.1016/S0169-5347(01)02137-1

Drechsler, M., Gerling, C., Keuler, K., Leins, J., Sturm, A., Wätzold, F., 2021. A quantitative approach for the design of robust and cost-effective conservation policies under uncertain climate change: The case of grasshopper conservation in Schleswig-Holstein, Germany. J. Environ. Manage. 296, 113201. https://doi.org/10.1016/j.jenvman.2021.113201

Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., Edworthy, A., Evans, M.J., Gibson, R., Heinsohn, R., Howland, B., Kay, G., Munro, N., Scheele, B.C., Stirnemann, I., Stojanovic, D., Sweaney, N., Villaseñor, N.R., Westgate, M.J., 2014. The Trajectory of Dispersal Research in Conservation Biology. Systematic Review. PLOS ONE 9, e95053. https://doi.org/10.1371/journal.pone.0095053

Gerling, C., Drechsler, M., Keuler, K., Leins, J., Radtke, K., Schulz, B., Sturm, A., Wätzold, F., 2021. Cost-effective conservation in the face of climate change: combining ecological-economic modelling and climate science for the cost-effective spatio-temporal allocation of conservation measures in agricultural landscapes.

Griffioen, R., 1996. Over het dispersievermogen van de Moerassprinkhaan. Nieuwsbr. Saltabel 15, 39–41.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Railsback, S.F., Vincenot, C.E., Berger, U., Gallagher, C., DeAngelis, D.L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A.S.A., Milles, A., Nabe-Nielsen, J., Polhill, J.G., Radchuk, V., Rohwäder, M.-S., Stillman, R.A., Thiele, J.C., Ayllón, D., 2020. The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. J. Artif. Soc. Soc. Simul. 23, 7.

Hanski, I., 1999. Metapopulation ecology. Oxford University Press.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biol. Conserv. 142, 14–32. https://doi.org/10.1016/j.biocon.2008.10.006

Heydenreich, M., 1999. Die Bedeutung der Heuschreckenart Stethophyma grossum L., 1758 (Caelifera: Acrididae) als Bestandteil eines Zielartensystems für das Management von Niedermooren.

Hulme, P.E., 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? J. Appl. Ecol. 42, 784–794. https://doi.org/10.1111/j.1365-2664.2005.01082.x

Ingrisch, S., 1983. Zum Einfluß der Feuchte auf die Schlupfrate und Entwicklungsdauer der Eier mitteleuropäischer Feldheuschrecken (Orthoptera, Acrididae). Dtsch. Entomol. Z. 30, 1–15. https://doi.org/10.1002/mmnd.19830300102

Ingrisch, S., Köhler, G., 1998. Die Heuschrecken Mitteleuropas, Die Neue Brehm-Bücherei. Westarp Wissenschaften, Magdeburg.

Joyce, C.B., Simpson, M., Casanova, M., 2016. Future wet grasslands: ecological implications of climate change. Ecosyst. Health Sustain. 2, e01240. https://doi.org/10.1002/ehs2.1240

Keller, D., 2012. Insect dispersal in fragmented agricultural landscapes. ETH Zurich. https://doi.org/10.3929/ETHZ-A-007619649

Keßler, T., Cierjacks, A., Ernst, R., Dziock, F., 2012. Direct and indirect effects of ski run management on alpine Orthoptera. Biodivers. Conserv. 21, 281–296. https://doi.org/10.1007/s10531-011-0184-z

Keuler, K., Radtke, K., Kotlarski, S., Lüthi, D., 2016. Regional climate change over Europe in COSMO-CLM: Influence of emission scenario and driving global model. Meteorol. Z. 25, 121–136. https://doi.org/10.1127/metz/2016/0662

Kleukers, R., Van Nieukerken, E., Odé, B., Willemse, L., Van Wingerden, W., 1997. De sprinkhanen en krekels van Nederland (Orthoptera).

Köhler, G., Weipert, J., 1991. Beiträge zur Faunistik und Ökologie des Naturschutzgebietes 'Apfelstädter Ried', Kr Erfurt-Land Teil IV Orthoptera: Saltatoria. Arch Nat Landschaftforschung 31, 181–195.

Koschuh, A., 2004. Verbreitung, Lebensräume und Gefährdung der Sumpfschrecke Stethophyma grossum (L., 1758) (Saltatoria) in der Steiermark. Joannea Zool. 26.

Leins, J.A., Banitz, T., Grimm, V., Drechsler, M., 2021. High-resolution PVA along large environmental gradients to model the combined effects of climate change and land use timing: lessons from the large marsh grasshopper. Ecol. Model. 440, 109355. https://doi.org/10.1016/j.ecolmodel.2020.109355

Levins, R., 1969. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. Bull. Entomol. Soc. Am. 15, 237–240. https://doi.org/10.1093/besa/15.3.237

Löffler, F., Poniatowski, D., Fartmann, T., 2019. Orthoptera community shifts in response to land-use and climate change – Lessons from a long-term study across different grassland habitats. Biol. Conserv. 236, 315–323. https://doi.org/10.1016/j.biocon.2019.05.058

Malkus, J., 1997. Habitatpräferenzen und Mobilität der Sumpfschrecke (Stethophyma grossum L. 1758) unter besonderer Berücksichtigung der Mahd. Articulata 12, 1–18.

Marshall, J.A., Haes, E.C.M., 1988. Grasshoppers and allied insects of Great Britain and Ireland. Grasshopp. Allied Insects G. B. Irel.

Marzelli, M., 1994. Ausbreitung von Mecostethus grossus auf einer Ausgleichs-und Renaturierungsfläche. Articulata 9, 25–32.

Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, B. Zhou (eds.), in press. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Mewes, M., Sturm, A., Johst, K., Drechsler, M., Wätzold, F., 2012. Handbuch der Software Ecopay zur Bestimmung kosteneffizienter Ausgleichszahlungen für Ma\s snahmen zum Schutz gefährdeter Arten und Lebensraumtypen im Grünland. UFZ-Bericht, Helmholtz-Zentrum für Umweltforschung.

Meyer, C., Reutter, M., Matzdorf, B., Sattler, C., Schomers, S., 2015. Design rules for successful governmental payments for ecosystem services: Taking agri-environmental measures in Germany as an example. J. Environ. Manage. 157, 146–159. https://doi.org/10.1016/j.jenvman.2015.03.053

Miller, J., Gardiner, T., 2018. The effects of grazing and mowing on large marsh grasshopper, Stethophyma grossum (Orthoptera: Acrididae), populations in Western Europe: a review. J. Orthoptera Res. 27(1), 91–96. https://doi.org/10.3897/jor.27.23835

Naujokaitis-Lewis, I.R., Curtis, J.M.R., Tischendorf, L., Badzinski, D., Lindsay, K., Fortin, M.-J., 2013. Uncertainties in coupled species distribution–metapopulation dynamics models for risk assessments under climate change. Divers. Distrib. 19, 541–554. https://doi.org/10.1111/ddi.12063

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. WIREs Clim. Change 5, 317–335. https://doi.org/10.1002/wcc.271

Oppel, S., 2005. Die Heuschreckenfauna der jungen Düneninsel Trischen im schleswig-holsteinischen Wattenmeer (Insecta: Saltatoria) 6.

Oschmann, M., 1969. Faunistisch-ökologische Untersuchungen an Orthopteren im Raum von Gotha. Hercynia - Ökol. Umw. Mitteleur. 6, 115–168.

Poniatowski, D., Beckmann, C., Löffler, F., Münsch, T., Helbing, F., Samways, M.J., Fartmann, T., 2020. Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. Glob. Ecol. Biogeogr. 29, 2190–2202. https://doi.org/10.1111/geb.13188

Poniatowski, D., Münsch, T., Bianchi, F., Fartmann, T., 2018. Arealveränderungen mitteleuropäischer Heuschrecken als Folge des Klimawandels. Nat. Landsch. 553–561. https://doi.org/10.17433/12.2018.50153645.553-561

Sonneck, A.-G., Bönsel, A., Matthes, J., 2008. Der einfluss von Landnutzung auf die Habitate von Stethophyma grossum (Linnaeus, 1758) an Beispielen aus Mecklenburg-Vorpommern. Articulata 23, 15–30.

Sörens, A., 1996. Zur Populationsstruktur, Mobilität und dem Eiablageverhalten der Sumpfschrecke (Stethophyma grossum) und der Kurzflügeligen Schwertschrecke (Conocephalus dorsalis). Articulata 11, 37–48.

Srivastava, V., Lafond, V., Griess, V. C., 2019. Species distribution models (SDM): applications, benefits and challenges in invasive species management. CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 14. https://doi.org/10.1079/PAVSNNR201914020

Stange, E.E., Ayres, M.P., 2010. Climate Change Impacts: Insects, in: John Wiley & Sons, Ltd (Ed.), Encyclopedia of Life Sciences. John Wiley & Sons, Ltd, Chichester, UK, p. a0022555. https://doi.org/10.1002/9780470015902.a0022555

Statistisches Amt für Hamburg und Schleswig-Holstein, 2021. Bodenflächen in Schleswig-Holstein am 31.12.2020 nach Art der tatsächlichen Nutzung. Statistisches Amt für Hamburg und Schleswig-Holstein, Hamburg.

Statistisches Bundesamt, 2021. Land- und Forstwirtschaft, Fischerei - Bodenfläche nach Art der tatsächlichen Nutzung. Statistisches Bundesamt (Destatis), Wiesbaden.

Sturm, A., Drechsler, M., Johst, K., Mewes, M., Wätzold, F., 2018. DSS-Ecopay – A decision support software for designing ecologically effective and cost-effective agri-environment schemes to conserve endangered grassland biodiversity. Agric. Syst. 161, 113–116. https://doi.org/10.1016/j.agsy.2018.01.008

Trautner, J., Hermann, G., 2008. Die Sumpfschrecke (Stethophyma grossum L., 1758) im Aufwind-Erkenntnisse aus dem zentralen Baden-Württemberg. Articulata 23, 37–52.

Uvarov, B., 1977. Grasshoppers and locusts. A handbook of general acridology Vol. 2. Behaviour, ecology, biogeography, population dynamics. Grasshopp. Locusts Handb. Gen. Acridology Vol 2 Behav. Ecol. Biogeogr. Popul. Dyn.

Van der Putten, W.H., 2012. Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts. Annu. Rev. Ecol. Evol. Syst. 43, 365–383. https://doi.org/10.1146/annurev-ecolsys-110411-160423

Van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos. Trans. R. Soc. B Biol. Sci. 365, 2025–2034. https://doi.org/10.1098/rstb.2010.0037

Van Strien, M.J., 2013. Advances in landscape genetic methods and theory: lessons learnt from insects in agricultural landscapes. ETH Zurich. https://doi.org/10.3929/ETHZ-A-009761395

Vinatier, F., Tixier, P., Duyck, P.-F., Lescourret, F., 2011. Factors and mechanisms explaining spatial heterogeneity: a review of methods for insect populations. Methods Ecol. Evol. 2, 11–22. https://doi.org/10.1111/j.2041-210X.2010.00059.x

Wingerden, W.K.R.E. van, Musters, J.C.M., Maaskamp, F.I.M., 1991. The influence of temperature on the duration of egg development in West European grasshoppers (Orthoptera: Acrididae). Oecologia 87, 417–423. https://doi.org/10.1007/BF00634600

Winkler, C., 2000. Die Heuschrecken Schleswig-Holsteins - Rote Liste, Rote Liste [Schleswig-Holstein]. Eigenverl, Flintbek.

Winkler, C., Haacks, M., 2019. Die Heuschrecken Schleswig-Holsteins, 4. Fassung, Stand der Daten: Dezember 2017. ed, Schriftenreihe: LLUR SH Natur RL$l27. Landesamt für Landwirtschaft, Umwelt und Ländliche Räume, Kiel.

11 Tables

Table 1: Yearly grassland mowing schedules as applied in the simulation runs. First column gives the names of the 18 mowing schedules that encode the calendar weeks of yearly mowing occurrence divided by a plus (+) symbol. An acronym of the schedule name is provided in the second column, encoding the relevant mowing week in its name. The last three columns give the actual yearly mowing days (first day of respective calendar week) per mowing schedule. Schedules that include cells containing a dash (encoded by '00' in the respective name) only have two mowing occurrences per year, all others have three. The first mowing schedule *M20+00+44* represents extensive mowing, while more intensive mowing schedules follow in the rows below the double line.

Schedule name	Acronym	Mowing days		
M20+00+44	*M00*	133	-	301
M00+22+44	*M22*	-	147	301
M00+23+44	*M23*	-	154	301
M00+24+44	*M24*	-	161	301
M00+25+44	*M25*	-	168	301
M20+26+44	*M26*	133	175	301
M20+27+44	*M27*	133	182	301
M20+28+44	*M28*	133	189	301
M20+29+44	*M29*	133	196	301
M20+30+44	*M30*	133	203	301
M20+31+44	*M31*	133	210	301
M20+32+44	*M32*	133	217	301
M20+33+44	*M33*	133	224	301
M20+34+44	*M34*	133	231	301
M20+35+00	*M35*	133	238	-
M20+36+00	*M36*	133	245	-
M20+37+00	*M37*	133	252	-
M20+38+00	*M38*	133	259	-

Table 2: Simulation parameters as used for the model extension and dispersal process of the large marsh grasshopper (LMG). The first column gives the parameter name and the respective symbol applied in equations. Second and third column contain the parameter's value and unit (if any). The fourth column gives a more detailed description of the parameter.

Parameter / State variable (symbol)	**Value**	**Unit**	**Description**
Dispersal radius ($\mathrm{rad}_{\mathrm{disp}}$)	1,500	m	Home range of the LMG given by the maximum covered distance of an individual (Griffioen, 1996)
Base dispersal rate ($rate_{disp}^{ima}$)	0.00595	day^{-1}	Daily dispersal rate of the LMG determined by the farthest disperser found in a 'mark and recapture' study (Malkus, 1997)
Dispersal preference ($pref^{near}$)	1.0		Preference of selecting a neighbor during the dispersal process, where higher values result in selection of closer neighbors
sight ($sight_{disp}$)	0.5		Ability to find a selected neighbor during a dispersal process
Decay rate (dec_{disp})	0.04		Distance dependent probability to survive the dispersal process
Climate Cell size ($size_{clim}$)	12,000	m	The size (width/height) of a square Climate Cell
Grassland Cell size ($size_{hab}$)	250	m	The size (width/height) of a square Grassland Cell (habitat)

Abbreviations: clim=climate, dec=decay, disp=dispersal, hab=habitat, ima=imago, pref=preference, rad=radius

12 Figures

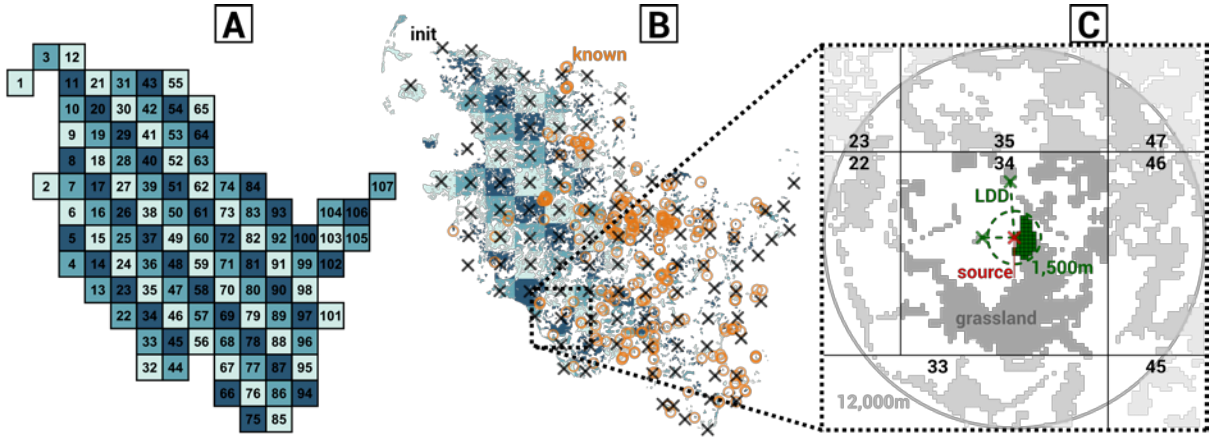

Figure 2: Distribution of 107 climate cells (A) and 72,929 grassland cells (B) in Schleswig-Holstein (SH), and grassland cells within a dispersal distance of > 12,000 m around the source habitat of a selected initial population (C). The numbers in A assign a unique ID to each climate cell. Turquoise colors in subplots A and B are used to highlight mapping of grassland cells to respective climate cells. In subplot B, black crosses mark the 107 initial populations that are closest to the respective climate cell's geometric center and orange circles known LMG locations in SH in the years 2000 to 2016. In subplot C, a red cross marks the source habitat of the initial population in climate cell 34. Green colors highlight grassland involved in dispersal: the dashed green circle around the source habitat represents the starting population's dispersal radius of 1,500 m; green cells are available grassland within this radius; and the two green crosses connected to the source habitat by dashed lines represent the habitats reached via long distance dispersal (LDD). LDD applies, if there are no cells within the 1,500m range of the source cell in either one of eight cardinal directions (North, Northeast, etc.). Grey cells depict the remaining grassland that can be reached over time through dispersal from cells other than the source habitat, where the shades of grey from dark to light represent: grassland within the source climate cell 34; grassland outside the source cell but within a 12,000 m dispersal distance; and grassland in a dispersal distance farther than 12,000 m. The four vertical and horizontal black lines delimit the source climate cell from its seven neighbors identified by black numbers. Note: here, there is no neighboring climate cell to the Southwest

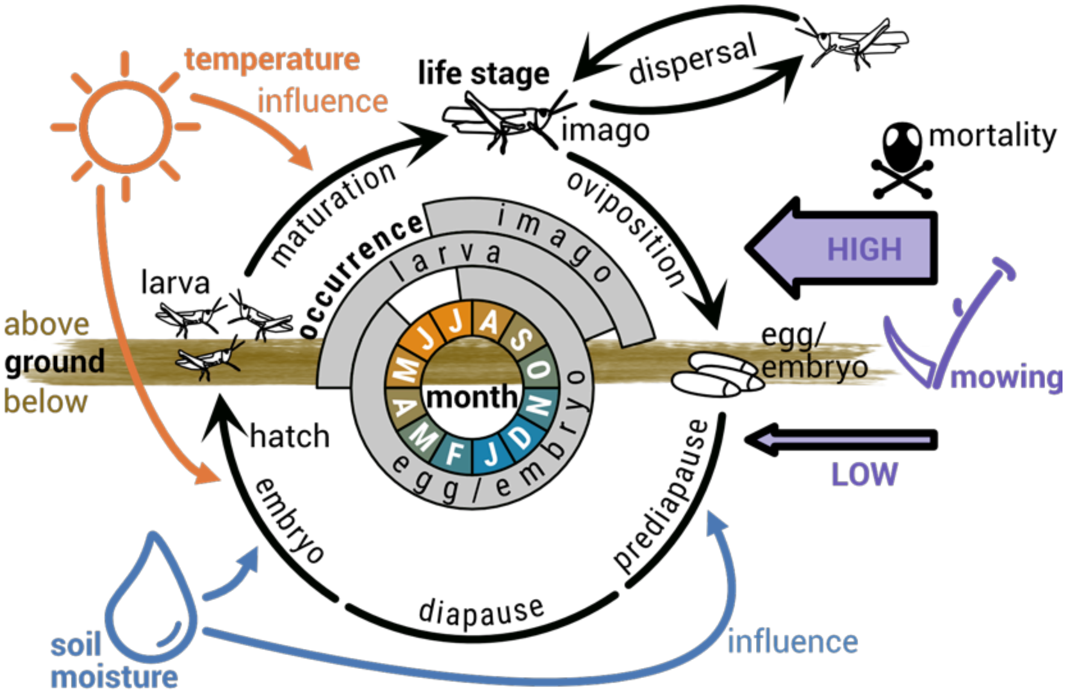

Figure 3: Yearly life cycle of the large marsh grasshopper, including the influence of external drivers. Black life stage symbols and arrows represent processes between and during life stages, where the life stage 'egg/embryo' is subdivided into three phases (broken arrow) and the dispersal process is directed to neighboring habitats. The typical ranges of the life stage occurrences are indicated in grey. The inner circle depicts months, where the color indicates seasonal changes in temperature. The influence of the external drivers of temperature, soil moisture and mowing is shown by colored symbols and arrows. Mowing impact is distinguished into high (aboveground) and low (belowground) mortality

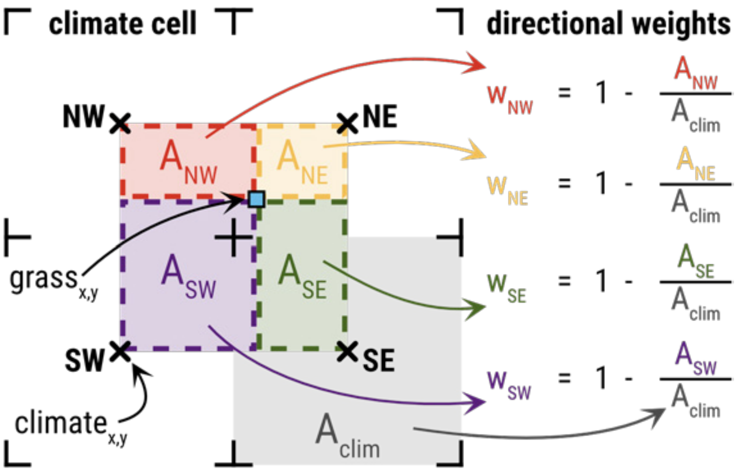

Figure 4: Calculation of the weights applied to bilinearly interpolate the climate values of four climate cells (black crosses) to achieve a distinct value for a grassland cell (blue square) that is enclosed by the climate cells. These directional weights are determined using the square area of a climate cell (A_{clim}, grey) and the rectangular directional areas (A_{NW}, red; A_{NE}, yellow; A_{SE}, green; A_{SW}, purple) formed between the grassland cell coordinate and the center of the respective climate cell in secondary cardinal direction (Northwest, NW; Northeast, NE; Southeast, SE; Southwest, SW). Climate cells closer to the grassland cell result in smaller areas while receiving larger directional weights (w_{NW}, w_{NE}, w_{SE}, w_{SW}), which is accounted for by building the inverse of the ratio from directional area to climate cell area

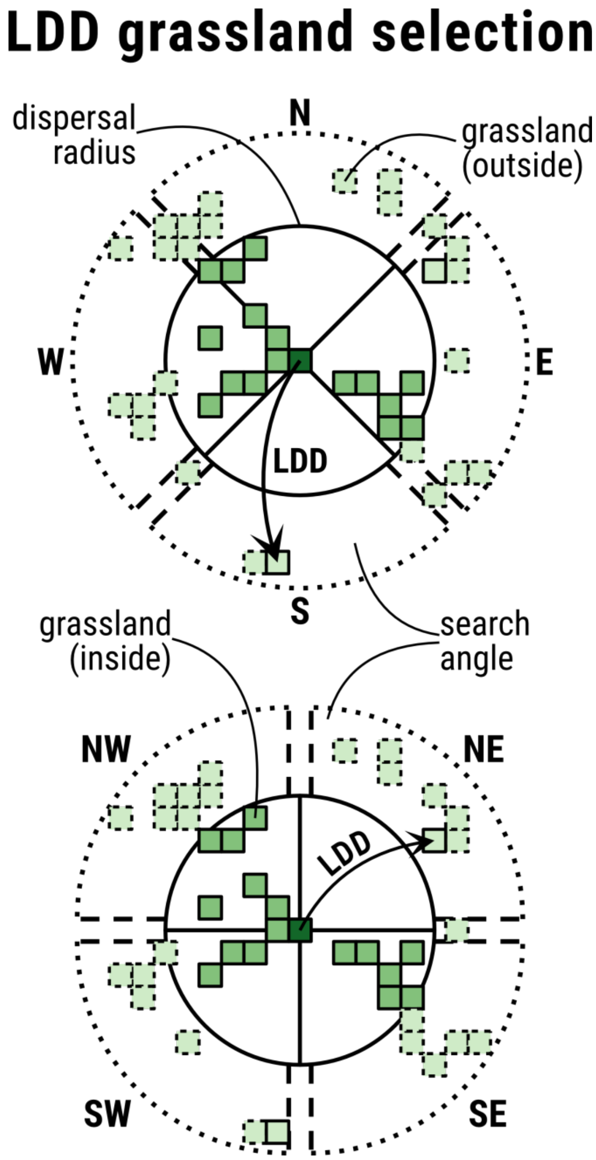

Figure 5: Determination of grassland cells for long distance dispersal (LDD) in cardinal (TOP) and secondary cardinal direction (BOTTOM) of a source habitat (dark green). The solid black circle encompasses grassland cells (medium green) within a defined dispersal radius. Light green cells represent grassland outside of the dispersal radius, where dashed cells are unreachable from the source habitat and solid cells are selected for LDD. Dashed black lines depict a direction's angle to search cells for LDD selection. Longer distances than indicated here are possible. Cells for LDD are only searched in case no grassland is found within the dispersal radius of either one the directions. Cells in straight secondary cardinal or cardinal direction (spaces between parallel dashed lines) are ignored for the search in cardinal or straight cardinal direction, respectively

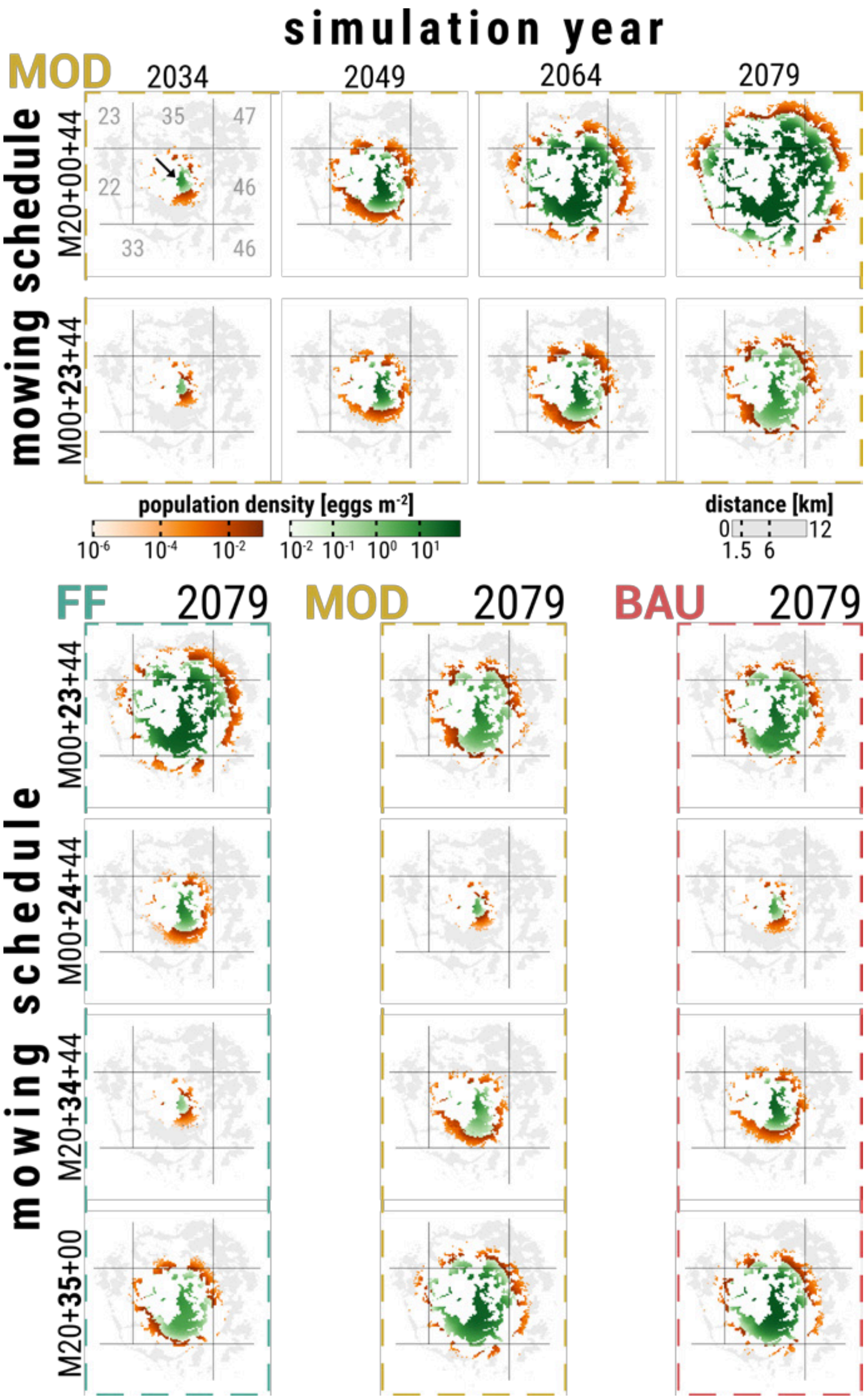

Figure 6: Spatial distribution of a LMG population dispersing from a singular source habitat in the center (black arrow in top left subplot) of climate cell 34. Each colored cell within the 20 subplots represents the population density in eggs m^{-2} (mean over 10 replicates) in a 6.25 ha grassland habitat inside a 16 km radius of the source habitat at the end of a simulation year. GREEN cells are considered habitats with an established LMG population, i.e., an imago life stage density ≥ 0.002 individuals m^{-2} during a simulation year; ORANGE cells represent unestablished populations at the cutting edge of the dispersal process, i.e., a imago life stage density < 0.002 individuals m^{-2}; GREY cells are habitats that are reachable at the end of the 60 year simulation time in case of ideal conditions with minimal disturbances (cf. top right subplot); WHITE areas were either unreachable or do not qualify as grassland. The grey grid lines delineate the climate cells from each other, where the grey numbers in the top left plot label the ID of the respective climate cell. The top two rows show – from left to right – the chronological LMG distribution progress after 15, 30, 45 and 60 simulation years exemplarily for the MOD climate change scenario (CCS), where the first row is the progress under ideal conditions (extensive mowing) and the second row in an environment disturbed by mowing schedule M00+23+44 (mowing in calendar week 23 instead of 20). Each of the 12 plots in the three bottom columns depict the LMG distribution at the end of the final simulation year 2079 depending on the CCS FF (first column), MOD (second) and BAU (third) as well as the applied mowing schedules M00+23+44 (first row), M00+24+44 (second), M20+34+44 (third) and M20+35+44 (last)

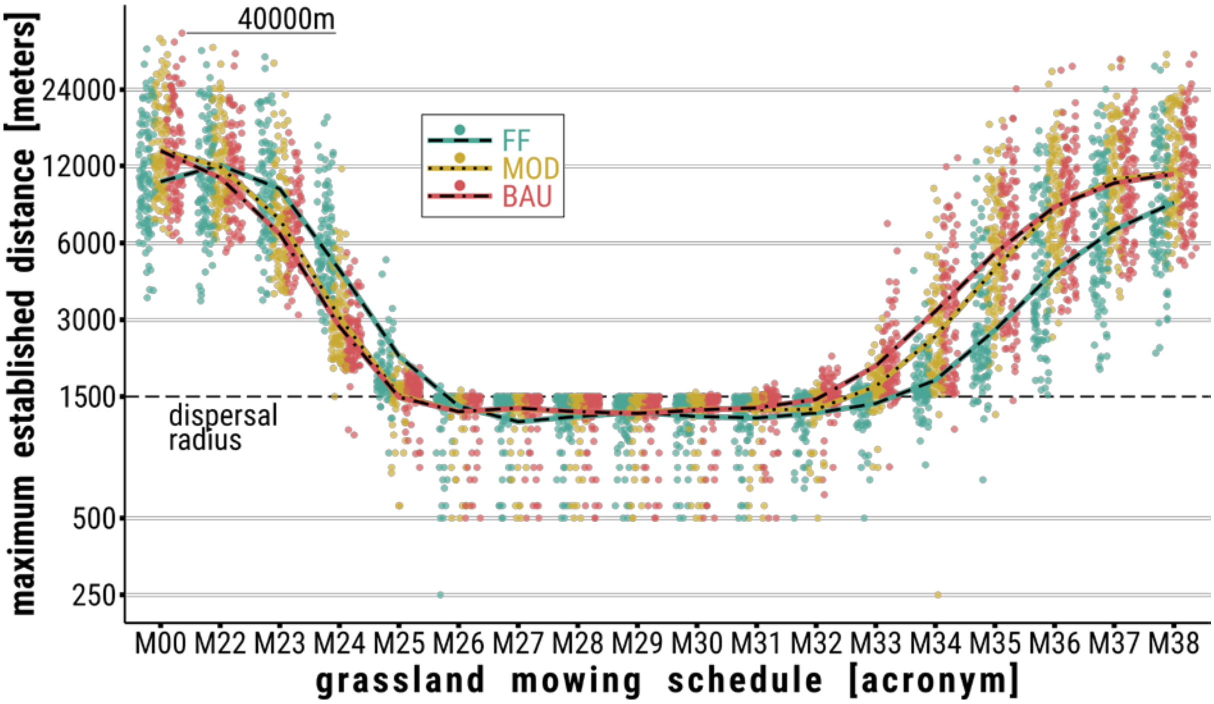

Figure 7: Distance in meters (y-axis) from a source habitat to the most distant established population in its neighborhood by the end of a simulation run in 2079 depending on mowing schedule (x-axis) and climate change scenario (CCS; green=FF, brown=MOD, pink=BAU). Each colored dot represents this distance value for either one of the 107 initial populations (or climate cells) averaged over ten replicates. The colored trend lines are distinguished by CCS and follow the mean for the distance value over the 107 cells in the study region depending on the applied mowing schedule. The black dashed line marks a distance of 1,500 m, i.e., the LMG dispersal radius and thus the usual home range threshold of the source habitat when ignoring potential long distance dispersal (LDD). Populations established directly through (LDD) from the source habitat were omitted in the calculating to avoid misleading maxima outside the dispersal radius

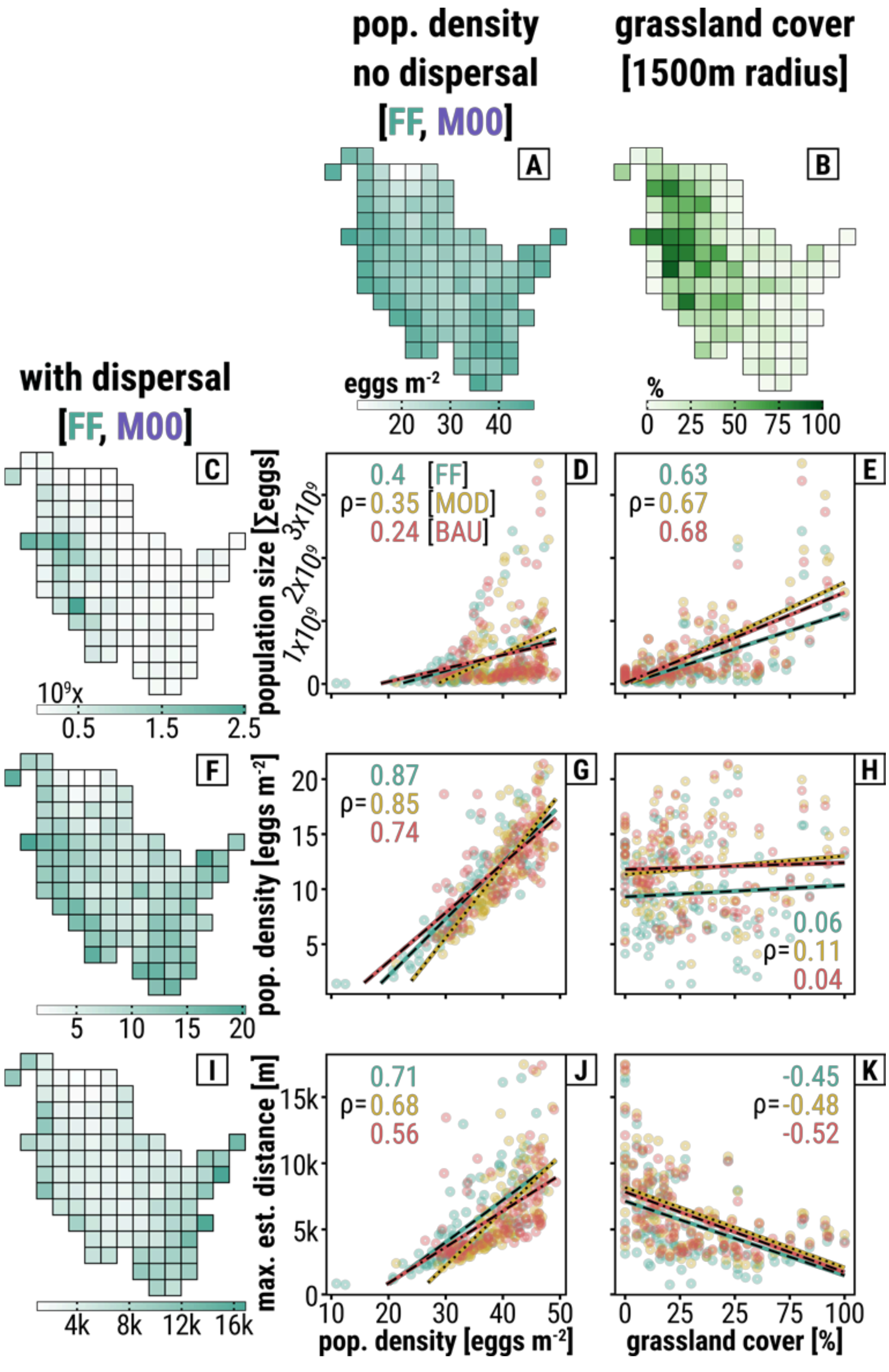

Figure 8: Spatial distribution of and correlation between evaluation parameters population size [Σ eggs], population density [eggs m^{-2}] and maximum established distance [meters] as well as regional grassland cover [in %]. Maps C, F and I show the spatial distributions of the results stemming from simulations with dispersal - exemplary for the FF climate change scenario (CCS), for simulations without dispersal (A) and the grassland cover in a radius ≤ 1,500 m of a respective source habitat (B). Each of the 107 cells in subplots A, C, F and I represent INDEPENDENT simulation runs, or rather their mean over 10 replicate runs (5 without dispersal), and depict the results of the dispersal process from a SINGLE initial population in the center of a cell. The six scatter plots correlate the evaluation parameters in the first column with the values in the first row for all three CCS FF (RCP 2.6, green color), MOD (RCP 4.5, brown) and BAU (RCP 8.5, pink). Each colored dot marks the resulting values in one of the 107 source grid cells. The colored numbers give the correlation coefficient ρ for the respective parameter combinations by CCS. The colored lines represent the respective linear regression, where dashed=FF, dotted=MOD and dash dotted=BAU. Note that the maps are shown exemplarily only for the FF scenario, as the qualitative outcome was similar for all three CCS

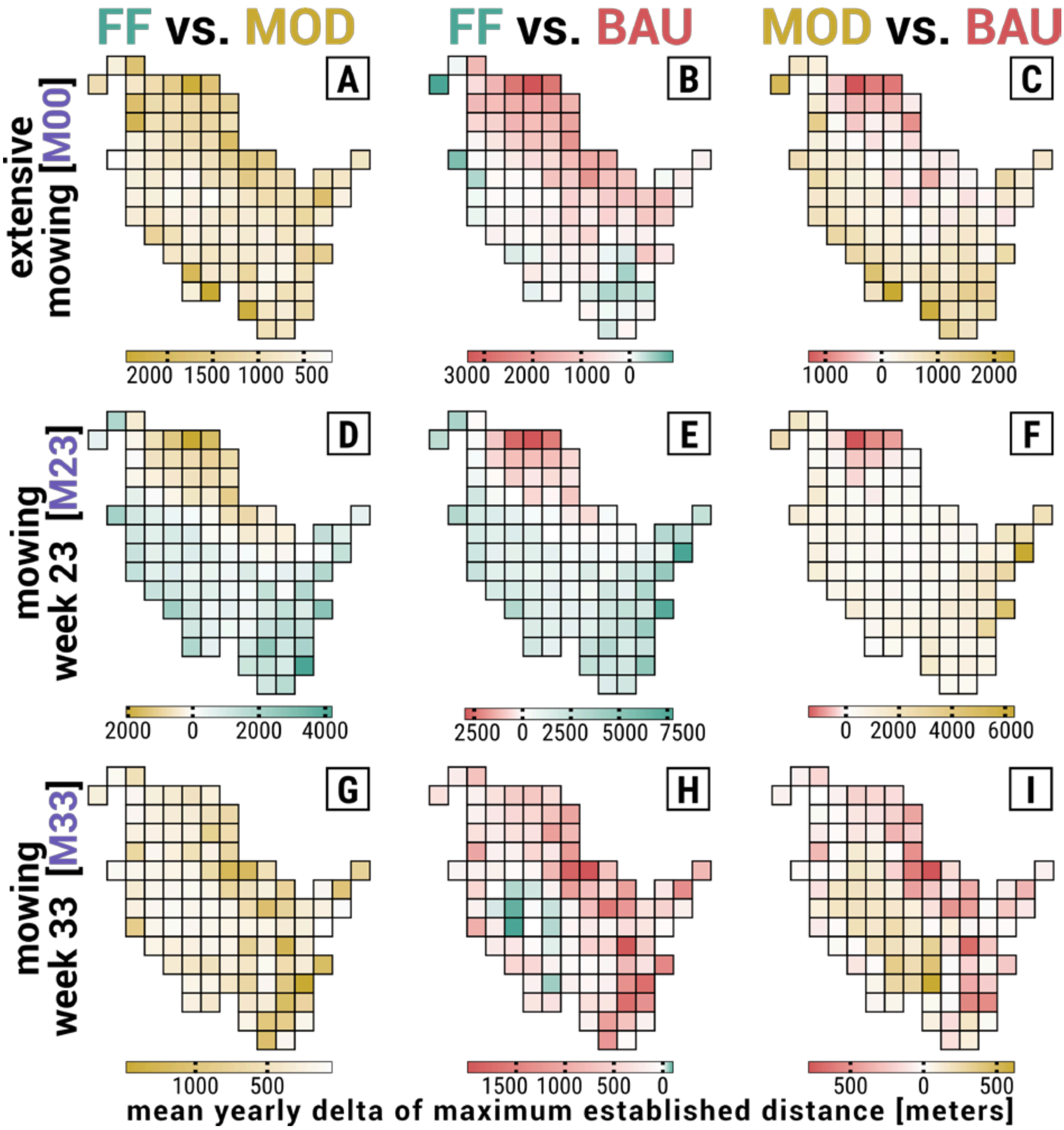

Figure 9: Difference (delta) in dispersal success in terms of mean population establishment distance [meters] between climate change scenarios (CCS) depending on source habitat and mowing schedule. First column: FF vs. MOD, second: FF vs. BAU, third: MOD vs. BAU. First row: reference scenarios with extensive mowing schedule M20+00+44 (M00), second row: deviating early mowing schedule M00+23+44 (M23), third row: additional late mowing schedule M20+33+44 (M33). Values were determined per replicate by subtracting the yearly established distance of the CCS mentioned second from the CCS mentioned first in the header and then calculating the replicate mean of absolute delta. Each of the 107 cells per subplot represent INDEPENDENT simulation runs, or rather their mean over 10 replicate runs, and depict the results of the dispersal process from a SINGLE initial population in the center of a cell. The cells' background colors highlight which of the respective CCS on average shows the higher differences during the 60 simulation years, where a LIGHTER color represents lower average difference. GREEN cells are in favor of FF, BROWN cells in favor of MOD and PINK cells in favor of BAU