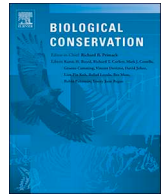




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Intense grazing of calcareous grasslands has negative consequences for the threatened marsh fritillary butterfly

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ABSTRACT

Grazing generally benefits grassland biodiversity as it prevents shrub and tree succession. However, too intense grazing may have negative effects for example many grassland insects. EU-subsidies for grazing of some habitats, aimed at promoting biodiversity, still require a relatively intense grazing, and could therefore have negative consequences for some species. We quantified how such grazing affects habitat quality for the marsh fritillary butterfly, and how this influence its colonization-extinction dynamics and persistence. Specifically, we studied a metapopulation on Gotland (Sweden), where the marsh fritillary occupies unfertilized calcareous grassland with a naturally slow succession. We quantified the difference in larvae autumn nests between grazed and ungrazed habitat, and used this difference to adjust the ‘effective area’ of 256 habitat patches in a 50 km² landscape. We then parameterized a metapopulation model based on the occurrence pattern of the adult butterfly, and simulated future population development under different grazing regimes. The results showed that ungrazed habitat harbored 4.8 times more nests than grazed habitat. Reducing the ‘effective area’ of grazed patches accordingly increased the local extinction probability and decreased colonization. Grazing all suitable habitat reduced the occupancy by over 80%, while no grazing increased the occupancy by up to 40%, based on projections of future dynamics. Current grazing is clearly too intense, and EU-subsidies are here, thus, a conservation measure with negative consequences for a threatened butterfly. To prevent this, subsidies for grazing need to be more flexible and better adapted to the prevailing soil conditions and requirements of the target species.

1. Introduction

Semi-natural grasslands are important for the biodiversity in European agricultural landscapes (e.g. Duelli and Obrist, 2003). The intensified agriculture (and forestry) has, however, led to a large loss and fragmentation of habitats for species associated with these grasslands (e.g. Cousins et al., 2015). In addition, abandoned management of remaining grasslands has in many places led to shrub and tree encroachment, which have had further negative consequences for many specialized species (e.g. Dover et al., 2010; Luoto et al., 2003; Wallis De Vries et al., 2002). Grazing is a common measure to prevent this development and has proven to be efficient for restoring and maintaining grassland biodiversity (e.g. Pöyry et al., 2004; Pykälä, 2003). The effect on biodiversity may, however, strongly depend on grazing intensity, where low or intermediate levels often seem most beneficial (e.g. Dumont et al., 2009; Wallis De Vries et al., 2007). If the grazing becomes too intense, it may instead have negative effects for some species,

such as many grassland insects (e.g. Dumont et al., 2009; Jerrentrup et al., 2014; Kruess and Tschardtke, 2002). However, financial support for grazing aimed at promoting biodiversity, e.g. EU-subsidies as part of the Common Agriculture Policy (CAP) (e.g. Brady et al., 2017; Kleijn et al., 2006), require an intense grazing regime. There is, thus, a risk that these subsidies aimed at promoting biodiversity, instead are detrimental for some species, and therefore constitutes an example of a conservation measure that potentially have negative impacts on biodiversity (e.g. Bulte and Rondeau, 2005; Haddad et al., 2014). However, for most species we do not know how grazing affects their populations and the quality of their habitat, but this needs to be quantified to understand their population dynamics and to be able to assess the effect of different management strategies.

Grassland butterflies constitute a species group that has experienced negative population trends due to the loss and changed management of semi-natural grasslands (Maes and Van Dyck, 2001; Warren et al., 2001). One reason is abandoned grazing (e.g. Thomas, 1980), and re-

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sumed grazing should therefore in general be positive for grassland butterflies (e.g. Pöyry et al., 2004). However, for many of these species grazing intensity is particularly important to consider, and it is clear that too intense grazing is negative (e.g. Ellis, 2003; Johansson et al., 2017; van Noordwijk et al., 2012; Schtickzelle et al., 2007). Reasons could be that intense grazing leads to a lower abundance of host plants and nectar resources (Bubová et al., 2015; Schtickzelle et al., 2007), or that the butterfly eggs and larvae are damaged or eaten by grazing animals (van Noordwijk et al., 2012). One of these butterflies is the marsh fritillary (*Euphydryas aurinia*) that due to its dramatic decrease in Europe is included in EU's Habitats Directive and is red-listed in several European countries (van Swaay and Warren, 1999; Warren, 1994). The species is associated with open moist grasslands with the host plant *Succisa pratensis* and a relatively low vegetation (e.g. Betzholtz et al., 2007; Konvicka et al., 2013). Suitable habitat most often need extensive grazing (e.g. Smee et al., 2011), but the most favourable conditions occurs at sites where the grazing was recently abandoned (Anthes et al., 2003), which agrees with several other grassland butterflies (Pöyry et al., 2004). The optimal management regime, however, most likely varies with the prevailing soil conditions. Poor soils may require less grazing to prevent succession compared to more productive soils, and this needs to be considered for achieving a suitable grazing regime.

The marsh fritillary, like many other butterflies, has been found to occur in metapopulations (e.g. Anthes et al., 2003; Bulman et al., 2007; Schtickzelle et al., 2005; Wahlberg et al., 2002). According to classical metapopulation theory, the probability of a species going locally extinct decreases with increasing area of the habitat patch, as large habitat patches can harbor larger local populations (Harrison et al., 1988). The local population size (and thus the local extinction probability) can also be strongly influenced by the quality of the habitat (e.g. Fleishman et al., 2002; Thomas et al., 2001), which often is neglected (as such data are often missing). However, including habitat quality, e.g. by taking grazing pressure into account, may improve models for local extinction considerably (Johansson et al., 2017). Taking habitat quality into account could be seen as an adjustment of the 'effective area' of a patch (Moilanen and Hanski, 1998). A low quality patch have a smaller 'effective area', and can thus be expected to harbor a smaller local population, compared to an equally sized high quality patch. The colonization probability is determined by connectivity to local populations in the surrounding landscape (Hanski, 1999), and because connectivity is influenced by the size of surrounding source populations, the colonization probability may also indirectly be affected by habitat quality in the surrounding landscape. For realistic projections of future persistence we need to understand how habitat quality affects the colonization-extinction dynamics of the species. This can then be used to evaluate the effect of different management strategies and conservation incentives, for a more efficient conservation of the species.

The aim of this study was to increase the understanding of how habitat quality affects the colonization-extinction dynamics and persistence of grassland butterflies. This is used to evaluate the potential effects of a common conservation measure, aimed at promoting habitat quality for grassland species. Specifically, we investigate the effect of EU-subsidies for grazing on the habitat quality for a Swedish metapopulation of the marsh fritillary by 1) quantifying the difference in larvae autumn nests between grazed and ungrazed habitat, 2) using the difference in larvae autumn nests to adjust the 'effective area' of all habitat patches for the entire metapopulation, 3) parameterizing a metapopulation model based on the occurrence pattern of the adult butterfly and observed inter-patch dispersal events, and 4) using the model to project future population dynamics under different grazing regimes in the landscape. We hypothesize that the current grazing intensity is too



Fig. 1. A marsh fritillary larvae autumn nest on the host plant (*Succisa pratensis*).

intense and reduces habitat quality for the marsh fritillary, which leads to increased local extinction and decreased colonization probabilities. Increasing the total area being grazed will therefore result in a lower occupancy over time. EU-subsidies for grazing, thus, have negative effects on the threatened marsh fritillary.

2. Material and methods

2.1. Study species

The marsh fritillary (*Euphydryas aurinia*) is classified as vulnerable (VU) in Sweden (Gärdenfors, 2015). The species is univoltine, with adults flying from late May to late June in Sweden. Females mate once and lay large egg batches (50–500 eggs/batch). Each female can lay several batches, but usually with fewer and fewer eggs (Porter, 1992). The egg batches are laid under leaves of the host plant *Succisa pratensis*, and after hatching the larvae spin a silken nest around the host plant (Fig. 1). Larvae feed and bask gregariously during sunny days until September, when they enter diapause (in the fourth instar) in a collective conspicuous nest (larvae autumn nests). The larvae become active again in early spring and resume feeding and basking together. They become more solitary at the end of the fifth instar, when their food needs increase. In total the larvae undergo six instars.

2.2. Study area and suitable habitat patches

The study was conducted in an area of 50 km² (10 km × 5 km) close

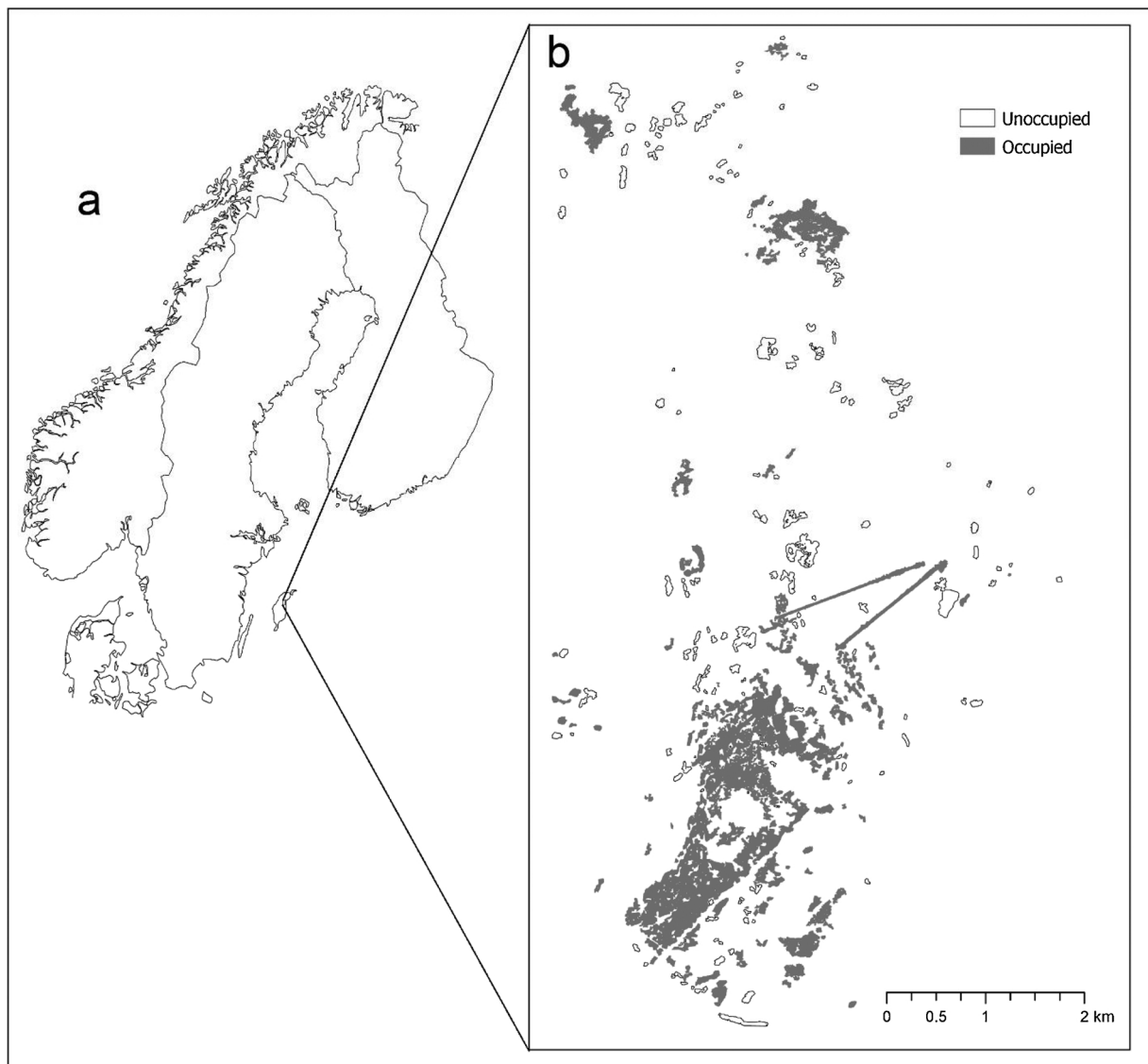


Fig. 2. The location of the study landscape on the island of Gotland outside the Swedish coast (a) and the spatial location of the 256 habitat patches (b), that are either occupied (dark grey) or unoccupied (white) by the marsh fritillary in 2018. The white area in between patches constitute unsuitable matrix.

to Slite on the island of Gotland in the Baltic Sea (Fig. 2), Sweden (midpoint of the area: 57°69'N 18°69'E). This study area includes all potential habitat patches that can be expected to be reachable for the marsh fritillary based on observed dispersal distances from an earlier mark-recapture study (Appendix A). In the study area the species occurs in wet parts of unfertilized calcareous wet grasslands that in most places remain naturally open due to the poor soil and slow accumulation of humus (Eliasson, 2008). In some parts of the habitat, the succession of grasses, shrubs and trees is further slowed down through the impact of frost phenomena during the flooded winter period, which prevents most plants from establishing. In such habitat the vegetation becomes very sparse, and *Succisa pratensis* is one of the few plant species that survive.

To identify potential habitat for the marsh fritillary in the study landscape we mapped the distribution of patches with host plants throughout the landscape and combined it with high resolution land cover data (Swedish land cover data, CadasterENV) and tree cover information from laser radar data (LiDAR). Potential habitat was defined as all open grasslands with occurrence of the host plant. The habitat could be either grazed or ungrazed, and grazing information was retrieved from the Swedish Board of Agriculture. Habitat patches were delimited based on the characteristics of the surrounding landscape

(e.g. Bulman et al., 2007). Discrete patches were defined as habitat areas separated by > 33.3 m of open habitat without the host plant, or > 10 m with forest barrier. These threshold values were based on observed movements between patches. In this way 256 separate habitat patches were identified within the study area (Fig. 2). The mean, median and max sizes of these patches were 0.74, 0.12 and 47.1 ha, respectively. Most patches were, thus, relatively small (90% were < 1 ha and 96% < 2 ha). There were, however, a few larger patches (10 patches > 2 ha), where the two largest clearly stand out with areas of 42.5 and 47.1 ha, respectively. The total area of all patches was 188.3 ha, of which 58.3 ha were grazed with an intensity required to receive EU subsidies. This means a yearly grazing that results in a low vegetation structure that is clearly affected by grazing animals. In the study area this means grazing from late May to late September with sheep or cattle (Angus and Charolais) with approximately 0.3 animals/ha.

2.3. Data collection

In this study we utilize three sources of field data on the marsh fritillary: 1) larvae autumn nests from September 2017 that are used to

quantify the difference in quality between ungrazed and grazed habitat, 2) the occurrence pattern (presence/absence) of the adult butterfly in the entire patch network from June 2018 that is used to fit a metapopulation model, 3) observed inter-patch dispersal events from a large mark-recapture study of adult butterflies that was conducted in June 2017 (the main results from this mark-recapture study will be presented elsewhere, but see [Appendix A](#) for information on observed dispersal). Here we only utilize the observed dispersal distances to set the spatial scaling in the metapopulation model (see *Modelling the colonisation-extinction dynamics*).

Larvae autumn nests were counted in September 2017. To be able to study the effect of grazing on the number of nests we distributed hectare grid cells over all suitable habitat in the landscape (the cells could thus also contain unsuitable habitat). We only included grid cells with either 100% grazed or 100% ungrazed habitat, and performed surveys in 331 of these cells in total (233 in ungrazed and 98 in grazed habitat). In each grid cell we randomly distributed four meter wide transects across the suitable habitat within the cell. The length of these transects differed depending on how much suitable habitat there was in the grid cell (sampling was only done in suitable habitat). The total area that transects covered in any plot ranged 121–1263 m² (mean = 669 m²). Within each transect, we then counted all larvae autumn nests when slowly walking along the transect. We also collected data on the vegetation using 0.5 m² circular plots (with a diameter of 80 cm) that were evenly distributed along the transects. The number of plots ranged 5–23 (mean = 11.4) depending on the total transect length within a grid cell. In each vegetation plot we then measured three variables that potentially could affect the species ([Anthes et al., 2003](#); [Betzholtz et al., 2007](#); [Bulman et al., 2007](#); [Smee et al., 2011](#)): 1) the vegetation height using a 17 cm wide sward ruler (the recorder stood 5 m in front of the ruler and noted the height where 50% of the width of the ruler was covered by vegetation), 2) the number of *Succisa pratensis* individuals (i.e. the host plant) and, 3) the length of the longest *S. pratensis* leaf.

The occurrence pattern of the adult butterfly was assessed during the flight period in late May to late June 2018. Each habitat patch was visited up to three separate days during the reproduction period on times of the day when the butterflies are highly active. If the species was not detected in a patch after three visits, it was considered to be unoccupied.

2.4. Quantifying the effect of grazing on butterfly larvae

To quantify the effect of grazing on the marsh fritillary we used data on larvae autumn nests in grazed and ungrazed habitat. Based on the observed data we modelled the number of autumn nests in a hectare grid cell using a generalized linear model with a negative binomial distribution (due to over-dispersion). As explanatory variables we included the categorical variable grazed/ungrazed, transect area (to account for the fact that the survey area differed between grid cells depending on the total transect length) and connectivity to surrounding habitat (to account for a potential spatial structure as a result of grid cells surrounded by much suitable habitat being more likely to be visited by egg-laying females than more isolated grid cells). Habitat connectivity of grid cell *i* (HS_{*i*}) was modelled as:

$$HS_i = \sum_{j=1}^n e^{-d_{ij} \times \alpha_h} PA_j \quad (1)$$

where d_{ij} is the center-to-center distance in kilometers between focal grid cell *i* and surrounding cells *j*, PA_j is the total area suitable habitat in plot *j*, and *n* the total number of grid cells. The parameter α_h sets the spatial scaling and was optimized based on the deviance profile (e.g. [Johansson et al., 2013](#)), i.e. we used the value of α_h that gave the best model fit ([Appendix A](#)). The two continuous variables, transect area and habitat connectivity (HS), were standardized before fitting the model. The fitted model was then used to predict the number of larvae autumn

nests in ungrazed and grazed habitat when keeping transect area and habitat connectivity to its average value (i.e. zero, as they were standardized). Then we used these predictions to calculate a ‘quality-quota’ (Q) between ungrazed (Pred_{ungra}) and grazed habitat (Pred_{graz}), which thus determines how large the difference in quality is between the two habitat types:

$$Q = \text{Pred}_{\text{ungr}} / \text{Pred}_{\text{graz}} \quad (2)$$

2.5. The effect of grazing on vegetation height and host plant characteristics

To analyze how the vegetation variables (i.e. vegetation height, number of *Succisa* individuals, and the length of the longest *Succisa* leaf) were affected by grazing, we compared each variable between grazed and ungrazed hectare grid cells. For each grid cell we used mean values for each variable from the vegetation plots within the cell and tested the difference between grazed and ungrazed habitat using generalized linear models with identity link functions (i.e. a normal distribution). All response variables were log-transformed to improve normality and tested against the explanatory variable grazing category (grazed/ungrazed). To test if differences in the vegetation height, number of host plants, and host plant size (leaf length) between grazed and ungrazed habitat could explain the difference in quality for butterfly larvae between grazed and ungrazed habitat, we also added the vegetation variables to the model for larvae autumn nests. All vegetation variables were log-transformed to improve normality and standardized to make parameter estimates comparable. Model selection was based on AIC, and the final model was the one with the lowest AIC.

2.6. Modelling the colonization-extinction dynamics

To model the colonization-extinction dynamics of the marsh fritillary we used the classical Incidence Function Model (IFM, [Hanski, 1994](#)). The original IFM uses patch area as a proxy for the local population size, and assumes that all patches have equal quality. The IFM can, however, include habitat quality by adjusting the ‘effective area’ of the patch based on different patch characteristics ([Moilanen and Hanski, 1998](#)). Here we account for habitat quality (the effect of grazing) by adjusting the area of grazed patches based on the estimated difference between grazed and ungrazed habitat in the number of larvae autumn nests. In practice, we calculated the ‘effective area’ of patches with grazing by dividing the grazed area with Q (see Eq. (2)), i.e. with how many times fewer larvae nests grazed habitat had compared to ungrazed habitat. For completely ungrazed patches the ‘effective area’ = the actual area. We used the Q for the model without vegetation variables. Then we parameterized the IFM based on the occurrence pattern (i.e. presence/absence) of the adult butterfly in the entire patch network in 2018, following [Oksanen \(2004\)](#). For the full IFM formulation and details about the parameterization process see [Hanski \(1994, 1999\)](#) and [Oksanen \(2004\)](#). Below we only describe the functions for the local extinction and colonization probabilities.

The extinction probability of patch *i* (E_{*i*}) was modelled as a function of effective patch area (A_{*i*}) as:

$$E_i = \frac{e}{A_i^x} \quad (3)$$

where *e* and *x* are model parameters. The colonization probability of patch *i* (C_{*i*}) was modelled as a function of connectivity (S_{*i*}):

$$C_i = \frac{S_i^2}{S_i^2 + y^2} \quad (4)$$

where *y* is a model parameter. Connectivity was further modelled as:

$$S_i = \sum_{j=1}^n e^{-d_{ij} \times \alpha_c} A_j p_j \quad (5)$$

Table 1

Description of the four simulated scenarios of grazing in the landscape with total area grazed and ungrazed habitat, and the total effective area.

Scenario	Description	Ungrazed	Grazed	Total effective area ^a
S0	The same grazing as today	130 ha	58.3 ha	142.1 ha
S1	Increased grazing following the most likely future grazing regime	99.5 ha	88.8 ha	118.0 ha
S2	No grazing at all	188.3 ha	0 ha	188.3 ha
S3	Grazing in all patches	0 ha	188.3 ha	39.2 ha

^a The area grazed habitat was divided by the quality quota (Q, see Eq. (2)).**Table 2**The parameter estimates (with SE) and p-values for the model of larvae autumn nests with or without information on host plant numbers and host plant size in 331 ha grid cells. Δ AIC = change in AIC when removing the variable from the final model.

Parameter	Without host plant info (AIC = 1359)			With host plant info (AIC = 1342)		
	Estimate	p-value	Δ AIC	Estimate	p-value	Δ AIC
Intercept	1.25 (0.087)	< 0.001		1.07 (0.090)	< 0.001	
Grazed habitat	-1.57 (0.19)	< 0.001	56.9	-1.15 (0.21)	< 0.001	27.2
Transect area	0.27 (0.083)	< 0.001	8.1	0.32 (0.081)	< 0.001	12.3
Habitat connectivity (HS) ^a	0.46 (0.082)	< 0.001	20.8	0.31 (0.083)	< 0.001	8.6
log(number of host plants)	-	-		0.24 (0.081)	0.004	5.7
log(maximum leaf length)	-	-		0.28 (0.090)	0.002	8.0

^a In the best model $\alpha_h = 5.6$, see Eq. (1) and Appendix A.

where d_{ij} is the distance in kilometers between focal patch i and source patch j , A_j is the 'effective area' of patch j , and $p_j = 1$ if the butterfly is present in patch j and $p_j = 0$ if the butterfly is absent. The 'effective area' is here, as in the function for E_i , used as a proxy for the local population size (i.e. like regular area is used in the original IFM). It does not mean any changes to patch geometry that may affect distances between patches. The spatial scaling parameter α can be estimated based on the spatial occurrence pattern when fitting the model (e.g. Hanski, 1999). However, due to the risk of parameter correlations, it may be better to estimate α based on separate data on observed dispersal distances (Hanski, 1999). As we have such information from an earlier mark-recapture study (Appendix A) we chose the latter approach and fitted a negative exponential function to the observed inter-patch dispersal distances (Appendix A). However, for comparison we also estimated α directly from the occurrence pattern, which gave a similar result (Appendix A).

2.7. Projections of future population dynamics under different grazing regimes

To illustrate the potential effects of grazing on the future metapopulation, the fitted IFM was used to simulate four future scenarios of grazing management in the landscape (Table 1). First, we simulated a scenario with the same grazing as today (S0, i.e. the baseline scenario). In this scenario we expect the occupancy to remain constant at the equilibrium level due to the assumptions of the IFM (Hanski, 1999). Second, we increased the grazing in 30.5 ha of the habitat (that today are ungrazed) based on information from farmers and the county administrative board about the most likely future grazing regime in the landscape (S1). We also simulated the two extremes: no grazing at all (S2) and grazing in the entire patch network (S3) to cover the whole range of potential effects grazing can have on the entire metapopulation. Each scenario started with the observed occurrence pattern in 2018 and we then followed the population dynamics 50 years into the future. During this period we believe that the ungrazed habitat will remain open, due to the naturally slow succession, based on historical aerial photos. Large proportions of the ungrazed habitat have not been grazed since approximately 1940. We ran 500 replicates of each scenario and calculated the number of occupied patches after 50 years.

For all analyses we used R.3.5.3 (R Core Team, 2019) with add-on

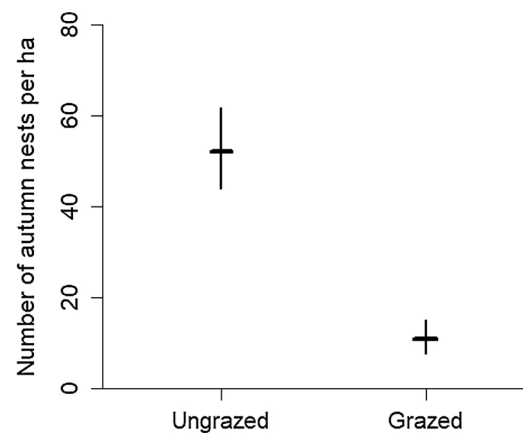


Fig. 3. The predicted number of marsh fritillary larvae autumn nests per hectare in ungrazed and grazed habitat. The thick horizontal lines show the mean and the thin vertical line the 95% confidence interval of the model prediction.

library MASS (Venables and Ripley, 2002) for the negative binomial models.

3. Results

In total we found 1026 marsh fritillary larvae autumn nests in 2017. Among these, 79 were found in grazed habitat (98 grid cells, within a total transect area of 5.89 ha) and 947 (in 233 grid cells, within a total transect area of 16.31 ha) in ungrazed habitat. Based on the statistical analysis ungrazed habitat clearly had more nests than grazed habitat (Table 2). Predictions from the model suggest that ungrazed habitat on average harbored 4.8 times more larvae autumn nests than grazed habitat (when taking transect area and habitat connectivity into account). The 'quality quota' (Q) was, thus, 4.8 (see Eq. (2)). This means that the 'effective area' of a grazed patch is only 21% of the 'effective area' of an ungrazed patch of the same size. If extrapolating into a density per hectare, the mean number of nests per hectare in ungrazed habitat was 52.0, while the corresponding number in grazed habitat was 10.8 (Fig. 3).

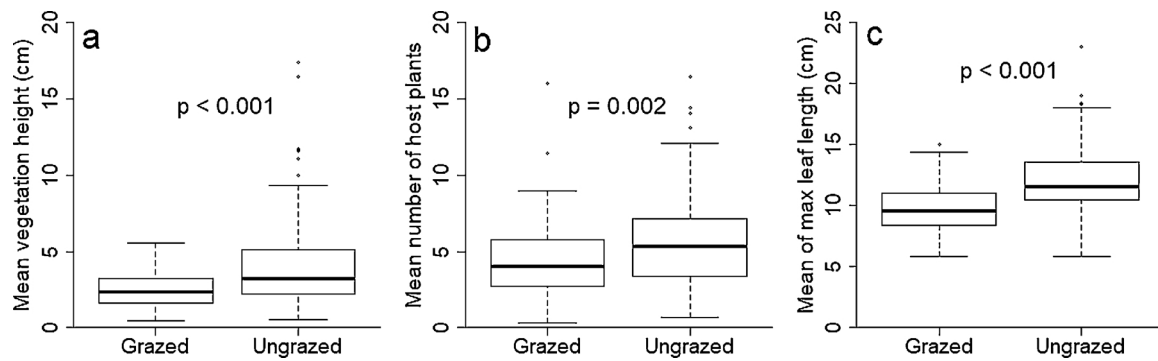


Fig. 4. The distributions of the (a) mean vegetation height, (b) mean number of host plants (*Succisa pratensis*), and (c) mean length of the longest host plant leaf in hectare grid cells situated in either grazed ($n = 98$) or ungrazed habitat ($n = 233$). The mean values are based on records from 0.5 m^2 sample plots (3788 in total) distributed among the 331 ha grids (i.e. on average 11.4 sample plots per hectare grid cell).

The mean vegetation was higher in ungrazed (mean = 3.9 cm) compared to grazed habitat (mean = 2.5 cm, Fig. 4). For the host plant *Succisa pratensis* there were more individuals in ungrazed (mean = 5.5) compared to grazed (mean = 4.4) habitat (Fig. 4), and the maximum length of the longest leaf was longer in ungrazed (mean = 12.1 cm) compared to grazed (mean = 9.8 cm). Both host plant numbers and the length of the longest leaf improved the model for the number of larvae autumn nests (Table 2), while the vegetation height did not (AIC decreased with 2.0 units when removing it from the model). When including information on the host plant, the effect of grazing category (grazed/ungrazed) was reduced but still improved the model (Table 2).

The number of occupied patches in 2018 was 101 (based on the survey of adult butterflies), which gives an occupancy of 0.395 among the 256 patches in the network. Projections of future population dynamics with the fitted IFM (for estimated model parameters, see Appendix A) showed that for the baseline scenario (i.e. S0, with grazing as it is today) the occupancy remained relatively unchanged after 50 years (Fig. 5) as expected (see above). However, when increasing the total area being grazed in accordance with the suggested future grazing regime (S1) the occupancy decreased to 0.316 on average, which is an average decrease of 22% compared to S0. The two extreme scenarios, with either no grazing at all (S3) or where all patches were grazed (S4), lead to an average occupancy of 0.564 (144.4 occupied patches) and 0.070 (18.0 occupied patches), respectively (Fig. 5). We observed no extinctions of the entire metapopulation in any of the scenarios within 50 years.

4. Discussion

Based on data from a large metapopulation of the marsh fritillary in Sweden we show that i) grazed habitat harbors almost five times fewer larvae autumn nests than ungrazed habitat, and ii) grazing leads to both fewer and smaller host plants. Moreover, based on projections of future metapopulation dynamics, we show that iii) the number of occupied patches may decrease by 22% if the most likely future grazing regime is implemented. Grazing all suitable habitat would reduce the metapopulation with over 80%, while less grazing in the landscape has the potential to increase the occupancy with up to 40%. EU-subsidies for grazing, aimed at promoting biodiversity, thus, instead have negative effects on a threatened grassland butterfly.

4.1. Grazing and habitat quality

We show a clear negative effect of grazing on the number of larvae autumn nests for the marsh fritillary. This shows that the current grazing pressure is clearly too intense and therefore reduces habitat quality, in accordance with our hypothesis. This is in line with several other studies showing that intense grazing can reduce habitat quality

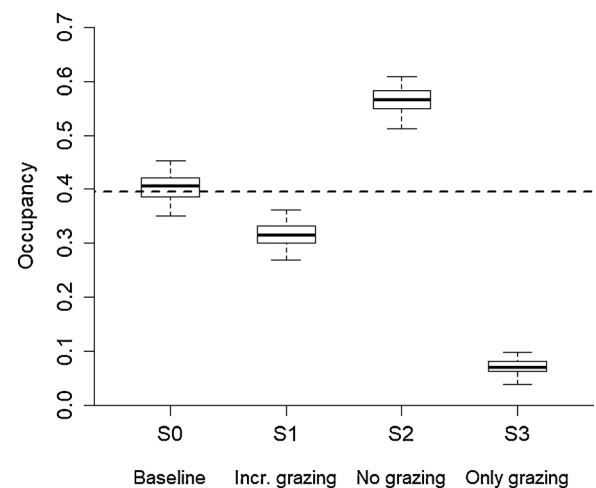


Fig. 5. The butterfly occupancy after 50 years, among the 256 patches, in four scenarios of future grazing in the landscape (see Table 1). The boxplots shows the median (thick horizontal line), the data between 25th-75th percentiles (box) and the 95% confidence limits (broken vertical line) from 500 replicates. The horizontal broken line shows the initial occupancy (i.e. observed in 2018).

for grassland butterflies (Ellis, 2003; Johansson et al., 2017; van Noordwijk et al., 2012; Schtickzelle et al., 2007) as well as other grassland insects (Jerrentrup et al., 2014; Kruess and Tschamtko, 2002). By adjusting the ‘effective area’ of grazed patches and fitting the classical IFM, we also show that habitat quality may have large effects on the colonization-extinction dynamics, which earlier has been emphasised (e.g. Fleishman et al., 2002; Thomas et al., 2001). Specifically, the local extinction probability increase if the focal patch is grazed (due to a smaller ‘effective area’ that should harbour a smaller local population) and the colonization probability decrease if the surrounding source patches are grazed. Hence, it is rather clear that EU-subsidies for grazing here result in a too intense grazing pressure that is detrimental for the marsh fritillary. This, thus, provide an example of a conservation measure, aimed at promoting a high biodiversity, that instead potentially have adverse effects (e.g. Bulte and Rondeau, 2005; Haddad et al., 2014)

In general grazing is necessary to prevent succession and maintain an open landscape in the long run, and low or intermediate levels of grazing have been shown to maintain habitat quality for many grassland species elsewhere, (e.g. Dumont et al., 2009; Wallis De Vries et al., 2007) including the marsh fritillary (Smee et al., 2011). A large challenge is, however, to adapt the grazing regime to the prevailing local conditions (Metera et al., 2010). Optimization of the grazing regime may involve not only changes in yearly stocking rates, but also e.g. the

timing of grazing, the livestock breed and could include different rotational systems that temporally excludes grazing (e.g. Dumont et al., 2007; Ravetto Enri et al., 2017). Using the IFM and the 'effective area' approach, one way to optimize could be to simulate how different combinations of grazed areas in the landscape affects the persistence of the species over time.

4.2. Future persistence under different grazing regimes

We show clear effects on the future metapopulation when the habitat patch quality (and thus 'effective patch area') changes due to an increase or decrease in the total area being grazed in the landscape, which is expected from metapopulation theory (Hanski, 1999). Our two extreme scenarios show how potent the grazing regime is for affecting the development of the future marsh fritillary metapopulation, as they suggest an eightfold difference in patch occupancy between no grazing (S2) and only grazing (S3). This also shows that the occupancy is not proportional to the total amount of ('effective') habitat area in the landscape (Hanski, 1998), which is only 4.8 times smaller in S3 compared to S2. The negative effect of increased grazing on the metapopulation is, thus, larger than expected from a solely 'reduced area perspective'.

Although we show clear negative effects of increasing the total area being grazed, our results suggest that it is unlikely that changes in the grazing regime alone will lead to extinction of the entire metapopulation within 50 years. In general the metapopulation, seems viable and robust to rather large landscape changes, compared to other metapopulations of the same species (Schtickzelle et al., 2005) and other grassland butterflies (e.g. Johansson et al., 2017). The main reason is the large total habitat area of 188.3 ha in our study landscape (where > 75% is high quality ungrazed habitat). Earlier projections of metapopulation persistence for the marsh fritillary in the UK have suggested that between 80 and 142 ha are required for a high (> 95%) probability of long-term (> 100 years) persistence (Bulman et al., 2007), which thus is less than the current amount of habitat in our landscape (also when accounting for the quality reduction caused by grazing, i.e. the 'effective area' = 142.1 ha). The species most likely also will survive a reduction of the effective area to 118 ha (as in S1), even if this will reduce the occupancy with > 20%. Our results suggest that the species may even survive in the most extreme scenario with grazing in all suitable habitat (S3, total effective area = 39.2 ha). A likely reason for this is the configuration of habitat in our landscape (e.g. Bulman et al., 2007), where the species rarely goes extinct in a few important large source patches. However, it should be remembered that we assume that the habitat quality in ungrazed patches remain constant over the 50-year period covered by our projections (due to the naturally slow succession). If this is not true, we may overestimate species persistence. Moreover, we do not account for a potential increase in environmental stochasticity e.g. caused by climate change.

4.3. The effect of too intense grazing on habitat quality for the marsh fritillary

One reason that too intense grazing reduce the habitat quality for the marsh fritillary could be that the host plants were both fewer and smaller in grazed compared to ungrazed habitat, which agrees with the effect of grazing on host plant abundance for other butterfly species (Schtickzelle et al., 2007). For the marsh fritillary higher host plant densities has earlier been shown to increase larvae abundance (Smee et al., 2011), and larger plants are often preferred for oviposition (Anthes et al., 2003). Moreover, host plant abundance has also shown positive effects on patch occupancy for the species (Bulman et al., 2007; Wahlberg et al., 2002). However, even if clearly significant, the effect size was relatively small (compared to the difference in larvae autumn nests) both for the number of host plants and the average sizes (roughly 20% lower in grazed habitat for both variables). Hence, host plant quality is most likely not the complete mechanism, and therefore a large unexplained difference

between grazed and ungrazed habitat still remained, even when controlling for average host plant numbers and sizes in the model. One reason for this could be that the eggs/larvae/autumn nests are eaten or trampled down by grazing animals, as shown for other species (van Noordwijk et al., 2012). Other possible reasons may be that the host plants grow more closely pressed to the ground in grazed habitat (and the leaves are therefore less exposed for egg-laying) or that the larvae cannot climb the *Succisa* inflorescences to avoid drowning when the habitat becomes flooded (as the inflorescence are often eaten by grazing animals, pers. obs.). Fewer nectar resources for egg-laying females in grazed habitat is also a possibility (Bubová et al., 2015). Understanding the complete mechanism for the negative effect of grazing thus requires further investigation. However, it is unlikely that the effect of grazing is a result of any systematic differences in other aspects of quality between grazed and ungrazed habitat. The reason is that the distribution of grazing mainly reflects landowner conditions (i.e. if specific landowners applies for EU-subsidies or not). Moreover, the large study area should buffer the risk of confounding factors.

5. Implications for conservation

To maintain high quality habitat for grassland butterflies, with an optimal balance of an open vegetation structure and a large abundance of the host and nectar plants, low intensity management (usually with light grazing) is often suggested (Ellis, 2003; Johansson et al., 2017; Schtickzelle et al., 2007). How to achieve 'low intensity' management, however, will depend on soil productivity, and it is therefore important that the grazing regime is adapted to the local conditions. More productive areas most likely require yearly grazing to prevent succession, where 'low intensity' can be achieved e.g. by regulating stocking rates, livestock breeds or by using rotational systems that excludes grazing during parts of the season (Ravetto Enri et al., 2017). However, in areas with naturally slow succession yearly grazing, even with low stocking rates, can be detrimental for some species. In our study landscape, grazing should preferably be excluded for entire patches during several years to benefit the marsh fritillary and other grassland insects, and it is unlikely that this would have any major negative effects on other grassland species. The grazing regime could follow a rotational scheme in the landscape, where grazing e.g. appears every fifth year in a particular patch. Such grazing regime may require that animals are kept on other land during years when grazing is excluded, which should be possible in our study landscape. However, this would need changes in the CAP, to allow more flexible payments for habitat management objectives and conservation of regional target species, rather than yearly grazing as such. Farmers must receive some economic support also in years when grazing is excluded, to retain grazing animals on other land. If the yearly intense grazing continues the marsh fritillary will decline, due to a reduction in the total 'effective area' of its habitat, as more patches most likely will be grazed in the future.

Declaration of Competing Interest

We have no conflicts of interest.

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Appendix A. Parameter estimation for the Incidence Function Model

We followed the method described in Oksanen (2004) to fit the Incidence Function Model (IFM, Hanski, 1994) based on the observed occurrence pattern of the adult butterfly in 2018. The spatial scaling parameter α can be estimated based on the spatial occurrence pattern when fitting the model (e.g. Hanski, 1999). However, due to the risk of parameter correlations, it may be better to estimate α based on separate data on observed dispersal distances (Hanski, 1999). As we have such information from the earlier mark-recapture study (where we observed 423 inter-patch dispersal events) we chose the latter approach and fitted a negative exponential function to the observed inter-patch dispersal distances (Fig. A1). However, for comparison we also estimated α directly from the occurrence pattern, which gave a similar spatial weighting (Fig. A1a). The α based on observed dispersal distances, was also within the 95% confidence limits of the α estimated from the occurrence pattern (Fig. A1c). For remaining parameters of the IFM, see Table A1.

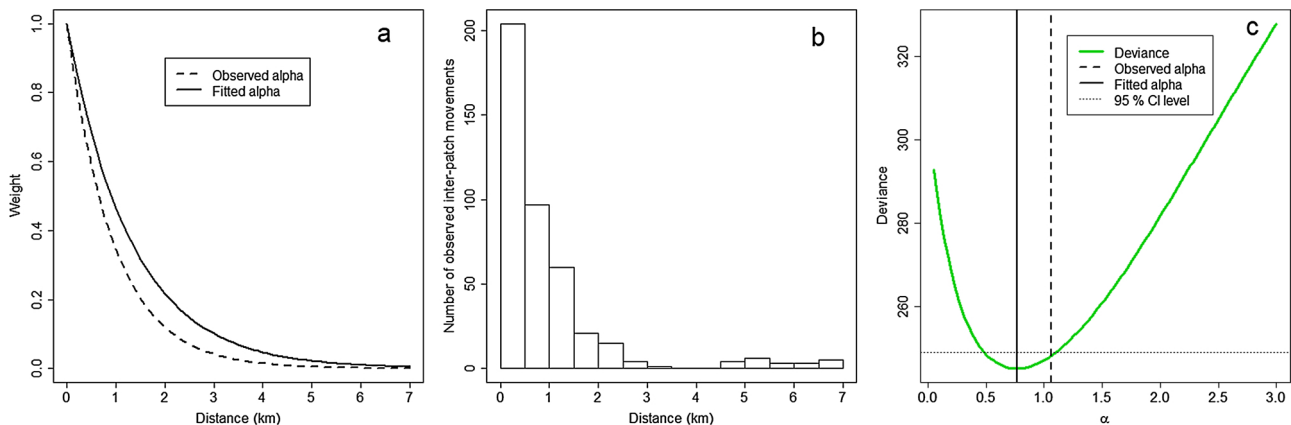


Fig. A1. a) Weight of the contribution of dispersal source patch j to the connectivity of focal patch i , given the observed (broken line) and fitted (whole line) spatial scaling parameter α as a function of distance (d_{ij}) between i and j (see Eq. (1)). The observed α is based on b) the distribution of inter-patch movements ($n = 423$, mean = 942 m, range = 40–6908 m), and the fitted α is based on c) the deviance profile when fitting the IFM with different values of α .

Table A1
The parameter estimates for the incidence function model.

Parameter	e	x	y	α
Estimate	0.0095	0.92	9531	1.06

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