

# Extreme weather affects colonization–extinction dynamics and the persistence of a threatened butterfly

Victor Johansson<sup>1</sup>  | Oskar Kindvall<sup>1</sup> | John Askling<sup>1</sup> | Markus Franzén<sup>2</sup> 

<sup>1</sup>Calluna AB, Linköping, Sweden

<sup>2</sup>Center for Ecology and Evolution in Microbial Systems, EEMiS, Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden

## Correspondence

Victor Johansson

Email: victor.johansson@calluna.se

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## Abstract

1. Extreme weather events can be expected to increase in frequency in the future. Our knowledge on how this may affect species persistence is, however, very limited. For reliable projections of future persistence we need to understand how extreme weather affects species' population dynamics.
2. We analysed the effect of extreme droughts on the host plant *Succisa pratensis*, colonization–extinction dynamics, and future persistence of the threatened marsh fritillary *Euphydryas aurinia*. Specifically, we studied a metapopulation inhabiting a network of 256 patches on Gotland (Sweden), where the summer of 2018 was the driest ever recorded. We analysed how the frequency and leaf size of host plants changed between 2017 and 2019, based on 6,833 records in 0.5-m<sup>2</sup> sample plots. Using turnover data on the butterfly from 2018 to 2019 we modelled local extinction and colonization probabilities. Moreover, we projected future population dynamics with an increasing frequency of extreme years under three different management strategies that regulate the grazing regime.
3. Our results show a substantial decrease in both frequency (46%) and size (20%) of host plants due to the drought, which taken together may constitute a 57% loss of food resources. The butterfly occupancy decreased by over 30% between 2018 and 2019 (from 0.36 to 0.27). The extinction probability increased with increasing 'effective area' of the patch (taking quality reduction due to grazing into account), and the colonization probability increased with increasing connectivity and ground moisture.
4. Projections of future dynamics showed an increasing risk of metapopulation extinction with increasing frequency of years with extreme droughts. The risk, however, clearly differed between management strategies. Less grazing in years with droughts decreased the extinction risk considerably.
5. *Synthesis and applications.* Extreme weather events can have profound negative impacts on butterflies and their host plants. For the marsh fritillary, an increased frequency of extreme droughts can lead to extinction of the entire metapopulation, even in a large and seemingly viable metapopulation. Increased grazing, due

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to fodder deficiency in dry years, may lead to cascading negative effects, while active management that reduce grazing in years with droughts can almost completely mitigate these effects.

#### KEYWORDS

climate change, drought, extreme weather, grazing, habitat quality, marsh fritillary, metapopulation, population persistence

## 1 | INTRODUCTION

Extreme weather events, such as severe heat waves, droughts and floods, can be expected to increase in frequency and intensity in the future as a direct effect of anthropogenic climate change (e.g. Christidis, Jones, & Stott, 2015; Meehl & Tebaldi, 2004; Ummenhofer & Meehl, 2017). These events may have profound effects on many ecosystems and species (Jiguet, Brotons, & Devictor, 2011; Kindvall, 1995; Maxwell et al., 2019; Parmesan, Root, & Willig, 2000); most often negative (Maxwell et al., 2019), but also positive effects have been shown (e.g. Brown, Sherry, & Harris, 2011; Carlsson & Kindvall, 2001). Changes in the magnitude and frequency of extreme weather events can have even larger impact on population persistence than increases in for example, average temperatures (e.g. Bauerfeind & Fischer, 2014; Parmesan et al., 2000). Therefore, there has been a relatively recent increasing focus on the effects of extreme weather events rather than long-term mean changes in climatic variables (e.g. Jentsch, Kreyling, & Beierkuhnlein, 2007). How the frequency of extreme weather events affects future population persistence has been identified as one important question for future research (Bailey & van de Pol, 2016). Moreover, the synergy between direct and indirect impacts of extreme weather needs further investigation (Chapman et al., 2014). For making projections of future persistence we need to understand how extreme weather events affect the population dynamics of different species.

Butterflies constitute one species group that most likely will be affected by an increasing frequency and intensity of extreme weather events (e.g. Ehrlich et al., 1980; Oliver et al., 2015; Piessens, Adriaens, Jacquemyn, & Honnay, 2009; Tack, Mononen, & Hanski, 2015). Many butterflies have already experienced negative population trends due to the loss and changed management of their habitat during the last century (Maes & Van Dyck, 2001; Warren et al., 2001), and there is a risk that an increase in extreme weather events will lead to further declines and even extinctions in the future (e.g. McLaughlin, Hellmann, Boggs, & Ehrlich, 2002; Thomas, Singer, & Boughton, 1996). The type of extreme weather event of significance for population change, however, seem to differ between species and different life-stages, and may include temperature, precipitation and drought extremes (e.g. Long et al., 2017; Oliver et al., 2015; Thomas et al., 1996; WallisDeVries, Baxter, & Van Vliet, 2011). There may also be interacting effects with habitat areas and its configuration in the surrounding landscape, where the negative effects of extreme weather can be lower in less fragmented landscapes (Oliver, Brereton, & Roy, 2013; Oliver et al.,

2015; Piessens et al., 2009). Moreover, large habitat heterogeneity may also reduce the impact of extreme weather, as shown for other insects (Kindvall, 1996). These interacting effects may open up the possibility that conservation measures can reduce the negative impacts of extreme weather events and also aid recovery (Oliver & Morecroft, 2014). However, this needs further investigation. We therefore need to study how the effect of extreme weather events on species persistence differs between different management strategies.

Metapopulation theory (Hanski, 1999) provides a conceptual framework for understanding butterfly persistence in fragmented landscapes. 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 harbour larger local populations (Harrison, Murphy, & Ehrlich, 1988). The colonization probability is determined by connectivity to local populations in the surrounding landscape (Hanski, 1999). However, the colonization-extinction dynamics can also be influenced by the quality of the habitat (e.g. Fleishman, Ray, Sjögren-Gulve, Boggs, & Murphy, 2002; Thomas et al., 2001), which is important to consider. One way to take habitat quality into account is by adjusting the 'effective area' of a patch (e.g. Moilanen & Hanski, 1998), where a low-quality patch has a smaller 'effective area' compared to an equally sized high-quality patch. For example, too intense grazing may reduce the habitat quality, and thus the 'effective patch area', for many grassland butterflies (Johansson, Kindvall, Askling, & Franzén, 2019; Moilanen & Hanski, 1998). It is also possible that habitat quality is further affected by extreme weather, for example, due to changes in abundance or quality of host plants (Curtis, Brereton, Dennis, Carbone, & Isaac, 2015; Gutbrodt, Mody, & Dorn, 2011). For realistic projections of future persistence, we therefore need to understand species' colonization-extinction dynamics in relation to both habitat quality and extreme weather events.

In the summer of 2018 a major drought hit southern Sweden (SMHI, 2018), which made it possible to study the effect of droughts on wild plant and animal populations. We used this opportunity and aimed this study at analysing the effect of extreme weather on host plants, colonization-extinction dynamics and population persistence of grassland butterflies. Using data on a metapopulation of the threatened marsh fritillary on Gotland (Sweden) before and after the drought we (a) quantify the effect of the drought on host plant frequency and leaf size, (b) record changes in occupancy after the drought, (c) model colonization and extinction probabilities based on the observed turnovers and (d) use these models to project the effect of an increase in the frequency of years with droughts on future metapopulation persistence under three different

management strategies. We hypothesize that host plants are fewer and smaller in years with droughts, and that butterfly patch occupancy is reduced the year following an extreme drought. Furthermore, we hypothesize that an increase in the frequency of years with droughts will have negative impacts on future persistence of the metapopulation.

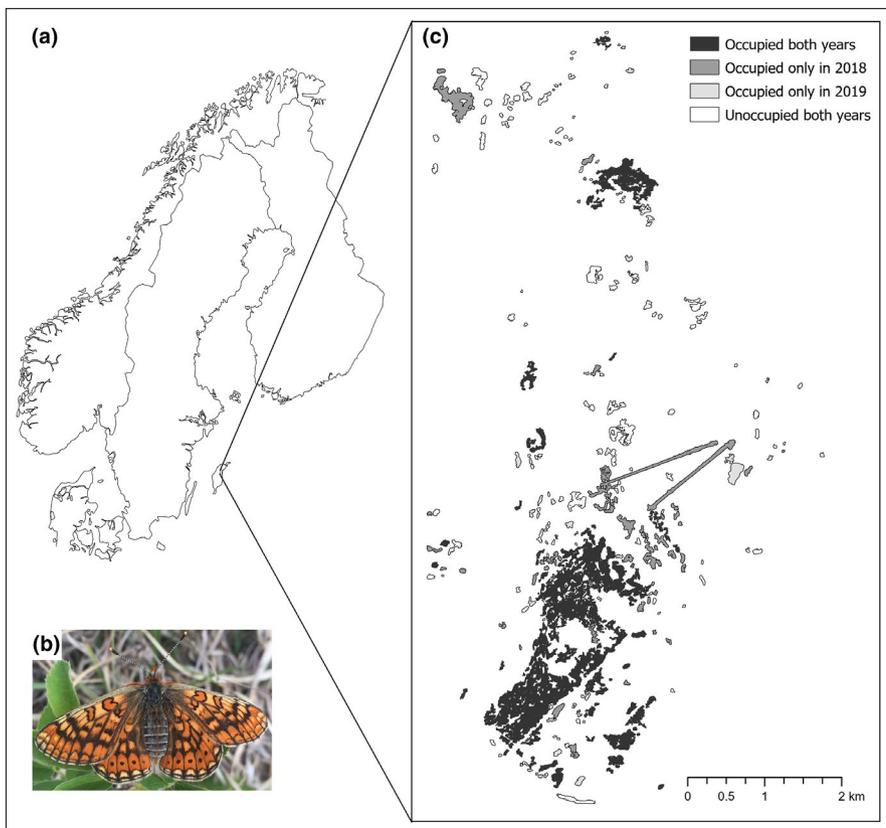
## 2 | MATERIALS AND METHODS

### 2.1 | Study species and study area

The marsh fritillary *Euphydryas aurinia* (Figure 1) has decreased dramatically in Europe due to habitat loss during the last century, and is therefore included in EU's Habitats Directive (Council Directive 92/43/EEC). The species is also red-listed in several European countries (Swaay et al., 2010) and classified as vulnerable (VU) in Sweden (Gärdenfors, 2015). The marsh fritillary is a univoltine species, with adults flying from late May to late June in Sweden. Females lay egg batches under leaves of the host plant *Succisa pratensis* (in other parts of its distribution, the marsh fritillary also utilizes other host plants; e.g. Singer, Stefanescu, & Pen, 2002), and after hatching the larvae spin a silken nest around the host plant. Larvae feed and bask gregariously during sunny days until September, when they enter diapause in a collective nest (larval autumn nests). The species is very sensitive to grazing, and the number of autumn nests is on average 4.8 times lower in grazed compared to ungrazed habitat (Johansson et al., 2019).

The study was conducted in an area of 50 km<sup>2</sup> (10 km × 5 km) close to Slite on the island of Gotland in the Baltic Sea (Figure 1),

Sweden (midpoint of the area: 57°69'N 18°69'E). In the study area, the species occurs in unfertilized calcareous grasslands. To identify potential habitat for the marsh fritillary in the study landscape we mapped the distribution of the host plant *S. pratensis* 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 and local farmers. 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 from an earlier mark-recapture study (Johansson et al., 2019). In this way 256 separate habitat patches were identified within the study area (Figure 1c). Normally, approximately 31% of the total patch area is grazed every year with an intensity resulting in a low vegetation structure that is clearly affected by grazing animals (which is required to receive EU subsidies for grazing). 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 on average. This is an intensity that is clearly too high for the marsh fritillary in the study area, and current grazing is therefore detrimental for the species (Johansson et al., 2019). It is likely that grazing becomes harmful already at low stocking rates, and due to the poor soil and slow accumulation of humus (Eliasson,



**FIGURE 1** The location of the study area on the island of Gotland outside the Swedish coast (a) and the occupancy of the marsh fritillary (b) in 2018 and 2019 among the 256 habitat patches (c)

2008) the habitat will remain naturally open for decades without any grazing. The drought in 2018 (SMHI, 2018) had large negative effects on for example, crop yields and hay production. Due to severe fodder deficiency in our study region farmers were allowed to distribute grazing animals over even larger areas than normal, including a nature reserve established to protect the marsh fringing from grazing animals. Approximately 50% of the total patch area was grazed in 2018.

## 2.2 | Data collection

Data on the host plant *S. pratensis* were collected in September 2017, 2018 and 2019. Surveys were done in hectare grid cells distributed over suitable habitat in the landscape. The number of cells differed between years; 383, 142 and 172 respectively. In each grid cell we randomly distributed 4-m 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). We avoided grid cells where the grazing changed in 2018 to be able to separate the effect of year and increased grazing. All sampling was done in 0.5 m<sup>2</sup> circular plots (80 cm in diameter) that were evenly distributed along the transects. The number of plots ranged 3–23 ( $M = 9.8$ ) depending on the total transect length within a grid cell. In each plot we recorded (a) the number of *S. pratensis* individuals and (b) 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 and 2019. 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.

## 2.3 | Data analysis

To put the 2018 drought into perspective we compared the monthly early summer (May–July) precipitation in 2018 with monthly precipitation in May–July for all years between 1860 and 2019. As the weather data availability differed between different weather stations, we combined data from three stations in the region (Visby 1860–1953, Rings 1954–1970 and Hejnum 1971–2019). We also tested if the inter-annual variation in early summer precipitation had changed over the whole period. To assess the variability in precipitation through time we used moving coefficient of variation (standard deviation/mean) along the entire time series (using 11-year windows, i.e. including 5 years before and after the focal year). We then used this coefficient of variation as the response variable in a generalized linear model (with normal distribution) with year as the explanatory variable.

To analyse differences in the number of host plants and the length of the longest leaf (as two separate response variables) among sample plots we used GLMM with hectare grid ID as a random effect (to account for the hierarchical structure of the data). As

fixed effects we included the two factor years (2017, 2018 or 2019) and grazing (ungrazed/grazed), and the continuous variable ground moisture index (GMI). The GMI combines information from topography, the depth of ground water and the soil type (Klein, 2019), and has been calculated across Sweden with a resolution of 10 m × 10 m. We used the GMI value of the pixel that the plot was situated in. The GMI was standardized to make parameter estimates comparable. For the number of host plants we used a negative binomial distribution (overdispersed count data) and for the length of the longest leaf we used a Gaussian distribution (normal).

We used observed turnovers of the adult butterfly between 2018 and 2019 to model local extinction and colonization probabilities (in two separate models), using generalized linear models with a logit link function (logistic regression). As explanatory variables we used patch area, connectivity, grazing and the mean GMI for the patch. Grazing was included as an adjustment of the 'effective area' of the patch (Moilanen & Hanski, 1998), as we earlier have shown that grazing reduces habitat quality (Johansson et al., 2019). Specifically, grazed areas were reduced 4.8 times and we then used this 'effective area' in the models (ungrazed areas remained unchanged). To test if the 'effective area' was a better proxy for the local population size compared to the actual area we tested both explanatory variables against observed extinctions. Connectivity ( $S_i$ ) was modelled as:

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

where  $d_{ij}$  is the distance in kilometres 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  $j$  in 2018 and  $p_j = 0$  if the butterfly is absent. The spatial scaling parameter  $\alpha$  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  $\alpha$  based on separate data on observed dispersal distances (Hanski, 1999). As we have such information from an earlier mark-recapture study (Johansson et al., 2019), we chose the latter approach and fitted a negative exponential function to the observed inter-patch dispersal distances (giving an  $\alpha$  of 1.06). All variables were standardized to make parameter estimates comparable. The 'effective area' of patches and connectivity was log-transformed to improve normality. We built the models based on AICc and the final models were the ones with the lowest AICc. For 'effective area' and connectivity (which includes the 'effective area' of source patches) we added two AICc units to account for the fact that the earlier estimated difference between grazed and ungrazed habitat constitutes an extra parameter in the models. For all analyses we used R.3.5.3 (R Core Team, 2019) with add-on library glmmTMB for the GLMMs.

To look for potential explanations for the overall effect of the extreme drought on metapopulation occupancy we compared the occupancy in 2019 with predictions of an incidence function model fitted to the 2018 occurrence pattern (Johansson et al., 2019; Appendix S1). First, we tested if the increased grazing (due to fodder deficiency) in 2018 could explain the occupancy in 2019 by adjusting

the 'effective area' of all patches where the grazed area increased in 2018, and then predicted how many colonizations and extinctions that should occur between 2018 and 2019. Second, we tested to adjust the 'effective areas' further by assuming a linear relationship to the change in overall larval food resources (host plants). To get the overall change in food resources we used the models for the frequency and leaf size of host plants (see above) to make predictions for 2017 and 2018. To get the average frequency and size (i.e. in two separate calculations) for the entire study area, predictions for grazed and ungrazed habitat were multiplied with the proportion grazed and ungrazed habitat in the study area, respectively, and then summed together. To remove the effect of larger areas being grazed in 2018 (which affect the mean frequency and size of host plants), we compared predictions for the proportion grazed/ungrazed habitat in 2017. We then calculated how large proportion of the frequency and size in 2017 that remained in 2018, and multiplied these two proportions to get the overall change in food resources. We then adjusted the 'effective area' of all patches in accordance with the overall change in food resources, and again predicted how many colonizations and extinction that should occur between 2018 and 2019.

## 2.4 | Projections of future population dynamics

To illustrate the potential effects of an increasing probability of extreme years on the future metapopulation persistence, we combined our turnover models (for extreme years) with the earlier fitted Incidence function model (for 'normal' years; Johansson et al., 2019; Appendix S1) to project future dynamics. For the projections, we adjusted the colonization model that was based on turnovers so that it only included connectivity (i.e. we refitted the model without GMI). The reason was to avoid the fact that damper patches have relatively high colonization probabilities even when the connectivity is close to zero, which could falsely reduce the extinction risk.

The grazing regime can have large effects on the species (Johansson et al., 2019), and we therefore compared three different grazing strategies in years with extreme droughts. First, the grazing increased to simulate fodder deficiency, as in 2018 (an increase from 31% to 50% of the total habitat patch area in the landscape). Second, the grazing continued as in 'normal' years (i.e. with grazing in 31% of the total area). Third, the grazing was completely prohibited in the

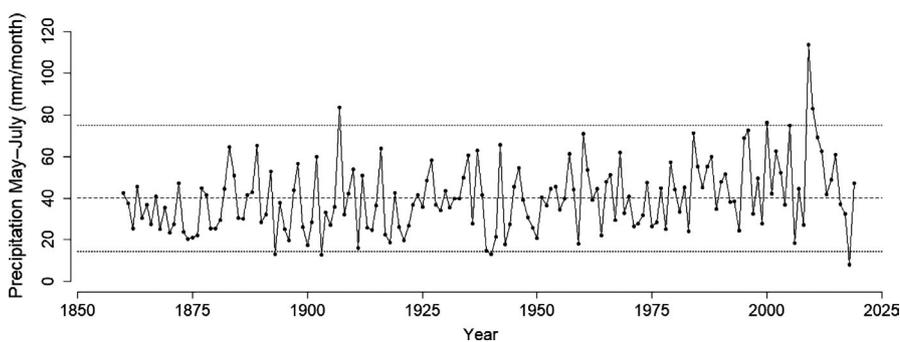
entire landscape (0% grazing) during years with extreme weather. As future climate projections are uncertain when it comes to how often weather extremes will occur (e.g. van Vuuren et al., 2011) we choose to test a wide range of probabilities for extreme droughts. All three management strategies were therefore combined with increasing probability of extreme droughts, from 0 to 0.5 (i.e. from no extreme years to extreme years every second year on average). For each strategy we tested 11 probabilities (0, 0.05, 0.10, 0.15, ..., 0.45, 0.50), and for each combination we ran 1,000 replicates (i.e.  $3 \times 11 \times 1,000 = 33,000$  projections in total) for 100 years into the future (as in Bulman et al., 2007). After 100 years we calculated the patch occupancy and extinction risk for the entire metapopulation (i.e. the proportion of replicates where patch occupancy was zero).

## 3 | RESULTS

The early summer precipitation (May–July) in 2018 on Gotland was the lowest ever recorded since measurements started in 1860 (Figure 2). The mean monthly precipitation during these 3 months in 2018 was only 8.3 mm, which is roughly 18% of the average precipitation for the period (40.1 mm/month) and clearly below the 95% confidence interval (Figure 2). Over the whole period there was no significant increase in the inter-annual coefficient of variation in the early summer precipitation ( $p = 0.83$ ; Appendix S2).

We observed substantial decreases in both the frequency and the leaf size of the host plant *S. pratensis* between 2017 and 2018 (Table 1; Figure 3). The average frequency decreased from 10.3 to 6.2 plants per  $m^2$  and the average leaf length from 11.6 to 9.4 cm. The predicted decrease in the frequency of host plants between 2017 and 2018 was 46% and the corresponding decrease in leaf size was 20%, when removing the effect of the larger total area being grazed in 2018 (which is needed as grazing reduces both plant frequency and size, Table 1). Taken together this could, thus, mean a total reduction of food resources for larvae by roughly 57% due to the drought (100% - remaining frequency 54%  $\times$  remaining size 80%). In 2019, the host plant remained at very similar levels of both frequency and size as in 2018, which was clearly lower than in 2017 (Table 1; Figure 3). The number of host plants increased with increasing GMI, while the maximum leaf length instead decreased.

We recorded 50 local extinctions and 19 colonizations in the patch network between 2018 and 2019. The number of occupied patches



**FIGURE 2** The average monthly precipitation in May–July from 1860 to 2019 (whole line), according to three weather stations (Visby 1860–1953, Rings 1954–1970 and Hejnum 1971–2019) on Gotland. Horizontal broken line shows the average monthly precipitation (40.1 mm) for the entire period and the dotted lines the 95% confidence limits

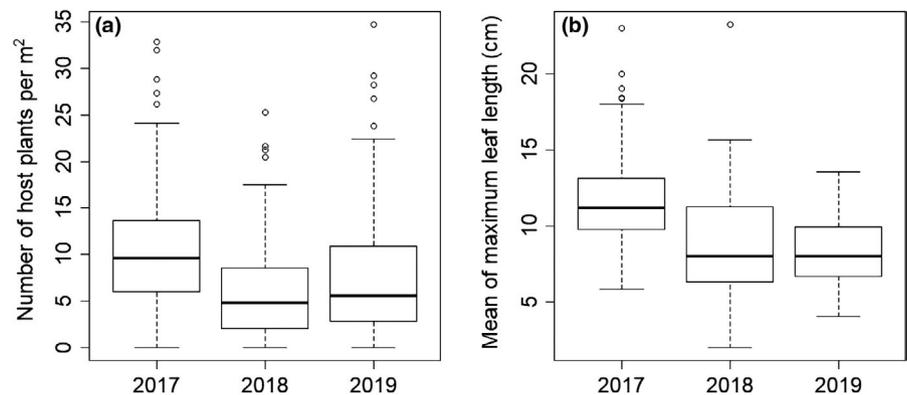
**TABLE 1** The parameter estimates (with SE) and *p*-values for the models of number of host plants *Succisa pratensis* and the length of the longest leaf

Variable	Number of host plants		Length of the longest leaf	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
Intercept	1.58 (0.039)	<0.001	12.2 (0.13)	<0.001
Grazing	-0.22 (0.064)	<0.001	-2.23 (0.21)	<0.001
Year 2018	-0.61 (0.050)	<0.001	-2.33 (0.19)	<0.001
Year 2019	-0.45 (0.037)	<0.001	-2.88 (0.13)	<0.001
GMI	0.07 (0.019)	<0.001	-0.18 (0.07)	0.006

Abbreviation: GMI, ground moisture index.

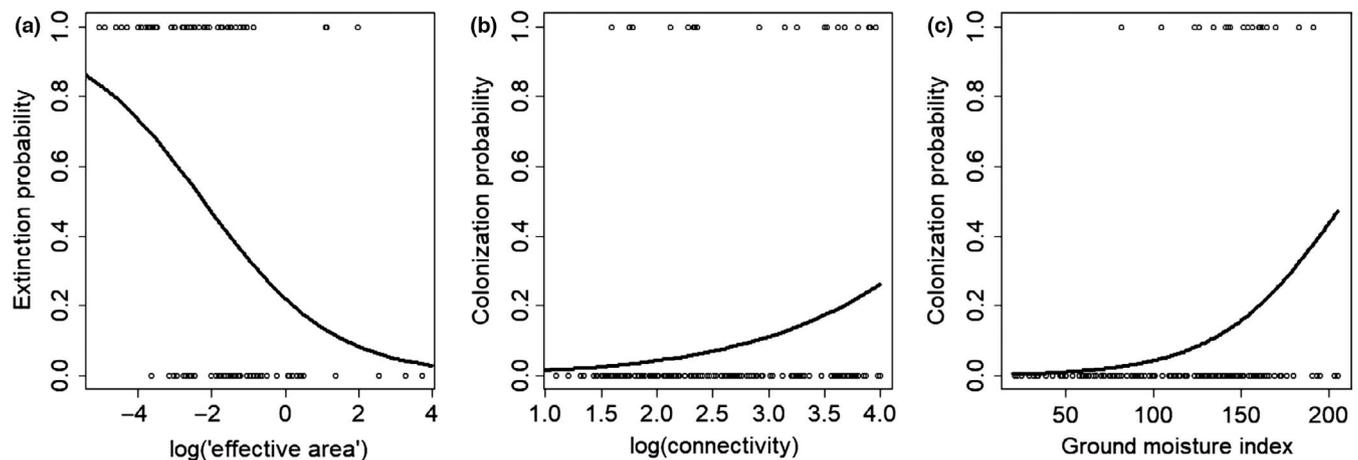
decreased from 101 in 2018 to 70 in 2019, which corresponds to a decrease in occupancy from 0.39 to 0.27 among the 256 patches. The expected occupancy when accounting for the increased area being grazed in 2018 was 0.36 based on predicted turnovers with the earlier fitted incidence function model (Appendix S1). If assuming a further linear reduction of the 'effective area' corresponding to the observed decrease in average frequency and size of the host plant, the incidence function model predicted an occupancy of 0.26. The local extinction probability increased with decreasing 'effective area' of the patch (Table 2; Figure 4). The 'effective area' was a stronger predictor than the actual area based on AICc (the AICc was 6.4 units higher for the latter). The colonization probability increased with increasing connectivity and increasing GMI (Table 1; Figure 4).

**FIGURE 3** The distributions of the (a) mean number of host plants *Succisa pratensis* and (b) mean length of the longest host plant leaf in hectare grid cells from 2017 to 2019. Each boxplot shows the median (the horizontal thick line) and the interquartile range (IQR, the box) with whiskers extending  $1.5 \times$  IQR out from the box

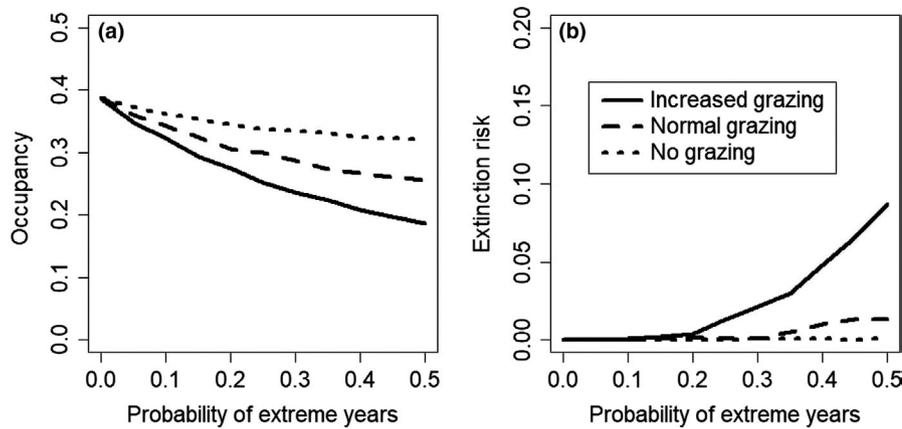


**TABLE 2** Parameter estimates (SE) of the final models for extinction and colonization probabilities.  $\Delta$ AICc = change in AICc when removing the variable from the final model

Variable	Extinction probability		Colonization probability	
	Estimate	$\Delta$ AICc	Estimate	$\Delta$ AICc
Intercept	-0.05 (0.22)		-2.53 (0.37)	
log('Effective area')	-0.99 (0.27)	13.5		
log(Connectivity)			0.78 (0.28)	4.6
Moisture index			1.20 (0.37)	12.5



**FIGURE 4** The extinction probability (a) in relation to the 'effective area' of a patch, and the colonization probability in relation to (b) connectivity and (c) the ground moisture index. Black dots are the observed data and whole lines the model predictions. In (b) and (c) predictions are made for the mean moisture index and connectivity respectively



**FIGURE 5** The mean occupancy (a) and extinction risk (b) after 100 years in relation to the probability of extreme drought events, with increased grazing (grazing in 50% of the habitat), normal grazing (grazing in 31%), or no grazing (0% grazing) in years with droughts

Patch occupancy decreased and the extinction risk for the entire metapopulation increased with increasing probability of years with extreme droughts (Figure 5). There were, however, clear differences in the effect of extreme droughts depending on the grazing strategy. The extinction risk was higher when assuming that the total area being grazed increased in years with extreme droughts (as it did in 2018), and lower when assuming that grazing instead was completely prohibited in years with extreme weather (Figure 5). In simulations with the highest probability (0.5), the patch occupancy after 100 years ranged 0.19–0.32 and the extinction risk ranged 0.1%–8.7% for the three strategies. We observed no extinction of the entire metapopulation within 100 years when assuming no extreme weather events.

## 4 | DISCUSSION

We show large effects of an extreme drought event on both the turnover of the marsh fritillary butterfly and the frequency and size of its host plant. The number of occupied patches decreased by over 30% and total host plant resources may have decreased by almost 60% due to the drought. An increase in the probability of years with extreme droughts will have strong effects on the future persistence of the marsh fritillary, and extinction of the entire metapopulation may occur already when the probability of extreme years exceeds 10% (i.e. one extreme drought event every decade on average). The effect, however, strongly depends on the management strategy in years with droughts; more grazing in years with droughts (due to fodder deficiency) have cascading negative impacts.

### 4.1 | The effect of extreme droughts on the marsh fritillary

We show that extreme droughts have clear negative effects on a threatened grassland butterfly. This agrees with our hypothesis and earlier studies showing that extreme weather events may have large impacts on butterfly populations (e.g. Oliver et al., 2015; Piessens et al., 2009; Tack et al., 2015; Thomas et al., 1996),

as well as on other organisms (Jiguet et al., 2011; Kindvall, 1995; Maxwell et al., 2019; Parmesan et al., 2000). In the present study, the occupancy of the marsh fritillary decreased by over 30% following a major drought. Only a small proportion of this decline can be explained by the increased grazing (due to fodder deficiency), while the main part seems to be related to effects directly linked to the extreme weather. The most likely reason is the substantial decrease in frequency and size of host plants due to the drought, which may have led to a 57% loss of food resources for marsh fritillary larvae throughout the landscape. A decrease in food resources is known to reduce larval abundance for the species (Botham et al., 2011; Smees, Smyth, Tunmore, French-Constant, & Hodgson, 2011), and for other specialized butterflies (Curtis et al., 2015), resulting in smaller and more extinction prone local populations. Interestingly, when assuming a linear reduction of the 'effective area' that corresponds to the overall loss of food resources our earlier developed incidence function model (Johansson et al., 2019) predicts turnovers that result in an occupancy very close to the observed one in 2019. It is, hence, very likely that the decrease in frequency and size of host plants reduces habitat quality, and thereby affects the colonization–extinction dynamics of the species which leads to the decrease in occupancy.

The frequency of years with extreme weather events can be expected to increase in the future (e.g. Christidis et al., 2015; Meehl & Tebaldi, 2004; Ummenhofer & Meehl, 2017). We can therefore expect negative impacts on the persistence of the marsh fritillary that could lead to extinction of the entire metapopulation, even in a relatively large metapopulation that has been suggested to be robust to rather substantial landscape changes (Johansson et al., 2019). The total habitat area (188.3 ha) in our study landscape exceeds the estimated total habitat area needed for long-term persistence (100 years) of the species (Bulman et al., 2007), which also agrees with our projections without taking extreme weather into account. However, when the probability of extreme droughts exceeds roughly 10%, the extinction risk start to increase. This highlights the importance of taking environmental stochasticity into account when projecting future dynamics (e.g. Lande, 1993), and also shows how potent the effect of increasing frequency of extreme weather can be, even on a seemingly viable metapopulation.

## 4.2 | Different management strategies in years with extreme droughts

Our projections show that the impact of extreme droughts on the future metapopulation persistence strongly depends on the management strategy in years with droughts. For the highest probability of extreme years tested (i.e. 0.5), the extinction risk was 87 times higher in the scenario with the largest negative effect compared to the one with least effect. Allowing grazing over larger areas in years with droughts (as in 2018) had cascading negative effects on the species, which highlights the synergy between indirect (increased grazing) and direct effects of the drought (Chapman et al., 2014). In contrast, no grazing instead almost completely mitigated the negative effects of droughts. The reason is that decreased grazing increases habitat amounts and leads to less fragmentation (as the 'effective area' increases due to ceased grazing), which to some extent buffer the negative effect of the extreme weather (Oliver et al., 2015). It is, hence, possible to reduce the impact of extreme weather by active changes in the grazing regime in years with droughts.

In the present landscape it would also be possible to strengthen the metapopulation by a general reduction in the grazed area (i.e. also in years without droughts, Johansson et al., 2019), which should make it more resilient to extreme weather events. This would most likely also benefit many other species that are sensitive to grazing in the study area and similar calcareous grasslands. It is, however, not a general management strategy that should be applied uncritically elsewhere, as it depends much on the poor soil conditions in our study area. In more productive areas grazing is necessary to prevent shrub and tree encroachment (e.g. Pöyry, Lindgren, Salminen, & Kuussaari, 2004), and some low intensity grazing may therefore be the best strategy to maintain high-quality habitat for the marsh fritillary (e.g. Munguira, Martín, García-Barros, & Viejo, 1997) and many other grassland butterflies (e.g. Johansson, Knape, & Franzén, 2017; Schtickzelle, Turlure, & Baguette, 2007). However, it is important that the grazing pressure does not increase in years with extreme weather, as too intense grazing generally seems detrimental for butterflies (e.g. Ellis, 2003; Johansson et al., 2017; Schtickzelle et al., 2007), and other grassland insects (e.g. Dumont et al., 2009; Jerrentrup, Wrage-Mönnig, Röver, & Isselstein, 2014; Kruess & Tschantke, 2002).

## 4.3 | Butterfly colonization-extinction dynamics in extreme years

We show that butterfly colonization-extinction dynamics are not only explained by connectivity and patch area (as in classical metapopulation theory, Hanski, 1999), but also by habitat quality (e.g. Fleishman et al., 2002; Thomas et al., 2001). The 'effective area', that is, the area adjusted for the negative impact of grazing, explained the extinction probability better than the actual patch area. This agrees with our earlier results showing that the number of larval autumn

nests was almost five times lower in grazed compared to ungrazed habitat (Johansson et al., 2019), which should increase the local extinction probability. An increased local extinction due to grazing has also been shown for other butterflies (Johansson et al., 2017; Moilanen & Hanski, 1998). Reasons could be that grazing leads to a lower abundance of host plants (Table 2; Schtickzelle et al., 2007) and nectar resources (Bubová, Vrabec, Kulma, & Nowicki, 2015), or that the butterfly eggs and larvae are damaged or eaten by grazing animals (van Noordwijk, Flierman, Remke, WallisDeVries, & Berg, 2012). Also the colonization probability was affected by habitat quality, as colonizations were more common in patches with a higher mean moisture index. It is possible that patches with high GMI are suboptimal (too wet) under normal years, but become more suitable in years with extreme droughts. This may lead to a shift in the metapopulation towards wetter habitat in dry years, and variation in ground moisture throughout the landscape may thus to some extent buffer the negative effect of extreme droughts. In more homogenous landscapes, the effect of extreme weather may be worse (Kindvall, 1996).

## 4.4 | Conclusions and conservation implications

There is a large probability that the frequency of extreme weather events will increase in the future, which most likely will have negative consequences for the marsh fritillary as well as other butterflies and their host plants (e.g. Oliver et al., 2013, 2015; Tack et al., 2015). It is possible that extreme droughts will occur more often than every ten years (which is the threshold where the extinction risk start to increase in our projections) during the coming centuries in Europe (e.g. Oliver et al., 2015). Taking climate change into account in future management plans is a major challenge, but probably of utmost importance for successful conservation of many threatened species (Butt et al., 2016; Maxwell et al., 2019). This includes highlighting potential interactions between extreme weather and different management strategies. For the marsh fritillary, as well as for many other grassland insects, it is important to prevent intensified grazing in years with droughts to avoid cascading negative effects. Preferably, grazing should even be reduced in dry years (primarily for areas with low productivity), at least leaving aside core patches. Future management could also include proactive actions, such as increasing habitat amounts, identifying and creating wetter patches and decreasing fragmentation to make populations more resilient to extreme events.

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## AUTHORS' CONTRIBUTIONS

V.J., O.K., J.A., M.F. conceived the ideas/methodology; O.K., J.A., M.F. collected data; V.J. analysed data and led manuscript writing; O.K., J.A., M.F. contributed to manuscript. All authors gave approval for publication.

## DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.s1rn8pk4k> (Johansson, Kindvall, Askling, & Franzén, 2020).

## ORCID

Victor Johansson  <https://orcid.org/0000-0003-1369-9351>

Markus Franzén  <https://orcid.org/0000-0001-8022-5004>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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