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ORIGINAL ARTICLE

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Quick recovery of a threatened butterfly in well-connected patches following an extreme drought

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Abstract

1. Extreme weather events are becoming more frequent due to climate change. We therefore need to understand how species respond to these events. In 2018, the worst drought ever recorded hit the island of Gotland in the Baltic Sea, which led to a major decline of the threatened marsh fritillary (*Euphydryas aurinia*) the succeeding summer.
2. We compared yearly occupancy among 256 habitat patches between 2018 and 2020 and analysed the colonisation–extinction dynamics between 2019 and 2020 in relation to patch area, connectivity, and habitat quality. Moreover, using capture-mark-release data in two patch clusters differing in connectivity, we also compared population sizes before and after the drought and analysed 'population growth rates'. We also compared yearly abundance of host plants (*Succisa pratensis*) over time.
3. Results show a remarkable recovery of the marsh fritillary. Both patch occupancy in 2020 and the number of individuals in the well-connected patch cluster were higher than before the drought. In contrast, host plants were fewer and smaller, which taken together suggest that the amount of food resources was roughly half in 2020 compared to the pre-drought conditions. Moreover, the butterfly population in the less connected patch cluster was eight times smaller compared to the population size before the drought. Local colonisations, extinctions, and population growth rates were explained by connectivity.
4. The ability to quickly recover after extreme droughts is promising in times of climate change. The significance of connectivity for the population dynamics during recovery highlights the importance of maintaining well-connected patch networks.

KEYWORDS
climate change, colonisation–extinction dynamics, extreme weather, metapopulation, population growth rate

INTRODUCTION

Extreme weather events will increase in frequency and intensity in the future due to climate change (e.g. Christidis et al., 2015; Meehl & Tebaldi, 2004; Ummenhofer & Meehl, 2017). These events may have large effects on many ecosystems and species (e.g. Maxwell et al., 2019; Neilson et al., 2020; Parmesan et al., 2000). Increasing magnitude and frequency of extreme weather events can have even

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larger impact on population persistence than increases in, for example, average temperatures (Bauerfeind & Fischer, 2014; Parmesan et al., 2000). Even though positive effects have been shown (Carlsson & Kindvall, 2001), the effects of extreme weather most often seem negative on population persistence (Maxwell et al., 2019). However, population responses to extreme weather are difficult to predict even with well-substantiated population models (Bergen et al., 2020). Increasing our understanding of how different species respond and recover after extreme weather events is therefore of utmost importance for successful species conservation in times of climate change.

Many butterfly species have already experienced negative population trends due to habitat loss and management changes during the last century (Maes & Van Dyck, 2001; Warren et al., 2021). There is a risk that an increase in extreme weather events will also lead to further declines and extinctions in the future (Johansson et al., 2020; McLaughlin et al., 2002; Piessens et al., 2009; Thomas et al., 1996). However, the effects of extreme weather will differ between species (Long et al., 2017; Oliver et al., 2015; Thomas et al., 1996), and the effect on long-term persistence will depend on their ability to recover after extreme weather events. The recovery may in turn be affected by the amount and configuration of habitat in the landscape; faster recovery can be expected in less fragmented landscapes (Oliver et al., 2013, 2015; Piessens et al., 2009). Larger areas of habitat are likely to provide a broader range of resources and microclimates compared to small areas (Oliver et al., 2010; Hodgson et al., 2011), and this heterogeneity may reduce the impact of extreme weather events and climatic variation in general (Kindvall, 1996; Nice et al., 2019; Suggitt et al., 2018).

The population dynamics of many butterflies fits metapopulation theory (e.g. Hanski, 1999). According to classical theory, the local extinction probability depends on patch size (as larger patches can harbour larger and less extinction prone local populations, Harrison et al., 1988), while the colonisation probability depends on connectivity to surrounding occupied patches (e.g. Hanski, 1999). Connectivity may, however, also affect local extinction probability through the so-called 'rescue effect' (Brown & Kodric-Brown, 1977), and patch size may affect colonisation probability (e.g. Hanski, 1999; Thomas & Jones, 1993) through a larger target area and potentially more resources that may attract immigrants. Moreover, the colonisation–extinction dynamics may also be influenced by habitat quality (e.g. Fleishman et al., 2002; Johansson et al., 2017). High-quality habitat can harbour larger local populations compared to habitat of lower quality (e.g. Johansson et al., 2019). Extreme weather events may affect habitat quality for butterflies, for example, due to changes in abundance or quality of their host plants (e.g. Gutbrodt et al., 2011; Johansson et al., 2020). Host plants may recover slowly after extreme weather events, as many plants have slow population dynamics (Helm et al., 2006), which can be expected to affect the population recovery of their associated herbivore (here butterfly).

During the summer of 2018, a major drought hit Europe, resulting in water shortages, crop failures, and fire outbreaks (Peters et al., 2020). The drought also had large impacts in many ecosystems, and clear negative effects were shown for, for example, several butterfly species (Bergen et al., 2020; Johansson et al., 2020). On the island of Gotland in the Baltic Sea (Sweden) May–July was the driest ever recorded since measurements started in 1860 (SMHI, 2018). This extreme drought had clear negative impacts on a large metapopulation of the threatened marsh fritillary the succeeding summer (i.e. in 2019, Johansson et al., 2020) when local extinctions had occurred in almost half (50) of the 101 patches, it occupied before the effect of the drought was evident (during the flight period in early summer 2018). The most likely reason for the decline was the almost 60% loss of its host plant (*Succisa pratensis*) throughout the landscape recorded in September 2018 (Johansson et al., 2020). The host plant abundance had not increased in September 2019, we therefore expected the butterfly to remain at relatively low population levels in 2020.

Our aim was to investigate how the marsh fritillary metapopulation and its host plants develop after the drought. Does the butterfly continue to decline or start to recover? Specifically, we (1) compare yearly patch occupancy from 2018 to 2020 (i.e. before and after the drought) and (2) analyse butterfly colonisation–extinction dynamics during the first year of recovery in relation to habitat quality (ground moisture and grazing), patch area and connectivity. Moreover, in two subsets of the network, we (3) compare population sizes before and after the drought using capture-mark-release data and (4) analyse population growth rates in 31-ha grid cells in relation to habitat quality, connectivity and preceding population densities. We also analyse (5) host plant abundance over time, using 8668 records from 0.5 m^2 sample points placed across the landscape. We hypothesised that the patch occupancy and population sizes (in the two subsets of the network) would be clearly lower in 2020 compared to the pre-drought conditions as the host plant had not recovered in September 2019. We also hypothesised that the host plant had not yet recovered to pre-drought conditions in September 2020.

METHODS

Study species and study area

The marsh fritillary [*Euphydryas aurinia* (Rottemburg, 1775)] is included in EU's Habitats Directive (Council Directive 92/43/EEC) and red listed in several European countries (van Swaay et al., 2010) due to its decrease during the last century. The species is univoltine, and adults fly from late May to late June in Sweden. Females lay egg batches under leaves of the host plant (see below), 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 larvae become active again in early spring and resume feeding. The host plant, *Succisa pratensis* (Moench), is a perennial polycarpic rosette herb living in low productive grasslands throughout Europe (Adams, 1955). The species flowers from August to September and mainly reproduce by seeds (Adams, 1955). Individual plants can live for over 25 years (Hooftman et al., 2003).

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The study was conducted in an area of 50 km^2 (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), where the marsh fritillary occurs in unfertilised calcareous grasslands. In previous studies (Johansson et al., 2019, 2020), we identified potential habitat for the species by mapping the distribution of 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). Suitable habitat was defined as all open grasslands where the host plant occurs. Discrete habitat patches were defined as habitat areas separated by >33.3 m of open habitat without the host plant, or >10 m with a forest barrier. In total, 256 separate habitat patches were identified within the study area (Figure 1), totalling an area of 188.3 ha of suitable habitat. Approximately 31% of the total patch area is grazed every year from late May to late September with sheep or cattle (Angus and Charolais) with approximately 0.3 animals/ha on average (the remaining 69% are unmanaged). We have earlier shown that this grazing intensity is detrimental for the species, reducing the habitat quality by almost 80% for the marsh fritillary based on the number of larval nests in grazed and ungrazed habitats (Johansson et al., 2019).

Data collection

The occurrence pattern of the adult butterfly in the entire patch network was assessed during the flight period in late May to late June 2018, 2019, and 2020. 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.

For two subsets (patch Clusters A and B) of the patch network (27.6 ha of ungrazed habitat, Figure 1e) we performed capture-mark-release (CMR) studies in 2017, 2019 and 2020 during the flight period (late May to late June). We chose these two clusters as they clearly differed in connectivity during recovery (the connectivity of the patches in Cluster A was on average 5.2 times higher compared to the patches in Cluster B, based on Equation 1). Butterflies were marked and recaptured along irregular routes focused to cover suitable habitat that was utilised by the butterflies. Each adult caught was marked individually using a permanent marker pen and immediately released at the point of capture. The surveys were performed between 9 a.m. and 5 p.m. Surveys were not performed in unfavourable weather conditions such as rain (within 1 h after rainfall) or temperatures below 17 °C.

Data on butterfly host plants were collected annually in September between 2017 and 2020. The sampling was done in hectare grid cells distributed over suitable habitat in the landscape. The number of cells differed between years: 383, 142, 172, and 147, respectively. In each grid cell, we randomly distributed 4-m wide transects across the suitable habitat within the cell. Within each transect, we collected data on the host plant using 0.5 m^2 circular plots evenly distributed along each transect. The number of plots ranged 3–23 (mean = 10.3) depending on the total transect length within a grid cell (which differed depending on the amount of suitable habitat in the grid cell). In each plot, we measured the number of *Succisa*

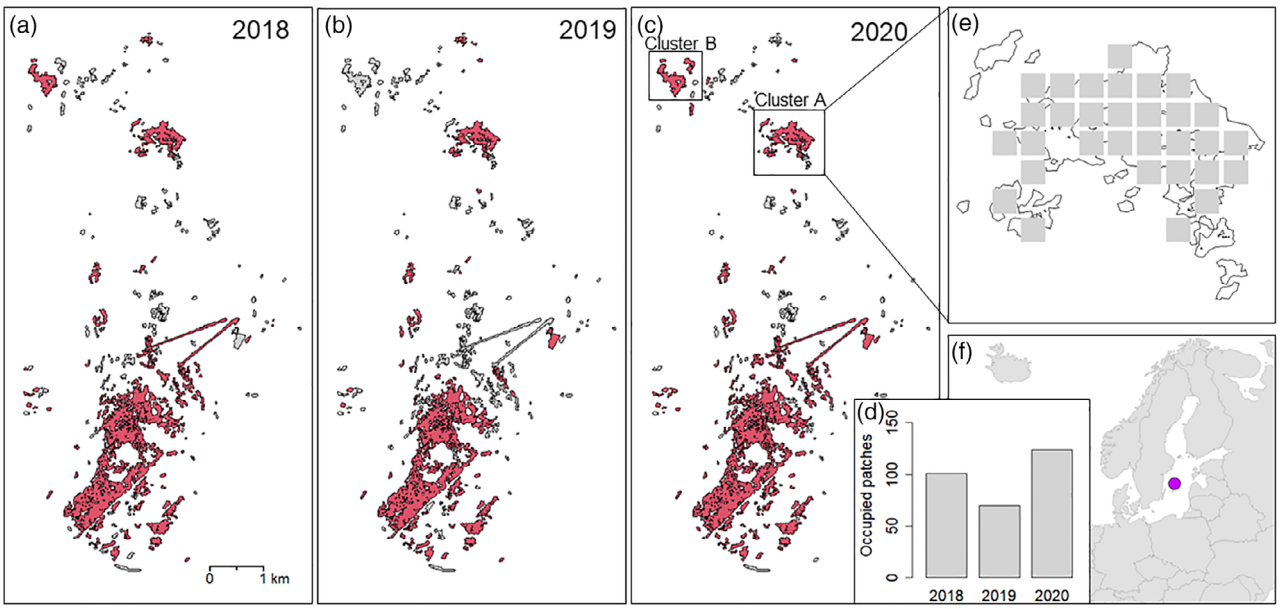

FIGURE 1 The study area with 256 habitat patches that are either occupied (red) or unoccupied (light grey) by the marsh fritillary in (a) 2018, (b) 2019, (c) 2020, and (d) the total number of occupied patches for each year. Mark-recapture studies were performed in two subsets of the patch network (patch Clusters A and B) where the population sizes (number of butterfly individuals) were estimated in 2017, 2019 and 2020. Within (e) 31-ha grid cells (grey squares, Cluster A), we also estimated the population growth rate after the drought (between 2019 and 2020). The study area is situated on (f) the Swedish island Gotland in the Baltic Sea (purple dot)

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pratensis individuals (i.e. the host plant) and the length of the longest *S. pratensis* leaf. We also recorded if the plot contained tussocks or not (1/0), as tussocks may affect both the number of plants and their size based on field experience. The total number of plots from the 4 years was 8668.

Statistical analysis

Local colonisation and extinction probabilities were modelled based on the observed turnovers between 2019 and 2020 using generalised linear models (GLMs) with a logit link function (logistic regression). As explanatory variables we included patch area, connectivity, mean ground moisture index (GMI, see Supporting information, Appendix S1) of the patch, and grazing (ungrazed/grazed). 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 patches j, A_j is the area of patch j, and $p_j = 1$ if the butterfly is present in patch j in 2019 and $p_j = 0$ if the butterfly is absent. The spatial scaling parameter α was based on observed inter-patch dispersal distances from a larger CMR-study in 2017 (giving an α of 1.06; Johansson et al., 2019). Patch area and connectivity were log-transformed to reduce skewness. All continuous variables were standardised. We built the models based on AICc and the final models were the ones with the lowest AICc.

Based on the CMR-data, population sizes were estimated for each year (2017, 2019, and 2020) in two subsets of the network (patch Clusters A and B in Figure 1) using Jolly–Seber–Schwarz–Arnason models (JSSA, Schwarz & Arnason, 1996) for open populations. For each year we used 10 days of CMR-data that were evenly distributed over the main flight period (covering 20–25 days depending on year and subset) to estimate the population size. We fitted year-and-subset-specific models as we wanted to compare population size between years within each cluster (and demographic parameters are likely to differ between years, Zimmermann, Blazkova, et al., 2011). Survival probabilities were time dependent (i.e. they were allowed to vary over the season when the model was fitted to the data), which is likely, for example, because of vanishing food supply (this also improved the models fit for every year based on the AIC, compared to constant probabilities). However, to reach model convergence, we had to keep capture probabilities and recruitment probabilities constant (but separately for each year and cluster).

For a more detailed analysis of the recovery of the population in the patches where CMR-data were collected we applied a 1-ha grid over the area (Figure 1e). We only included grid cells where the species was found both in 2019 and 2020 (31 in total, all in Cluster A). We then calculated the 'population density' in each grid cell and year based on the number of unique butterfly individuals observed within the grid cell and the amount of suitable habitat in the cell (which ranged 0.06–0.97 ha). For each grid cell, we then calculated the grid-cell-specific population growth rate (R_i) as:

$$R_i = \frac{N_{i,2020}}{N_{i,2019}} \quad (2)$$

where $N_{i,2019}$ and $N_{i,2020}$ are the estimated 'population densities' in grid cell i for 2019 and 2020, respectively. We then modelled the population growth rate (R) using a GLM with log-normal distribution

TABLE 1 Parameter estimates (SE) of the final models for extinction and colonisation probabilities

	Extinction probability		Colonisation probability	
Variable	Estimate	ΔAICc	Estimate	ΔAICc
Intercept	−3.10 (0.65)		−0.99 (0.19)	
log(Patch area)			0.84 (0.20)	19.6
log(Connectivity)	−1.05 (0.41)	4.9	0.90 (0.21)	21.1

Abbreviation: ΔAICc, change in AICc when removing the variable from the final model.

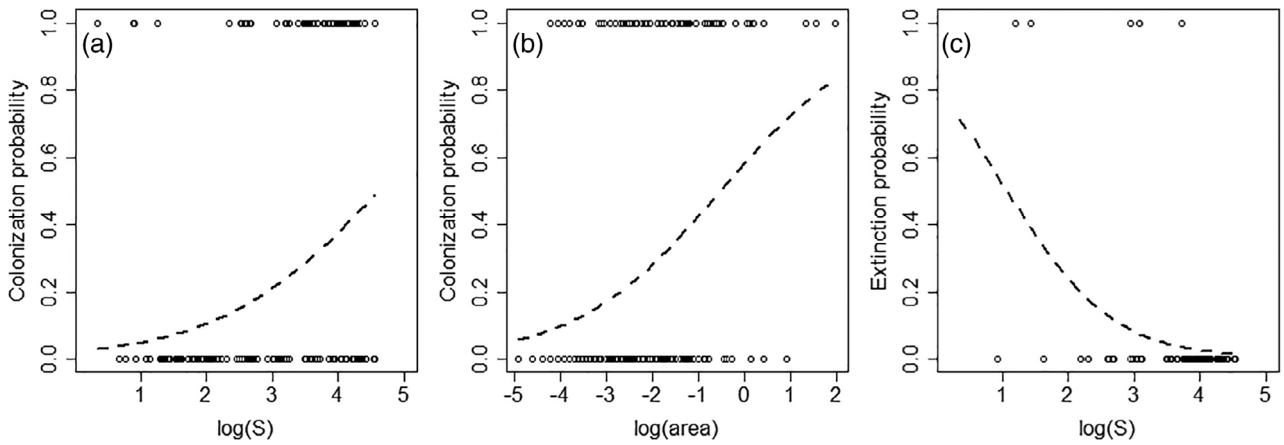

FIGURE 2 The colonisation probability in relation to (a) connectivity (S) and (b) patch area, and the extinction probability in relation to (c) connectivity. Dots are observed data, and broken lines are model predictions (see Table 1)

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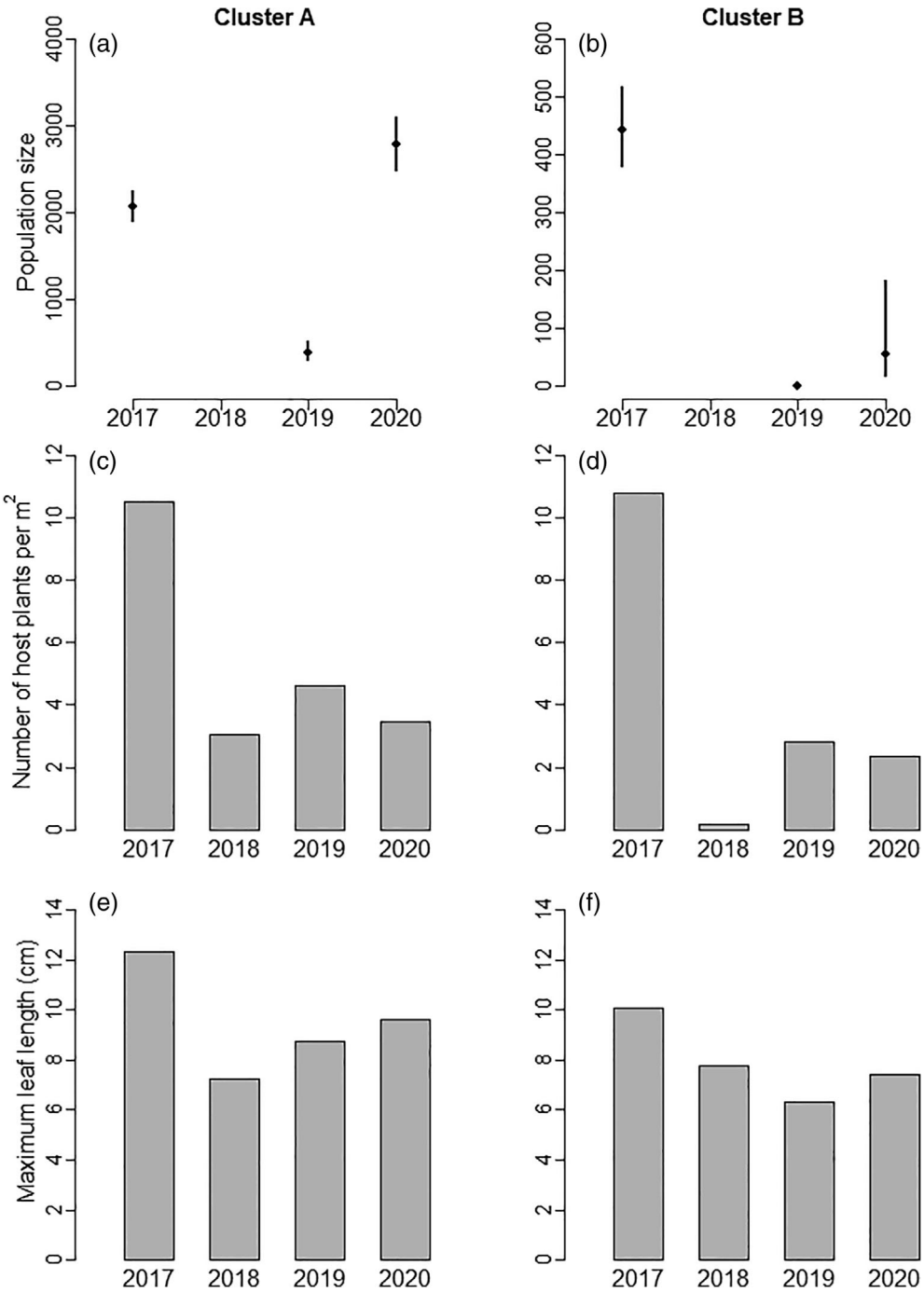

FIGURE 3 The estimated population sizes of the marsh fritillary (black dots = mean and vertical lines = 95% confidence intervals) in 2017, 2019 and 2020 for the two subsets (patch Clusters A and B) (a and b) in the network where capture-mark-release (CMR) data were collected (see Figure 1), and the yearly corresponding average number of host plants (c and d), and the mean length of the longest leaf (e and f) between 2017 and 2020. In 2019, the species went extinct from all patches in (b). For 2018, we did not perform any CMR

based on the explanatory variables mean GMI, post-drought host plant abundance (see below), the population density in 2019, and grid cell connectivity (GS_i). Grid cell connectivity was modelled as:

$$GS_i = \sum_{j=1}^{n} e^{-d_{ij} \times \alpha_h} N_{j,2019} \quad (3)$$

where d_{ij} is the centre-to-centre distance in kilometres between focal grid cell i and surrounding cells j, and $N_{j,2019}$ is the number of unique individuals in 2019 in cell j. The spatial scaling parameter α_h was based on the distribution of observed inter-grid-cell movements from all 3 years with CMR data (giving an α of 5.3, Appendix S1, Figure S2). For host plant abundance, we separately tested the number of

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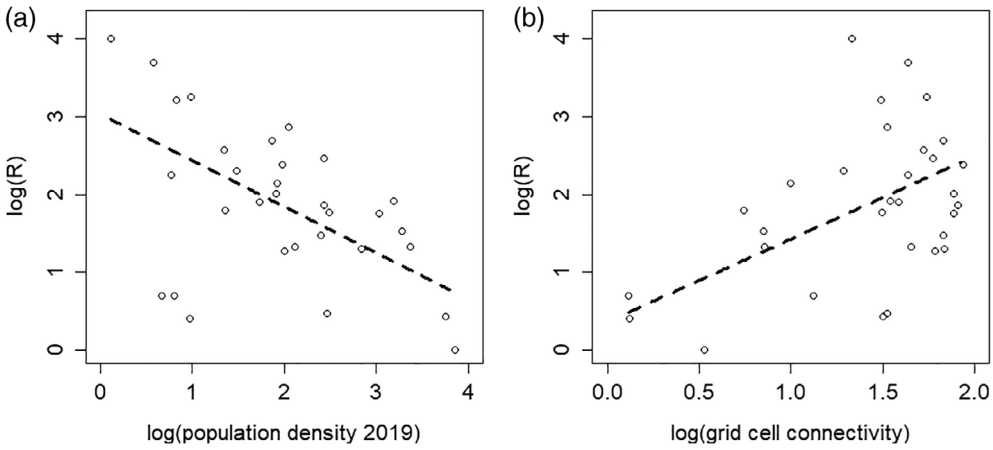

FIGURE 4 The grid cell population growth rate (*R*) between 2019 and 2020 in relation to (a) grid cell population density 2019 and (b) grid cell connectivity. Dots are estimated grid cell population growth rates, and broken lines are model predictions (see Table 2)

individuals, maximum leaf size, and the product of the two (as a measure of total biomass) based on average values from both post-drought years. The population density in 2019 and grid cell connectivity were log-transformed, and all explanatory variables were standardised.

To analyse the number of host plants and the length of the longest leaf (as two separate response variables), we used generalised linear mixed models (GLMMs) with hectare grid ID as a random effect to account for the hierarchical structure of the data. As explanatory variables (fixed effects), we included year as a factor with four levels (2017, 2018, 2019 or 2020), we also included grazing (grazed or ungrazed) and presence of tussocks (present or absent), and the continuous variable GMI (see Appendix S1 for details). For the number of host plants, we used a negative binomial distribution (over-dispersed counts) and for the leaf length we used a Gaussian distribution (normal).

To compare the drought in 2018 with other years, we used the longest annual precipitation time series available from May to July between 1860 and 2020. 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 1971–2020). Based on the average monthly precipitation (between May and July) for each year, we calculated an overall mean and associated 95% confidence interval for the entire period.

TABLE 2 Parameter estimates (SE) of the final model for the grid cell population growth rate (R) between 2019 and 2020

	Estimate (SE)	ΔAICc
Intercept	1.86 (0.12)	
log(population density in 2019)	−0.59 (0.13)	15.7
log(grid cell connectivity)	0.54 (0.13)	13.8

Abbreviation: ΔAICc, change in AICc when removing the variable from the final model.

All analyses were performed using R.4.0.3 (R Core Team 2020) with add-on library glmmTMB 1.0.2.1 for the GLMMs and openCR 1.5.0 for the JSSAs.

RESULTS

We recorded 59 local colonisations and 5 extinctions in the patch network between 2019 and 2020. The number of occupied patches increased from 70 in 2019 to 124 in 2020, corresponding to an increase in occupancy from 0.27 to 0.48 among the 256 patches. The colonisation probability increased with increasing connectivity and patch area (Figure 2, Table 1). Most colonisations (90%) took place within 0.5 km from occupied patches in 2019 (Figure S1), but a few colonisations occurred up to 2 km from any occupied patch in 2019. The extinction probability increased with decreasing connectivity (Figure 2, Table 1).

In patch Cluster A, the number of marked individuals from the CMR studies varied between years: 1002 (33% were recaptured) in 2017, 149 (24% were recaptured) in 2019, and 1022 (22% were recaptured) in 2020. The corresponding figures for subset B were 262 (44% were recaptured) in 2017, 0 in 2019, and 17 (12% were recaptured) in 2020. The estimated population size in subset A in 2019 (mean = 385, SE = 53.9) was significantly smaller compared to both 2017 (mean = 2059, SE = 88.7) and 2020 (mean = 2772, SE = 157.1), based on the non-overlapping confidence intervals for the yearly population size estimates (Figure 3a). The number of individuals in 2019 was on average 5.3 times smaller compared to the pre-drought population in 2017, while the population size in 2020 instead was 1.3 times larger compared to 2017 (which also was a significant difference based on the confidence intervals, Figure 3). For patch Cluster B, the population of 442 (SE = 35.0) individuals went extinct in 2019. The species recolonised in 2020, but the estimated population size of 55 (SE = 33.6) individuals was considerably smaller compared to the pre-drought condition (Figure 3b). In patch Cluster A, the population growth rate between 2019 and 2020 ranged 1.0–55.0

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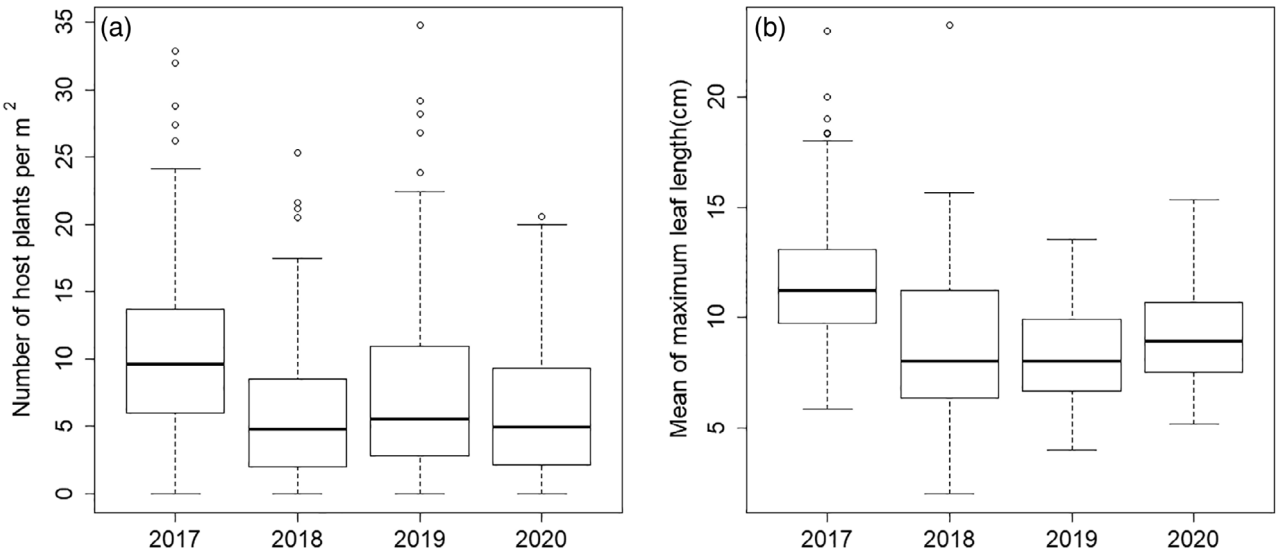

FIGURE 5 The distribution of the (a) mean number of host plants (*Succisa pratensis*) and (b) mean length of the longest leaf in hectare grid cells from 2017 to 2020

(mean = 10.3, SE = 2.13). The growth rate increased with increasing grid cell connectivity and declined with increasing population density in 2019 (Figure 4, Table 2), while GMI and host plant abundance had no clear effect (both variables increased AICc).

The host plants (*S. pratensis*) were still fewer and smaller in 2020 compared to the pre-drought conditions in 2017 (Figure 5, Table S1). At the hectare grid cell level, the average frequency in 2020 (6.1 plants/m^2) was only 60% of the frequency in 2017 (10.2 plants/m^2), while the average leaf length in 2020 (9.1 cm) was 81% of the leaf length observed in 2017 (11.2 cm). Taken together, this may thus mean that the amount of food resources was still roughly half in 2020 compared to the pre-drought conditions (60% × 81% = 49%), even if the sizes of plants seemed to have recovered slightly (Figure 5). Patch Cluster A (see Figure 1) roughly followed the pattern of the entire landscape (Figure 3c,e), while the host plant in Cluster B decreased more due to the drought (and was also slightly more behind in the recovery, Figure 3d,f).

The average monthly precipitation in May–July 2019 and 2020 was 47.3 mm and 41.9 mm, respectively, which is 5.8 and 5.2 times more than the drought year of 2018 (8.13 mm). The average for the entire period between 1860 and 2020 was 40.1 mm (Figure S3).

DISCUSSION

We show a remarkable recovery of the threatened marsh fritillary only 1 year after a major population decline caused by the worst drought ever recorded on Gotland. Both patch occupancy in the entire landscape and population density in one of the patch clusters (A) had increased to pre-drought levels or above. In contrast, host plants were still both fewer and smaller throughout the landscape compared to the pre-drought conditions. Even though the loss of host plants was extremely severe in the more isolated patch cluster (B), the butterfly was able to recolonise, but had not yet reached pre-drought population densities.

Population decline after the drought

Due to the drought in 2018, the occupancy of the marsh fritillary decreased by over 30% in its 256 patch network on Gotland (Johansson et al., 2020). Here, we show that the negative effect of the drought is even more evident for the population size (i.e. number of individuals), which was reduced by over 80% compared to the pre-drought conditions in patch Cluster A (Figure 4). In Cluster B, the species went completely extinct after the drought. Even if we do not estimate population sizes in the entire patch network this still indicates that changes in patch occupancy due to extreme weather may underestimate changes in the total population size, even if the two population measures are usually correlated (e.g. Johansson et al., 2017). The strong decline in our butterfly population due to the 2018 drought agrees with the well-studied Glanville fritillary in Finland (Bergen et al., 2020), which is also in line with other studies showing that extreme weather events may have large impacts on butterfly populations (Oliver et al., 2015; Piessens et al., 2009; Thomas et al., 1996) as well as on other species (e.g. Kindvall, 1995; Maxwell et al., 2019; Parmesan et al., 2000).

Population recovery after the drought

We show a remarkable recovery of the marsh fritillary after the extreme drought in 2018. Both the number of occupied patches and population size (in patch Cluster A, where it survived) were above the pre-drought conditions already 1 year after the decline. This is a fast recovery compared to several other butterfly populations and

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communities after severe droughts (De Palma et al., 2017; Oliver et al., 2013; Piessens et al., 2009), and the recovery of other species after extreme weather events in general (Neilson et al., 2020). We do not think that this is due to exceptionally beneficial post-drought years for the species, at least not weather-wise (the average precipitation suggested that 2019 and 2020 were rather 'normal' years, Figure S3), but we can expect higher population growth rates due to a decreased competition (i.e. negative density dependence – Zimmermann, Blazkova, et al., 2011; Neilson et al., 2020). However, the most important reason for the fast recovery of our metapopulation is most likely that the patch network is relatively large and well connected. The amount and configuration of habitat in the landscape are important for recovery, and faster recovery can be expected in less fragmented landscapes (Oliver et al., 2013, 2015; Piessens et al., 2009). Larger areas of habitat are also likely to provide a broader range of resources and microclimates (Oliver et al., 2010, Hodgson et al., 2011), which is known to buffer against climate extremes (Kindvall, 1996; Nice et al., 2019; Suggitt et al., 2018). 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), and earlier projections of future dynamics in our network suggest that the metapopulation is viable and robust to rather substantial landscape changes (Johansson et al., 2019, 2020). Our metapopulation should therefore have rather good conditions to recover after a major perturbation, in contrast to, for example, several other more fragmented European metapopulations of the marsh fritillary (Bulman et al., 2007; Schtickzelle et al., 2005). Hence, for other metapopulations of the species, we should probably expect a slower recovery, which may also be true for other rare butterflies and many other insects living in fragmented landscapes (Oliver et al., 2015).

Interestingly, the overall recovery of the marsh fritillary metapopulation does not seem to be related to a recovery of its host plant (*Succisa pratensis*), as host plants were still both fewer and smaller compared to the pre-drought conditions. Moreover, we do not find any relationship between host plants abundance and the population growth rates in the hectare grid cells. This is somewhat surprising as host plant availability have been shown to affect both larval abundance (e.g. Johansson et al., 2019; Konvicka et al., 2003; Smee et al., 2011) and the occurrence of adult butterflies for the species (Betzholtz et al., 2007; Wahlberg et al., 2002). The result is also in contrast to Piessens et al. (2009) that showed a rather strong association between butterfly and host plant recovery. We do not know, however, whether the current availability of host plants in our landscape will be enough to maintain the current butterfly population density over time. Larvae may require less host plant biomass shortly after a drought due to an increase in nutrient availability and a reduction of defence compounds in drought-stressed host plants (Gutbrodt et al., 2011; White, 2009). Moreover, it is likely that larval survival in general is higher after the drought due to a potential reduction of parasitic wasps after a major decline in the butterfly population (e.g. Lei & Hanski, 1997). However, both host plant chemistry and the abundance of parasites over time needs further investigation. It is possible that the marsh fritillary will decline within a few years again (if host plants remain fewer, and build up defence compounds, at the same time as parasitic wasps increase again), and it is therefore important to follow future population dynamics.

Population dynamics during recovery

The colonisation probability of empty patches between 2019 and 2020 increased with increasing connectivity, which is consistent with metapopulation theory (Hanski, 1999) and earlier studies of the marsh fritillary (e.g. Johansson et al., 2020). This also agrees with metapopulation structures of the species in other parts of Europe (e.g. Anthes et al., 2003; Bulman et al., 2007; Hula et al., 2004; Schtickzelle et al., 2005). Most colonisations occurred within a few 100 m from any of the occupied patches in 2019, which suggest a limited dispersal ability in line with many other butterflies (e.g. Cassel-Lundhagen & Sjögren-Gulve, 2007; Johansson et al., 2017). However, the species still managed to recolonise patch Cluster B (Figure 1), which has required dispersal events of at least 1.2 km. This suggests that, even if most movements are short (Figure S2, Junker & Schmitt, 2010), the species is capable of longer dispersal events (Hula et al., 2004; Zimmermann, Fric, et al., 2011). The colonisation probability also increased with increasing patch area. This relationship has been less emphasised in theory but has been shown empirically for butterflies (Thomas & Jones, 1993) and other insects (Ranius et al., 2014). Larger patches may both be easier to find and provide more resources for immigrants, which should increase their propensity to colonise the patch (Englund & Hambäck, 2007; Franzén & Nilsson, 2010). Patch size is likely a more important predictor of colonisation during recovery, as proportionally more large patches may be empty after a major perturbation compared to a 'normal' year. In contrast, the extinction probability was not explained by patch area, which disagrees with metapopulation theory, and earlier studies of the species (Johansson et al., 2019, 2020; Wahlberg et al., 2002). One reason for this could be that only five extinctions were recorded between 2019 and 2020, making it more difficult to find any clear relationships. However, even though the number of local extinctions were few, we found an effect of connectivity, which may suggest a so called 'rescue effect', i.e. that local population are rescued from extinction by immigration (Brown & Kodric-Brown, 1977).

The population growth rate (R) was lower in hectare grid cells with relatively high population density in 2019. This may suggest a density dependence (e.g. Marini & Zalucki, 2017), where densely populated grid cells cannot increase much compared to grid cells that were less densely populated the year before. The population growth rate was also affected by grid cell connectivity, and it was higher in hectare cells surrounded by densely populated grid cells in the preceding year (2019). This may suggest that movements also on a relatively small scale are restricted, which is also evident from the recaptures in all 3 years. Most individuals were

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recaptured within a few 100 m from the grid cell it was first found in (Figure S2).

Conclusions and implications for conservation

We show that the threatened marsh fritillary is able to recover quickly after major population declines due to extreme weather, which is promising in times of climate change when the frequency of extreme weather events can be expected to increase (e.g. Christidis et al., 2015; Meehl & Tebaldi, 2004; Ummenhofer & Meehl, 2017). However, it should be remembered that our patch network is relatively large and well connected. Smaller and more fragmented metapopulations may be less resilient (Oliver et al., 2013, 2015; Piessens et al., 2009). Based on the population dynamics in our study, fragmentation affects recovery, as all three measures of population dynamics (colonisations, extinctions, and population growth rates) depended on connectivity. It is, thus, important to maintain and preferably increase the connectivity throughout the patch network to enhance the resilience after extreme weather events. This does not necessarily imply creation of more physical connections, such as corridors and steppingstones, but could just as well be improvement of the quality of existing habitat. Increased quality should result in larger and more stable source populations (which is an important part of connectivity, see Equation 1). In our study landscape this may rather easily be achieved by reducing the grazing pressure (Johansson et al., 2019, 2020), which also seems warranted for other similar species (e.g. Johansson et al., 2017; Kruess & Tscharntke, 2002).

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CONFLICT OF INTEREST

The authors do not have any conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Victor Johansson, Oskar Kindvall, John Askling and Markus Franzén originally formulated the idea and developed methodology, Oskar Kindvall, John Askling, Demieka Seabrook Säwenfalk, Hannah Norman and Markus Franzén conducted fieldwork, Victor Johansson performed statistical analyses, and Victor Johansson, Oskar Kindvall, John Askling, Demieka Seabrook Säwenfalk, Hannah Norman and Markus Franzén wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author on request

REFERENCES

Adams, A.W. (1955) *Succisa pratensis* Moench. *Journal of Ecology*, 43, 709–718.

Anthes, N., Fartmann, T., Hermann, G. & Kaule, G. (2003) Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine *Euphydryas aurinia* colonies. *Journal of Insect Conservation*, 7, 175–185.

Bauerfeind, S.S. & Fischer, K. (2014) Simulating climate change: temperature extremes but not means diminish performance in a widespread butterfly. *Population Ecology*, 56, 239–250.

Bergen, E.v., Dallas, T., DiLeo, M.F., Kahilainen, A., Mattila, A.L.K., Luoto, M. et al. (2020) The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation. *Conservation Biology*, 34, 1503–1511.

Betzholtz, P.-E., Ehrig, A., Lindeborg, M. & Dinnétz, P. (2007) Food plant density, patch isolation and vegetation height determine occurrence in a Swedish metapopulation of the marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (*Lepidoptera*, *Nymphalidae*). *Journal of Insect Conservation*, 11, 343–350.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445–449.

Bulman, C.R., Wilson, R.J., Holt, A.R., Bravo, L.G., Early, R.I., Warren, M.S. et al. (2007) Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. *Ecological Applications*, 17, 1460–1473.

Carlsson, A. & Kindvall, O. (2001) Spatial dynamics in a metapopulation network: recovery of a rare grasshopper *Stauroderus scalaris* from population refuges. *Ecography*, 24, 452–460.

Cassel-Lundhagen, A. & Sjögren-Gulve, P. (2007) Limited dispersal by the rare scarce heath butterfly—potential consequences for population persistence. *Journal of Insect Conservation*, 11, 113–121.

Christidis, N., Jones, G.S. & Stott, P.A. (2015) Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nature Climate Change*, 5, 46–50.

De Palma, A., Dennis, R.L.H., Brereton, T., Leather, S.R. & Oliver, T.H. (2017) Large reorganizations in butterfly communities during an extreme weather event. *Ecography*, 40, 577–585.

Englund, G. & Hambäck, P.A. (2007) Scale dependence of immigration rates: models, metrics and data. *Journal of Animal Ecology*, 76, 30–35.

Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C.L. & Murphy, D.D. (2002) Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology*, 16, 706–716.

Franzén, M. & Nilsson, S.G. (2010) Both population size and patch quality affect local extinctions and colonizations. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 79–85.

Gutbrodt, B., Mody, K. & Dorn, S. (2011) Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos*, 120, 1732–1740.

Hanski, I. (1999) *Metapopulation ecology*. Oxford, UK: Oxford University Press.

Harrison, S., Murphy, D.D. & Ehrlich, P.R. (1988) Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *The American Naturalist*, 132, 360–382.

Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, 9, 72–77.

Hodgson, J.A., Moilanen, A., Wintle, B.A. & Thomas, C.D. (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48, 148–152.

17524598, 2022, 5, Downloaded from https://resjournals.onlinelibrary.wiley.com/doi/10.1111/icad.12574 by Statens Beredning, Wiley Online Library on [04/11/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hooftman, D.A., van Kleunen, M. & Diemer, M. (2003) Effects of habitat fragmentation on the fitness of two common wetland species, *Carex davalliana* and *Succisa pratensis*. *Oecologia*, 134, 350–359.

Hula, V., Konvička, M., Pavlicko, A. & Fric, Z. (2004) Marsh fritillary (*Euphydryas aurinia*) in The Czech Republic: monitoring, metapopulation structure, and conservation of an endangered butterfly. *Entomologica Fennica*, 15, 231–241.

Johansson, V., Kindvall, O., Askling, J. & Franzén, M. (2019) Intense grazing of calcareous grasslands has negative consequences for the threatened marsh fritillary butterfly. *Biological Conservation*, 239, 108280.

Johansson, V., Kindvall, O., Askling, J. & Franzén, M. (2020) Extreme weather affects colonization-extinction dynamics and the persistence of a threatened butterfly. *Journal of Applied Ecology*, 57, 1068–1077.

Johansson, V., Knape, J. & Franzén, M. (2017) Population dynamics and future persistence of the clouded Apollo butterfly in southern Scandinavia: the importance of low intensity grazing and creation of habitat patches. *Biological Conservation*, 206, 120–131.

Junker, M. & Schmitt, T. (2010) Demography, dispersal and movement pattern of *Euphydryas aurinia* (*Lepidoptera*: *Nymphalidae*) at the Iberian Peninsula: an alarming example in an increasingly fragmented landscape? *Journal of Insect Conservation*, 14, 237–246.

Kindvall, O. (1995) The impact of extreme weather on habitat preference and survival in a metapopulation of the bush cricket *Metrioptera bicolor* in Sweden. *Biological Conservation*, 73, 51–58.

Kindvall, O. (1996) Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology*, 77, 207–214.

Konvicka, M., Hula, V. & Fric, Z. (2003) Habitat of pre-hibernating larvae of the endangered butterfly *Euphydryas aurinia* (*Lepidoptera*: *Nymphalidae*): what can be learned from vegetation composition and architecture? *European Journal of Entomology*, 100, 313–322.

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, 16, 1570–1580.

Lei, G.-C. & Hanski, I. (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. *Oikos*, 78, 91–100.

Long, O.M., Warren, R., Price, J., Brereton, T.M., Botham, M.S. & Franco, A.M.A. (2017) Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology*, 86, 108–116.

Maes, D. & Van Dyck, H. (2001) Butterfly diversity loss in Flanders (North Belgium): Europe's worst case scenario? *Biological Conservation*, 99, 263–276.

Marini, L. & Zalucki, M.P. (2017) Density-dependence in the declining population of the monarch butterfly. *Scientific Reports*, 7, 13957.

Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A. et al. (2019) Conservation implications of ecological responses to extreme weather and climate events. *Diversity and Distributions*, 25, 613–625.

McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences*, 99, 6070–6074.

Meehl, G.A. & Tebaldi, C. (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, 305, 994–997.

Neilson, E.W., Lamb, C.T., Konkolics, S.M., Peers, M.J.L., Majchrzak, Y.N., Doran-Myers, D. et al. (2020) There's a storm a-coming: ecological resilience and resistance to extreme weather events. *Ecology and Evolution*, 10, 12147–12156.

Nice, C.C., Forister, M.L., Harrison, J.G., Gompert, Z., Fordyce, J.A., Thorne, J.H. et al. (2019) Extreme heterogeneity of population response to climatic variation and the limits of prediction. *Global Change Biology*, 25, 2127–2136.

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, 13, 473–484.

Oliver, T.H., Brereton, T. & Roy, D.B. (2013) Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, 36, 579–586.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton, T., Prudhomme, C. & Huntingford, C. (2015) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, 5, 941–945.

Parmesan, C., Root, T.L. & Willig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, 81, 443–450.

Peters, W., Bastos, A., Ciais, P. & Vermeulen, A. (2020) A historical, geographical and ecological perspective on the 2018 European summer drought. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, 20190505.

Piessens, K., Adriaens, D., Jacquemyn, H. & Honnay, O. (2009) Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia*, 159, 117–126.

Ranius, T., Bohman, P., Hedgren, O., Wikars, L.-O. & Caruso, A. (2014) Metapopulation dynamics of a beetle species confined to burned forest sites in a managed forest region. *Ecography*, 37, 797–804.

R Core Team. (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schtickzelle, N., Choutt, J., Goffart, P., Fichefet, V. & Baguette, M. (2005) Metapopulation dynamics and conservation of the marsh fritillary butterfly: population viability analysis and management options for a critically endangered species in Western Europe. *Biological Conservation*, 126, 569–581.

Schwarz, C.J. & Arnason, A.N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, 52, 860–873.

Smee, M., Smyth, W., Tunmore, M., ffrench-Constant, R & Hodgson, D. (2011) Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (*Euphydryas aurinia*) in SW England. *Journal of Insect Conservation*, 15, 153–163.

SMHI. (2018). SMHI summary annual report 2018.

Suggitt, A.J., Wilson, R.J., Isaac, N.J.B., Beale, C.M., Auffret, A.G., August, T. et al. (2018) Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, 8, 713–717.

Thomas, C.D. & Jones, T.M. (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, 62, 472–481.

Thomas, C.D., Singer, M.C. & Boughton, D.A. (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *The American Naturalist*, 148, 957–975.

Ummenhofer, C.C. & Meehl, G.A. (2017) Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 372, 20160135.

Swaay, C. van, Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašic, M., Settele, J., Verovnik, R., Verstrael, T., Warren, M., Wiemers, M., & Wynhoff, I. (2010) European Red List of butterflies.

Wahlberg, N., Klemetti, T. & Hanski, I. (2002) Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography*, 25, 224–232.

Warren, M.S., Maes, D., Swaay, C.A.M.v., Goffart, P., Dyck, H.V., Bourn, N. A.D. et al. (2021) The decline of butterflies in Europe: problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences*, 118, e2002551117.

White, T.C.R. (2009) Plant vigour versus plant stress: a false dichotomy. *Oikos*, 118, 807–808.

Zimmermann, K., Blazkova, P., Cizek, O., Fric, Z., Hula, V., Kepka, P. et al. (2011) Demography of adults of the marsh fritillary butterfly, *Euphydryas aurinia* (*Lepidoptera*: *Nymphalidae*) in The Czech Republic: patterns across sites and seasons. *European Journal of Entomology*, 108, 243–254.

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Zimmermann, K., Fric, Z., Jiskra, P., Kopeckova, M., Vlasanek, P., Zapletal, M. et al. (2011) Mark-recapture on large spatial scale reveals long distance dispersal in the Marsh Fritillary, *Euphydryas aurinia*. *Ecological Entomology*, 36, 499–510.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Table S1 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.

Figure S1. The distribution of distances to nearest occupied patch for all colonised patches between 2019 and 2020.

Figure S2. The distribution of the total number (from 2017, 2019 and 2020) of observed movements (n = 614) between hectare grid cells (based on the grid cell centroids) in the subset of patches used for capture-mark-release studies (see Figure 1).

Figure S3. The average monthly precipitation in May–July from 1860 to 2020 (whole line) close to the study area. Horizontal broken line shows the average monthly precipitation (40.1 mm) for the entire period and the dotted lines the 95% confidence limits.

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