



The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation

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Abstract: The ecological impacts of extreme climatic events on population dynamics and community composition are profound and predominantly negative. Using extensive data of an ecological model system, we tested whether predictions from ecological models remain robust when environmental conditions are outside the bounds of observation. We observed a 10-fold demographic decline of the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation on the Åland islands, Finland in the summer of 2018 and used climatic and satellite data to demonstrate that this year was an anomaly with low climatic water balance values and low vegetation productivity indices across Åland. Population growth rates were strongly associated with spatiotemporal variation in climatic water balance. Covariates shown previously to affect the extinction probability of local populations in this metapopulation were less informative when populations were exposed to severe drought during the summer months. Our results highlight the unpredictable responses of natural populations to extreme climatic events.

Keywords: climate change, drought, extinction, extreme climatic events, metapopulation dynamics, population decline

El Efecto de la Sequía Estival sobre la Previsibilidad de las Extinciones Locales en una Metapoblación de Mariposas

Resumen: Los impactos ecológicos de los eventos climáticos extremos sobre las dinámicas metapoblacionales y la composición de la comunidad son profundos y predominantemente negativos. Con los extensos datos de un sistema de modelos ecológicos probamos si las predicciones de los modelos ecológicos todavía son sólidos cuando las condiciones ambientales se encuentran fuera de los límites de observación. Observamos una declinación demográfica ocurrir diez veces en la metapoblación de la mariposa *Melitaea cinxia* en las Islas Åland de Finlandia durante el verano de 2018. Usamos datos climáticos y satelitales para demostrar que ese año fue una anomalía al contar con valores bajos de balance hídrico e índices bajos de productividad de la vegetación en todas las islas. Las tasas de crecimiento poblacional estuvieron fuertemente asociadas con la variación espaciotemporal del balance hídrico climático. Las covarianzas que previamente han afectado a la probabilidad de extinción de las poblaciones locales de esta metapoblación fueron menos informativas cuando las poblaciones estuvieron expuestas a sequías severas durante los meses de verano. Nuestros resultados resaltan las respuestas impredecibles de las poblaciones naturales ante los eventos climáticos extremos.

Palabras Clave: cambio climático, declinación poblacional, dinámicas metapoblacionales, eventos climáticos extremos, extinción, sequía

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摘要: 极端气候事件会对种群动态和群落组成产生深远的生态影响,且主要为负面影响。本研究利用生态模型系统的大量数据,测试了在环境条件超出观测范围时,生态模型的预测结果是否仍然稳健。我们观测到在 2018 年夏天,芬兰奥兰群岛的庆网蛱蝶 (*Melitaea cinxia*) 集合种群的种群数量下降了十倍,同时气候和卫星数据表明奥兰群岛当年出现了气候异常,气候水平衡值和植被生产力指数都很低。种群增长率与气候水平衡的时空变化密切相关。当种群面临夏季严重干旱时,之前研究发现在这个集合种群中会影响当地种群灭绝概率的协变量不再能提供丰富信息。我们的研究结果强调了自然种群会对极端气候事件产生不可预测的响应。【翻译:胡怡思;审校:聂永刚】

关键词: 气候变化, 极端气候事件, 干旱, 集合种群动态, 种群下降, 灭绝

Introduction

One of the major challenges in conservation science is to identify the species and populations that are most vulnerable to extinction. Long-term monitoring of ecological model systems, both at local and global scales, has facilitated conservation objectives by identifying the factors affecting population declines and extinctions (Hanski et al. 1995; Pimm et al. 2014; Dornelas et al. 2019). Ecological models aiming to improve understanding of population dynamics in temporally varying environments have been employed to shed light on which regions should receive priority for conservation and to predict which species and populations are most vulnerable (e.g., Franklin et al. 2014; Oliver et al. 2015). In temporally autocorrelated environments, where conditions tend to change gradually, these predictions may be reliable over short time scales and can, therefore, be used to make conservation more effective.

When populations are exposed to conditions that are beyond the normal range, such as in the case of extreme climatic events (ECEs), the factors underlying population dynamics may be less relevant and consequently predictions relying on these factors less reliable. Extreme climatic events have increased in recent decades in frequency and in intensity and duration (Jentsch et al. 2007; Coumou & Rahmstorf 2012; Ummenhofer & Meehl 2017). Recent studies demonstrate that even a single ECE, such as a flood or a drought, can have profound impacts on natural populations (Bailey & van de Pol 2016; Altwegg et al. 2017; Grant et al. 2017) and can even cause the collapse of an entire ecosystem (Anderson et al. 2017; Harris et al. 2018). For example, a pan-tropical episode of coral bleaching, triggered by a marine heatwave in 2016, eradicated over 60% of the coral communities in the Great Barrier Reef (Hughes et al. 2017).

Assessments of ECEs and their impacts are generally conducted by performing perturbation experiments (e.g., Bokhorst et al. 2008; Pansch et al. 2018) or by opportunistically taking advantage of a rare event (e.g., Smith 2011; Grant et al. 2017; Latimer & Zuckerman 2019). The latter type often concentrate on a single population and relatively small spatial scales or lack long-term ecological monitoring of the system prior to the ECE (but see Thibault & Brown 2008; Campbell-Staton

et al. 2017). We studied a dramatic demographic decline of the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation on the Åland archipelago in southwestern Finland due to a severe drought in the summer of 2018. This iconic butterfly metapopulation has become an important ecological model system for studying factors affecting local population dynamics and extinction risks in fragmented landscapes (Hanski 1998; Ovaskainen & Saastamoinen 2018). Ongoing systematic monitoring of the system provides a unique opportunity to improve the understanding of how large spatially structured natural populations respond to extreme climatic conditions and to study how ECEs affect the value of predictive models.

Since 1993, the occupancy and abundance of local populations of the butterflies, across a network of about 4400 dry meadows, have been systematically monitored. Estimates of local population sizes are acquired during autumn when all potential habitat patches are surveyed for the presence of the winter nests (details are given in Ojanen et al. [2013]). Despite increasing year-to-year fluctuations (Hanski & Meyke 2005; Tack et al. 2015), the overall size of the metapopulation has remained relatively stable; about 20% of available habitat patches are occupied each year. Survey data have been used to demonstrate that the long-term persistence and population dynamics (local extinctions and recolonizations) of the metapopulation largely depend on the number of available habitat patches, their area, and their spatial configuration (i.e., connectivity) (Hanski & Ovaskainen 2000; Dallas et al. 2019). Other key factors affecting local extinctions and population dynamics are habitat quality (e.g., number of host plants) (Harrison et al. 2011; Schulz et al. 2019) and genetic characteristics of individuals (Saccheri et al. 1998; Niitepöld & Saastamoinen 2017).

Annual changes in population size across the metapopulation are mainly driven by the growth rates of local populations over summer ($r = 0.96$), rather than being associated with variation in overwinter mortality ($r < 0.01$) (Tack et al. 2015). Moreover, we recently demonstrated that variation in population growth rates is strongly associated with variation in temperature

and precipitation across the habitat patch network (Kahilainen et al. 2018). Spatial variability in these climatic conditions contributes to the overall stability of the metapopulation by ensuring that local extinctions are compensated by stable or increased population sizes and colonization rates in other areas of the metapopulation. As climatic conditions have become more homogeneous across Åland in the last decade, the Glanville fritillary metapopulation has become more spatially synchronous in its demographic dynamics (Kahilainen et al. 2018), potentially making it more vulnerable to large-scale environmental perturbations (Hanski & Woiwod 1993). We sought to identify the key anomalies that occurred in the summer of 2018 on the Åland islands and demonstrate that exposure to these extremes was sufficient to drive the regional population declines of the butterfly observed across the metapopulation. We also explored how the ECE affected the performance of ecological models by testing whether the covariates that had been identified previously as affecting local extinctions in this system remained informative under extreme climatic conditions.

Methods

Long-Term Data Survey

On the Åland islands, the Glanville fritillary inhabits dry meadows and pastures with at least 1 of its 2 larval host plants present, ribwort plantain (*Plantago lanceolata*) or spiked speedwell (*Veronica spicata*). The entire study region (50 × 70 km) has been mapped for potential habitat patches (total 4415 patches as of September 2015). The population occupancy (presence of a larval nest within a habitat patch) and abundance (total number of larval nests within a habitat patch) are assessed annually when the larvae have entered the overwintering stage in their conspicuous larval nests. All the habitat patches on the archipelago are inspected with the help of approximately 50 field assistants. In the field, the locations of the larval nests are marked and data are stored into the Earth-Cape database (Ojanen et al. 2013). The occupancy and abundance data are composed of raw counts, which is a function of population size but also of detection probability. Estimates from control surveys conducted before 2018 suggest that the presence of the butterfly may be missed in up to 15% of the occupied patches; nondetection mainly occurs with very small populations (Hanski et al. 2017).

Climatic and Vegetation Index Data

Normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) values were derived from Moderate Resolution Imaging Spectrometer

(MODIS) (resolution 250 m) (Guay et al. 2014). Both NDVI and EVI data are available on a 16-day basis for a 2000–2018. Data were derived from bands 1 and 2 of the MODIS on board NASA's Terra satellite. A time series of NDVI and EVI observations can be used to examine the dynamics of the growing season and ecosystem function and to monitor phenomena, such as droughts. The EVI is an optimized vegetation index designed to enhance the vegetation signal by improving sensitivity in high biomass regions and improving vegetation monitoring through a decoupling of the canopy background signal and a reduction in atmosphere influences. We calculated NDVI and EVI values for each of the 4415 habitat patches from April to August. Monthly temperature and precipitation values and water balance (precipitation - potential evaporation) were derived from Jomala weather station (60.18° N, 19.99° E, 11 m asl) database. Climatic water balance was calculated as precipitation minus potential evapotranspiration. Potential evapotranspiration is the amount of evaporation and transpiration that would occur if a sufficient water source were available and was calculated using the Penman-Monteith equation (Guo et al. 2016). Based on values of climatic water balance, a time-series of the standardized precipitation-evapotranspiration index (SPEI) was calculated (Vicente-Serrano et al. 2009). An important advantage of the SPEI is that it can be computed at different time scales (i.e., it is possible to incorporate the influence of a variable range of past values in the computation). For example, an SPEI-3 value implies that data from the current month and those of the past 2 months were used to compute the drought index.

Population Growth Rate Model

Following an analysis pipeline developed for the Glanville fritillary metapopulation (Kahilainen et al. 2018), we fitted a Bayesian linear mixed-effects model to study the association between weather conditions and population growth rate at the regional scale. Instead of using temperature and precipitation values, we used monthly water balance indices, which are more explicitly associated with drought conditions. These values were computed for the whole study area at the spatial resolution of 1 km² based on national climate station observations from 1993 to 2018. National observations were supplemented by records from the surrounding countries, and kriging interpolation was applied to account for topography and water bodies (Aalto et al. 2016). We focused on the dynamics of groups of spatially clustered semi-independent habitat patch networks (SINs) (Hanski et al. 2017) instead of local populations because populations in individual patches frequently go extinct and estimates of population growth at this spatial scale would, therefore, be very heterogeneous. Furthermore, we focused on a subset of 33 SINs that

are considered viable in terms of the spatially explicit metapopulation theory and were occupied most of the study period (Hanski et al. 2017). Yearly population growth rates (r) were derived as:

$$r_{\text{SIN},t} = \log \left[\frac{(N_{\text{SIN},t} + 1)}{(N_{\text{SIN},t-1} + 1)} \right], \quad (1)$$

where $N_{\text{SIN},t}$ is the number of overwintering larval nests found in an SIN in the fall of year t . A single nest was added to both the numerator and the denominator to account for the occasional event that all patches in an SIN were unoccupied. We then extracted water balance data for each SIN (see Climatic and Vegetation Index Data in Methods) and fitted a linear mixed model for population growth rate with the water balance values across different life-history stages of the butterfly as covariates (Radchuk et al. 2013). To reduce the number of variables in the model and keep those from months known to be of importance for population growth (Tack et al. 2015; Kahilainen et al. 2018), an averaged water balance value (September–February) was included to reflect the conditions during the diapause period. In the model, we included a random intercept and a first-order autocorrelation term for each SIN. We implemented the model in Stan statistical modeling platform (Carpenter et al. 2017) and used R packages brms (version 2.7.0; Bürkner 2017) and RStan (2.17.3; Stan Development Team 2018) as its interface. For further details regarding the analysis pipeline and implementation of the model, see Kahilainen et al. (2018). From the model, we then obtained fitted annual growth rates for each of the 33 SINs included in the data and compared these with the observed growth rate values.

Extinction Probability Model

We fitted a linear mixed-effect model (logit link function) with data on binary patch extinction calculated for each year of the survey from 1999 to 2018 to examine whether the high extinction rates in 2018 could be attributable to covariates previously recognized as affecting the extinction probability of local populations (Hanski et al. 1995; Saccheri et al. 1998). Year was included as a random effect. Environmental variables included as fixed effects were the natural logarithm of patch area, amount of the dominant host plant in each patch estimated on a scale of 1–3, percentage of host plants that were dried out, and percentage of the patch that was grazed (see Ojanen et al. [2013] for details). Historical contingency was accounted for by considering the natural logarithm of the number of larval nests in each focal patch in the previous year and the number of larval nests in the neighborhood of each focal patch in the previous year, defined as:

$$S_i = \log \left(\sum e^{d_{ij}} N_j \right), \quad (2)$$

where d_{ij} is the distance between focal patch i and j and N_j is the number of nests in patch j in the previous year. We trained the model with 80% of the data, and subsequently assessed model performance—quantified using the area under the receiver operating characteristic (AUC)—on the remaining 20% of the data. As a general rule, an AUC score of ≤ 0.7 is considered poor discrimination, $0.7 \leq \text{AUC score} < 0.8$ is considered fair, and $0.8 \leq \text{AUC score} < 0.9$ is considered good discrimination (Swets 1988). This procedure was repeated 10 times to assess the sensitivity of model performance to the train-test split.

Results

Demographic Declines across the Butterfly Metapopulation in 2018

Despite systematic surveying efforts, an all-time low of only 91 larval nests were recorded during the autumn survey in 2018 (average number of nests recorded each year was 2750) (Fig. 1). The number of occupied habitat patches was an order of magnitude lower than in any average year ($n = 54$) (Fig. 1a), and only a single colonization event was recorded. The number of larval nests recorded within the occupied habitat patches was approximately 65% below average (Supporting Information).

Deviations from Past Climatic Conditions

Like many regions in Northern Europe, the habitat patches on the Åland Islands received remarkably low levels of precipitation in the summer of 2018. The effect of this shortage was intensified by record-breaking temperatures (Supporting Information), resulting in the lowest climatic water balance values on record at the Jomala weather station in Åland (1960–2018; Fig. 2a). Consequently, the summer of 2018 was anomalous also in terms of primary productivity. Satellite-derived vegetation indices (NDVI and EVI), available since 2000, showed low levels of vegetation productivity within the pastures and dry meadows inhabited by the butterfly in 2018 (Fig. 2b). The latter likely also reflected reduced host-plant quality and availability during the periods when the post- and prediapause butterfly larvae were feeding (Fig. 1b).

Drought and Regional Population Declines

Overall, monthly water balance indices—especially the water deficits during May and July—were highly associated with population declines at the SIN level (Fig. 3 & Supporting Information). With few exceptions, the model residuals for 2018 were negative, indicating that

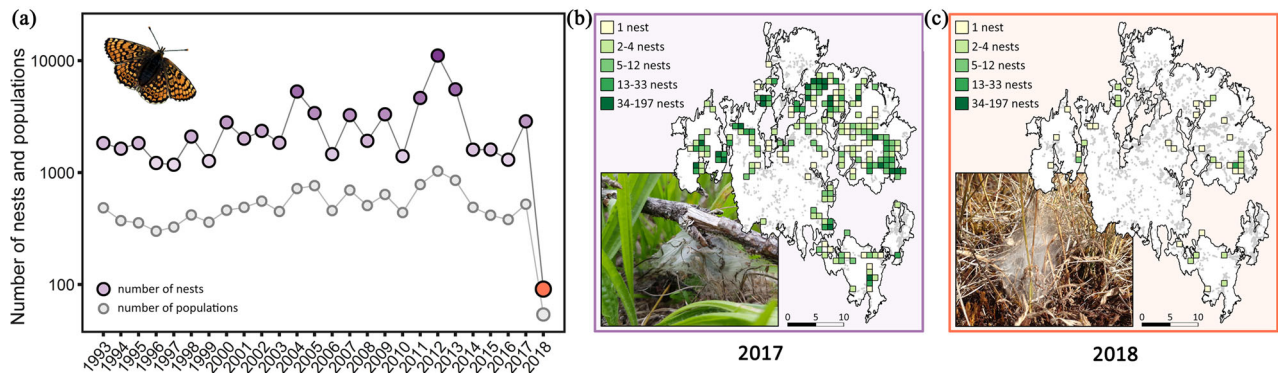


Figure 1. (a) Population dynamics of the Glanville fritillary butterfly metapopulation on the Åland islands, Finland (y-axis, 10-log scale; colored circles, nest counts; gray circles, occupied habitat patch counts; photograph, female Glanville fritillary butterfly by Tari Haabtela) and the number of larval nests per square kilometer (colored squares) found during autumn surveys in (b) 2017 under average climatic conditions (gray circles, surveyed but unoccupied habitat patches; photograph, larval nests on a typical *Plantago lanceolata* host plant by Ana Salgado) and (c) 2018 under extreme climatic conditions (i.e., drought) (gray circles, surveyed but unoccupied habitat patches; photograph, larval nests on *P. lanceolata* affected by drought by Felix Sperling).

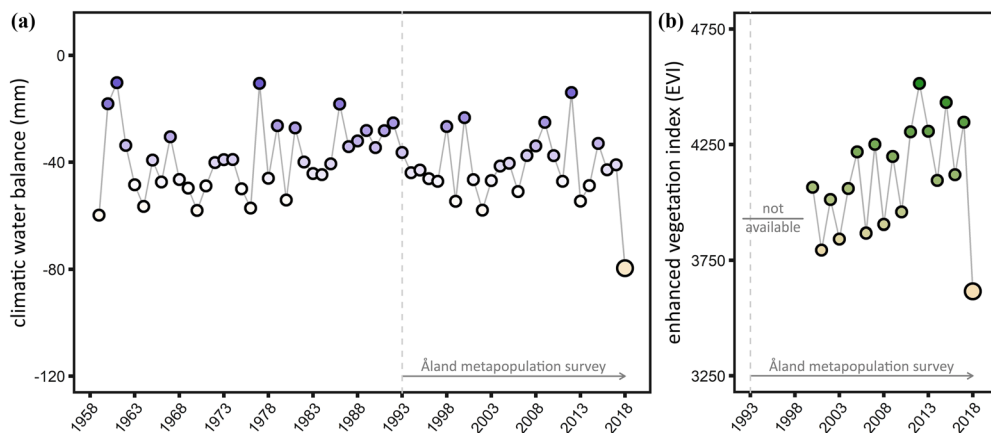


Figure 2. On the Åland islands, mean (a) water balance (precipitation - potential evapotranspiration) in April–August 1961–2018 derived from the Jomala climate station database and (b) enhanced vegetation index (measure of plant productivity) in the 4415 habitat patches of the Glanville fritillary butterfly in June–August 2000–2018 derived from bands 1 and 2 of the MODIS on the Terra satellite. All climatic variables and monthly values are represented in Supporting Information.

the observed declines in most SINs were more severe than suggested by the model fit (Fig. 3). Indeed, SIN-level population declines in 2018 were among the most dramatic ones observed since the start of the annual survey; nearly, 80% of the growth rate values fell within the lowest 5th percentile (Fig. 3 & Supporting Information).

Summer Drought and Predictability of Local Extinctions

We confirmed the previously identified factors affecting extinction probability of local populations in this system: the probability of extinction was lower in habi-

tat patches that were large and well connected. Patches with low population densities in the previous year, with low availability of host plants, or used for livestock grazing had higher extinction probabilities (Supporting Information). The mean AUC score for our environmental extinction model across the 20 years was 0.76, which implies that model covariates predicted the extinction of a local population reasonably well. Model covariates were more likely to predict the extinction probability correctly in the years prior to the ECE of 2018 (Fig. 4a). The AUC scores varied significantly across years; the lowest values were observed in years characterized by water deficits during summer (Fig. 4b).

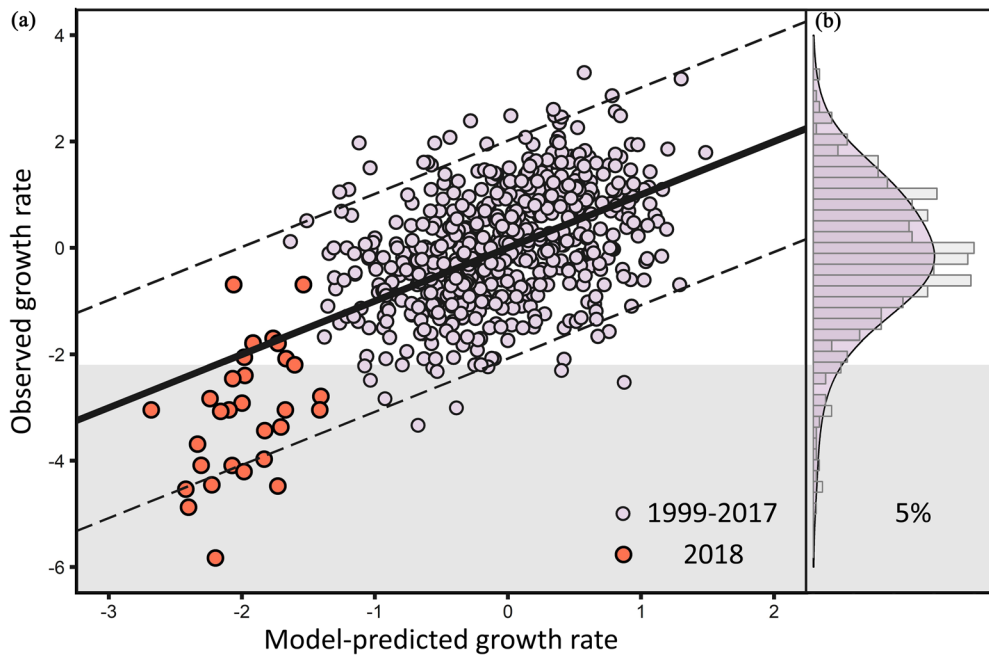


Figure 3. (a) Relationship between observed and fitted population growth rates of the Glanville fritillary butterfly populations in the Åland islands from a linear mixed-effects model with water balance values across the butterfly's life cycle as predictors of population growth rate at the semi-independent network level (light purple circles, observations for 1999–2017; red circles, observations for 2018; dashed lines, 95% interval of model residuals) and (b) distribution of population growth rate values from 1999 to 2018 (shaded area, values in the lowest 5% range of the population growth rate distribution).

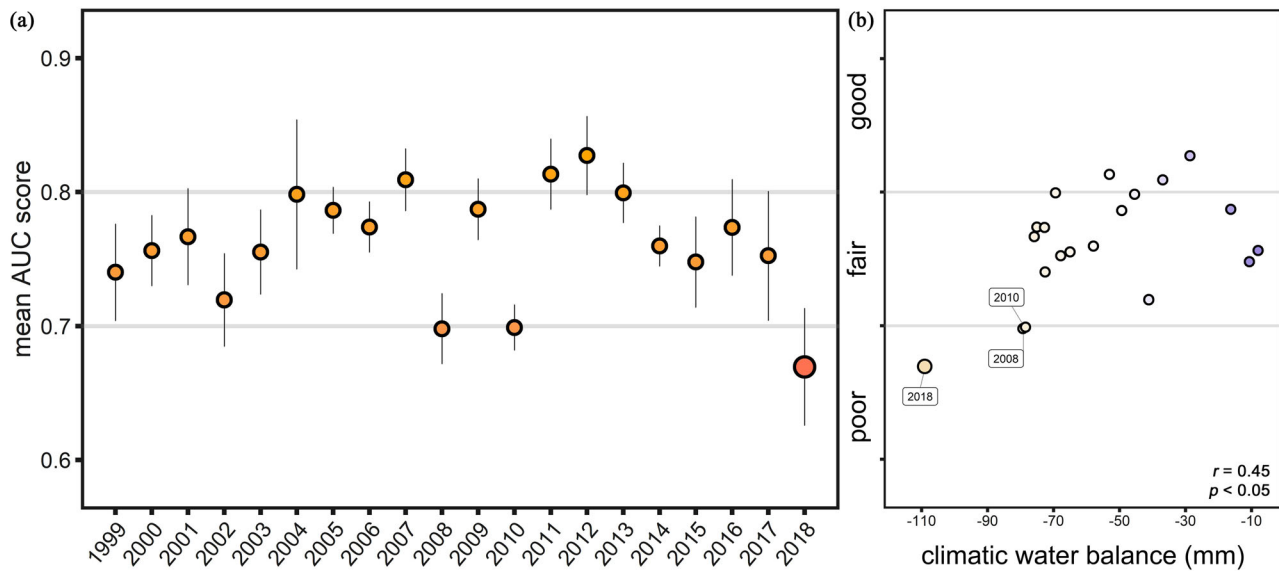


Figure 4. (a) The predictability of local extinctions in a butterfly metapopulation—quantified using the area under the receiver operating characteristic curve (AUC)—for 1999–2017 (model training, 10 random subsets with 80% of the data; plotted values, mean; error bars, SE; discrimination: poor; $AUC \leq 0.7$; fair, $0.7 \leq AUC < 0.8$; good, $0.8 \leq AUC < 0.9$ [Swets 1988]) and (b) AUC as a function of the mean water balance (precipitation - potential evapotranspiration) in May–July (r , Spearman's rho). The predictability of local extinctions is low for years characterized by water deficits during summer.

Discussion

The ongoing climate crisis is expected to result in a rapid increase in the frequency, intensity, and duration of ECEs (e.g., Sun et al. 2014; Fischer & Knutti 2015). Owing to the profound impacts these ECEs can have on ecological functioning, the vulnerability of natural populations to the impacts of climate change may be severely underestimated (Anderson et al. 2017; Ummenhofer & Meehl 2017).

The Åland islands, like many other regions across the northern hemisphere, underwent a severe drought in the summer of 2018. Using extensive long-term data of the spatially structured natural population of the Glanville fritillary butterfly, we demonstrated that both the climatic conditions during the summer and biological response of the metapopulation exceeded the 5% threshold values typically used to define ECEs (van de Pol et al. 2017). The majority of studies investigating the impacts of ECEs have focused on the ability of organisms to cope with the direct effects of the extreme environmental conditions. For example, the overwintering life stages of some species of butterfly are very sensitive to warm winter temperatures (Radchuk et al. 2013; Roland & Matter 2016). Although an organism's critical physiological limits are likely important risk factors (Hoffmann & Sgrò 2018), extinctions of local populations could also be triggered indirectly (Maron et al. 2015). Our estimates of the occupancy and abundance of local populations across the archipelago were based on data collected in the autumn; hence, they only represent populations that survived the potentially harsh summer conditions. Therefore, we could not infer whether the population declines and local extinctions were triggered directly by the arid conditions or indirectly by, for example, climate-induced restrictions in resource availability (Maron et al. 2015; Johansson et al. 2020). Nonetheless, using satellite-derived vegetation indices, we found that productivity was substantially reduced within the habitat patches of the butterflies in 2018. These data suggest that the severe drought negatively affected the quality and availability of the host plants of these herbivorous insects, making resources scarce when demands were high. These results are in line with detailed observations made in 12 focal patches in 2018, where despite observing large numbers of clutches in early summer, only 2 larval nests were found in autumn (Salgado et al. 2020). The host plants are known to recover quickly from drought, and the proportion of desiccated host plants in the habitat, as assessed during the survey in autumn, is a poor predictor of plant condition during larval development (Tack et al. 2015).

We explored whether the strong deviations from usual conditions influenced our ability to forecast the short-term biological response of the metapopulation at regional and local scales. We demonstrated that the population growth rates at regional scales (i.e., level of SINKS

[Hanski et al. 2017]) were positively associated with climatic water balance during summer months (Supporting Information). In other words, population sizes of this drought-sensitive butterfly species declined in years characterized by water deficits during summer (see also Tack et al. [2015] and Kahilainen et al. [2018]). This result strongly points toward climatic conditions as the key driver of the dramatic decline of the metapopulation in 2018. In addition, we found that the relationship between the climatic variables and the biological response of the metapopulation was primarily linear (i.e., model residuals of 2018 were negative, but generally did not exceed model confidence limits [Fig. 3]) (van de Pol et al. 2017). These results highlight that our detailed understanding of the population dynamics of this ecological system allowed us to—at least in part—forecast the observed population declines in response to the described extreme event.

Although we were able to capture climate-induced changes in dynamics at regional scales, we were less successful in predicting the extinction probabilities of local populations in 2018 (Fig. 4a). In general, the model covariates, such as habitat size and connectivity, were likely to predict the extinction probability correctly. In 2018, even populations inhabiting large and well-connected patches with a high abundance of nests in the previous year went extinct. This suggests that summer droughts, and in particular the extreme climatic conditions of 2018, may force the population over a threshold in which local extinctions are driven by factors other than those highlighted in previous studies of the system (reviewed in Ovaskainen & Saastamoinen [2018]). Hence, uncharacterized ecological variables, such as the water-holding capacity of the patch or the microhabitat heterogeneity within each meadow or pasture, may potentially be important determinants of population persistence under arid environmental conditions. In addition, interactions with other species in the community (e.g., parasitoids or predators) may be different in dry years. Finally, because annual overwinter survival varied from 0.41 to 0.83 (Tack et al. 2015), extending the current models to include variables that capture variation in winter conditions could improve their predictive value. Despite our use of a systematic and methodical protocol, the probability of detecting the presence of the butterfly is lower in very small populations than in large populations (Hanski et al. 2017). Hence, strong climate-induced declines in population sizes may, therefore, contribute to decreased detection rates (and, consequently, an overestimation of the biological response). Other variables, such as reduced nest sizes or shifts in habitat choice, may also negatively affect detectability under climatic extremes. However, our surveying protocol dictates that when a patch is judged unoccupied, it should immediately be resurveyed with the same effort (Ojanen et al. 2013). Owing to this safeguard mechanism, the

majority of the patches were surveyed twice in 2018, reducing the potential influence of the ECE on nest detectability.

The documentation of the demographic crash of the Glanville fritillary metapopulation highlights the vulnerability of natural populations and underscores the importance of long-term monitoring programs to effectively document the consequences of ECEs on species, population, and community dynamics. Our results further demonstrate that ECEs can impede conservation efforts by reducing the value of predictive models (Matter & Roland 2017). For example, even within this extensively understood study system, any effort to potentially mitigate the impacts of the ECE on local populations would likely have failed because we would not have been able to predict which local populations were most vulnerable. The long-term implications of the ECE of 2018 are yet to be realized, but rapid recovery may be possible due to the high fecundity of the species (Saastamoinen 2007). Continuation of the metapopulation survey in the future could, therefore, reveal whether and how the remaining populations bounce back from this rare disruption in extinction-colonization dynamics. This then also provides a unique and exciting opportunity to study the long-term ecological and evolutionary impacts of an ECE in a spatially structured population.

Acknowledgments

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Supporting Information

An overview of the Glanville fritillary metapopulation long-term data (Appendix S1), the meteorological and vegetation index data (Appendix S2), and the estimated coefficients for the population growth rate model (Appendix S3) and the extinction probability model (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than regarding the absence of the material) should be directed to the corresponding author.

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