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Increasing frequency of low summer precipitation synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary butterfly

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Climate change is known to shift species' geographical ranges, phenologies and abundances, but less is known about other population dynamic consequences. Here, we analyse spatio-temporal dynamics of the Glanville fritillary butterfly (*Melitaea cinxia*) in a network of 4000 dry meadows during 21 years. The results demonstrate two strong, related patterns: the amplitude of year-to-year fluctuations in the size of the metapopulation as a whole has increased, though there is no long-term trend in average abundance; and there is a highly significant increase in the level of spatial synchrony in population dynamics. The increased synchrony cannot be explained by increasing within-year spatial correlation in precipitation, the key environmental driver of population change, or in *per capita* growth rate. On the other hand, the frequency of drought during a critical life-history stage (early larval instars) has increased over the years, which is sufficient to explain the increasing amplitude and the expanding spatial synchrony in metapopulation dynamics. Increased spatial synchrony has the general effect of reducing long-term metapopulation viability even if there is no change in average metapopulation size. This study demonstrates how temporal changes in weather conditions can lead to striking changes in spatio-temporal population dynamics.

1. Introduction

Long-term viability of metapopulations is enhanced by independent dynamics in the constituent local populations [1,2]. When local dynamics are independent, decline in the sizes of some populations is compensated for by increase in the sizes of other populations, and hence the size of the metapopulation as a whole remains relatively constant. For this to happen, the spatial scale of environmental stochasticity needs to be small, or otherwise environmental stochasticity needs to be weak and local population dynamics are dominated by demographic stochasticity. If, in contrast, long-range environmental stochasticity is strong, the independence of local dynamics is diminished, the effective number of (independent) local populations is reduced [3] and metapopulation fluctuations increase, which decreases the probability of long-term survival. While rarely quantified for natural systems, theoretical [4] and laboratory [5] studies have highlighted the importance of spatial variation in growth rate in balancing out population fluctuations at the metapopulation level.

Many studies have examined spatial synchrony in population dynamics from a more general perspective, examining the possible causes of synchrony [6–10]. The two causes most discussed are dispersal and spatial autocorrelation in the factors affecting population growth, i.e. spatially correlated environmental stochasticity. Extreme weather events and high amplitude of year-to-year changes in weather across large areas are especially potent in synchronizing dynamics.

Therefore, climate change may influence spatial synchrony of population dynamics, though this has remained little studied. Most ecological studies related to climate change have analysed changes in species' geographical ranges [11–14] and abundances [11,13,15], where the driving forces are thought to be the mean values of climatic variables, typically some measure of temperature. Many recent theoretical [16], modelling [17,18], experimental [17,19–22] and observational [23–25] studies indicate that climatic variability and climatic extremes may have a similar or even stronger impact than the respective mean values on species dynamics. Once again, however, these studies have generally examined the impact of environmental variation on the geographical ranges and mean abundances of species, whereas practically no studies have analysed the impact of climatic variability on more complex aspects of population dynamics, such as the amplitude or spatial synchrony of population dynamics.

Here, we examine the effects of spatial and temporal variation in precipitation on the growth rate of a uniquely well-studied metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) [26]. We report a significant increase in temporal fluctuations of the size of the metapopulation and a striking increase in the spatial extent of synchrony in regional dynamics during 21 years. To explain these patterns, we test two mutually non-exclusive hypotheses. First, the increase in fluctuations and spatial synchrony may be due to increasingly uniform (more spatially correlated) weather conditions driving reduced spatial variation in the growth rate of populations across the metapopulation. Second, the increase in spatial synchrony may be caused by increased year-to-year variation in critical weather conditions, leading to increased frequency of especially unfavourable weather conditions, which may synchronize the dynamics across the metapopulation. Our results support the latter hypothesis.

2. Material and methods

(a) Study system

The Glanville fritillary inhabits a large network of 4000 dry meadows with one or both of its two host plant species, *Plantago lanceolata* and *Veronica spicata*, within an area of 50 × 70 km in the Åland Islands in southwest Finland. The meadows are generally small, with an average area of 0.17 ha (no meadow is greater than 10 ha; [26]). The Glanville fritillary metapopulation has been surveyed annually since 1993 [27]. Every meadow is visited in August–September by 50–70 field assistants, and the conspicuous silken webs spun by larval family groups are counted. The larval groups consist of *ca* 100 full-sibling larvae in the autumn, at the time of the survey, during which the probability of detecting a larval group is around 0.5 [27,28]. The locations of the larval groups are marked with GPS and wooden sticks, which facilitates checking their presence or absence in the following spring to assess over-winter survival.

The Glanville fritillary exhibits classic metapopulation dynamics in the 4000 meadow network [2,26]. Local populations are generally small (median size has been two larval family groups in the 11 487 yearly estimates of local population sizes in 1993–2013) and have a high risk of extinction (annual extinction risk of local populations ranging from 0.19 to 0.60 in 1994–2013; extinction risk is inversely related to population size [2,29]).

The network of 4000 meadows has been subdivided into 86 semi-independent sub-networks with SPOMSIM [30], which uses a hierarchical connectivity-based clustering algorithm. While doing the clustering, we used previously estimated parameter

values ($b = 0.5$, $c = 0.5$ and $q = 1.5$, where b and c define the scaling of emigration and immigration as functions of habitat patch area, respectively, and q is a parameter of the geometric average linkage method used in clustering). Different sub-networks are so isolated from each other that there is only limited dispersal between them [31]. Mark–recapture studies show that the average lifetime dispersal distance is *ca* 1 km [32–34].

(b) Precipitation

Previous studies have shown that larval survival in July is threatened by hot and dry weather that leads to withering of the host plants in the generally dry meadows, while high precipitation in August reduces population growth rate [28,35]. To investigate the impact of spatial variation in rainfall, we used monthly data from the weather radar located in Korppoo, southwest Finland (60°7'42" N, 21°38'34" E). The original data has spatial resolution of *ca* 0.8 km², from which we interpolated an estimate of monthly precipitation for every habitat patch. The radar data were available for the years 1998–2012. The data are most accurate for 2000–2012, because of longer radar maintenance breaks in 1998–1999, but the breaks do not bias the estimate of within-year spatial variation in precipitation. No comparable remote-sensed temperature data are available that would cover the entire patch network, but this is not a big limitation because previous studies indicate that precipitation during summer strongly affects host plant quality and is thereby the critical weather variable [27,28,35].

To model long-term year-to-year dynamics in the size of the entire metapopulation in 1993–2013, for which period we have no matching weather radar data, we used long-term data on monthly average precipitation from the Jomala weather station, which is located near the centre of the main Åland Island (60°10'41.64" N, 19°59'11.95" E).

(c) Plant dryness

Plant dryness was recorded for each meadow during the autumn survey. For each plant population, the field assistants estimated the percentage of *P. lanceolata* individuals that were withered. These data are available for all the years except 1994 and 2011.

(d) Spatial synchrony

We characterized spatial synchrony in population growth rate from one year to another using two different measures. The first measure, which we call metapopulation coherence, characterizes the extent to which annual changes in metapopulation size in the 86 sub-networks compensate each other. We calculated the *per capita* change in the size of the metapopulation in sub-network i as $\Delta_i = \log[(N_{i,t} + 1) / (N_{i,t-1} + 1)]$, where $N_{i,t}$ is the size of the metapopulation in sub-network i in year t . Metapopulation coherence is defined as

$$\text{abs}[\Sigma(\Delta_i)] / \Sigma[\text{abs}(\Delta_i)].$$

The term $\Sigma[\text{abs}(\Delta_i)]$ gives the sum of the absolute values of *per capita* change in the different sub-networks and is used to normalize metapopulation coherence. At the same time, $\Sigma[\text{abs}(\Delta_i)]$ is a convenient measure of the magnitude of metapopulation changes. If changes in different sub-networks occur in different directions, such as illustrated for the year 1997 in figure 1*f*, increasing (positive Δ_i) and decreasing (negative Δ_i) regional changes compensate each other and metapopulation coherence is low. In the opposite case, illustrated by the year 2010 (figure 1*e*), metapopulations in most sub-networks either increase or decrease (as in figure 1*e*), and metapopulation coherence is high. To generate a null distribution for metapopulation coherence in the case when there is no temporal association of the Δ_i values, we calculated metapopulation coherence by sampling a value for each sub-network at a random time and repeated random sampling 10 000 times to

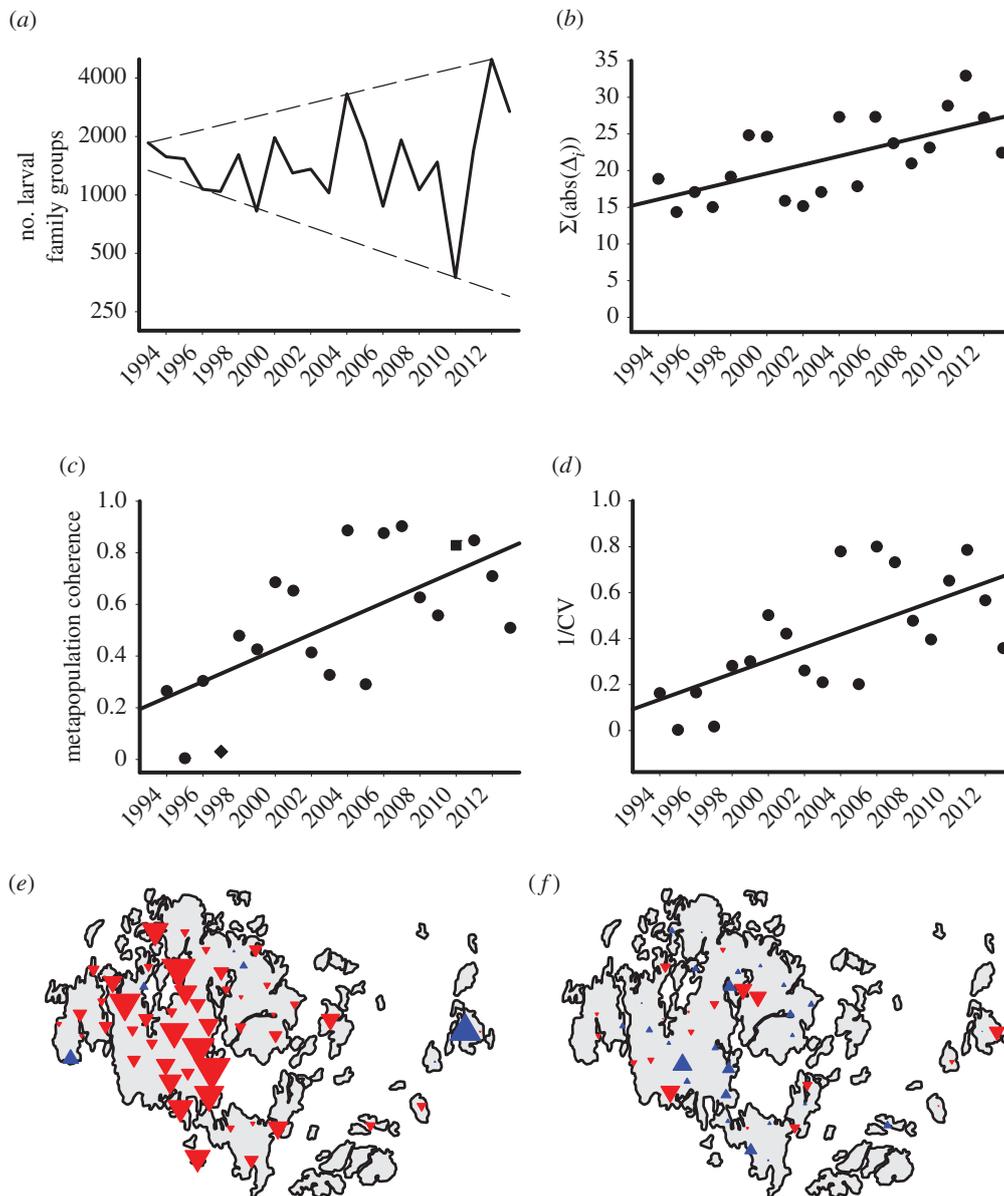


Figure 1. Time series showing increasing fluctuations in the size of the Glanville fritillary metapopulation (a), magnitude of *per capita* changes in 86 sub-networks (b), metapopulation coherence (c) and inverse of CV in *per capita* changes in 86 sub-networks (d). The measures in (c,d) are two complementary measures of spatial synchrony (see §2d). The lower and upper dashed lines in (a) show the 10% and 90% quantile regression lines, respectively. The black solid lines in (b–d) are linear regression lines (all $p < 0.002$). (e,f) Spatial patterns in *per capita* growth rate in the sub-networks in a year of high ((e), 2010, marked with a square in (c)) and in a year with low spatial synchrony ((f), 1997, marked with a diamond in (c)), respectively. Blue and red triangles indicate positive and negative growth rate, respectively. Comparable maps for all the years are presented in the electronic supplementary material, figure S1.

generate a distribution. The upper tail of this distribution gives a threshold for assessing the significance of the observed values.

Our second measure characterizes spatial synchrony as the inverse of the coefficient of variation (CV) calculated for *per capita* changes in abundance from year $t - 1$ to year t in each of the sub-networks. As growth rate can be negative or positive, we report the absolute value of $1/\text{CV}$. This measure of spatial synchrony, which has been previously used by Post & Forchhammer [36] in a comparable context, reflects relative dispersion.

(e) Data analyses

Temporal increase in the amplitude of fluctuations of the metapopulation as a whole was tested with quantile regression using the package *quantreg* [37] in R v. 2.15.1 [38]. We examined the effects of metapopulation size in the previous year ($\log_{10}(N_{t-1})$), log-transformed rainfall in July, log-transformed rainfall in August and the percentage of dry plants on the logarithm of metapopulation change ($\log_{10}(N_t/N_{t-1})$). We selected *a priori* a set of ecologically

plausible models and used the function *model.sel* in the package *MuMIn* v. 1.13.4 to rank the models based on their Akaike information criterion for finite sample sizes (AICc) [39,40]. We evaluated the evidence in favour of each model based on its Akaike weight, which reflects the relative likelihood of the model given the data; as the Akaike weights are normalized across the set of candidate models, they can be interpreted as probabilities [41]. As plant dryness was not recorded in 1994 and 2011 (§2c), we repeated the analysis twice, first for the full set of models and data for 19 years (excluding 1994 and 2011), then for the entire time series of 21 years but excluding models that included plant dryness (see table 1 and the electronic supplementary material, table S1, for the *a priori* models). When analysing the annual change in the size of the metapopulation, we excluded populations not surveyed for the full period (cf. [26]). While calculating spatial variation in growth rate and over-wintering survival, and correlation between growth rate and precipitation, we included those sub-networks in which abundance in year $t - 1$ exceeded 10 larval groups, thus avoiding problems with zero and very small population sizes.

Table 1. The set of *a priori* selected models explaining the log-transformed *per capita* change in metapopulation size in 1993–2013, excluding the years 1994 and 2011 for which no data on plant dryness was available. (K is the number of parameters in the model. Models are ranked based on the difference in AICc values (Δ AICc) between the focal model and the best model in the set. Akaike weights reflect the likelihood of a model relative to all the other models in the set.)

model	K	AICc	Δ AICc	Akaike weight
density dependence + rainfall July	4	2.6	0	0.500
rainfall July	3	3.7	1.11	0.286
density dependence + rainfall July + rainfall August	5	5.9	3.35	0.094
rainfall July + rainfall August	4	6.6	4.09	0.065
density dependence	3	8.0	5.43	0.033
density dependence + plant dryness	4	10.8	8.20	0.008
density dependence + rainfall August	4	11.1	8.52	0.007
intercept only	2	12.5	9.94	0.003
plant dryness	3	13.6	11.02	0.002
rainfall August	3	14.6	12.06	0.001

3. Results

(a) Long-term dynamics

There has been no increasing or decreasing trend in the size of the metapopulation as a whole over the 21 years (figure 1; linear regression: $F_{1,19} = 0.45$, $p = 0.51$), but several statistics show that the amplitude of fluctuations has significantly increased. There is a nearly significant difference in the slopes of the lower and upper quantile regression lines (figure 1a; $p = 0.06$), a highly significant increase in year-to-year changes in the number of larval groups (linear regression: $F_{1,18} = 12.94$, $p = 0.002$) and a highly significant increase in the magnitude of *per capita* changes in the 86 sub-networks ($\Sigma[\text{abs}(\Delta_i)]$; figure 1b; linear regression: $F_{1,18} = 13.23$, $p = 0.002$). Both measures of spatial synchrony show a highly significant increase over the years (figure 1c,d; linear regressions: $F_{1,18} = 13.85$, $p = 0.002$ and $F_{1,18} = 14.15$, $p = 0.001$). In the null distribution for metapopulation coherence, values greater than 0.44 are in the 1% upper tail, that is, these values indicate significant coherence. Based on this criterion, 8 out of the 12 years from 1994 until 2005 show no significant coherence, whereas all the 8 years from 2006 onwards show significant metapopulation coherence.

(b) Survival over winter and summer

To explain the causes of increasing synchrony over the years (figure 1c,d), we focus on two life-history stages in which there is much year-to-year variation and which greatly affect population dynamics, namely over-winter mortality of diapausing larvae and mid-summer survival of young larvae. In the present data, the average annual over-winter survival in the 86 sub-networks has varied between 41% and 83%, but there is no temporal trend in mean survival nor in the standard deviation among the sub-networks (linear regression of log survival versus year: $F_{1,17} = 0.19$ and $p = 0.67$; linear regression of the standard deviation versus year: $F_{1,17} = 0.04$ and $p = 0.85$). It is hence unlikely that changes in over-winter mortality would explain the long-term increase in spatial synchrony (figure 1c,d).

We cannot measure the survival of young larvae in summer as such, because it is not possible to gather data

on the numbers of egg clusters laid by females in hundreds of populations. Instead, we have analysed the change in the number of larval groups from spring (previous generation) to autumn, $\log(N_{\text{autumn}}/N_{\text{spring}})$, though this is affected by the reproductive success of butterflies in June as well as by larval survival until the autumn. This measure has been highly variable, the annual mean value in the 86 sub-networks ranging from 0.57 to 6.02, but with no temporal trend in the mean nor in the standard deviation (linear regression of log summer change versus year: $F_{1,17} = 0.21$ and $p = 0.65$; linear regression of the standard deviation versus year: $F_{1,17} = 0.01$ and $p = 0.92$). However, the absolute value of the relative change, $\text{abs}(\log[N_{\text{autumn}}/N_{\text{spring}}])$, shows an increasing trend ($F_{1,17} = 3.64$ and $p = 0.07$), suggesting increasing variation in the survival of young larvae over the years. In any case, the change over summer drives the annual change in population size, as these two variables are highly correlated ($r = 0.96$, $p < 0.001$; log-transformed variables), while there is no correlation between annual change and change over winter ($r < 0.01$), nor between change over winter and change over summer ($r = 0.22$, $p = 0.36$).

(c) Spatial variation in precipitation and change in population size

July and August rainfall had a positive and a negative effect, respectively, on *per capita* annual growth rate in the 86 sub-networks (figure 2a,b). The relationships are highly significant when data are pooled for all the years (July: $F_{1,429} = 64.04$, $p < 0.0001$; August: $F_{1,429} = 85.29$, $p < 0.0001$), but the effects are weak and inconsistent among the years (figure 2a,b). These results do not support the hypothesis that increased spatial synchrony in the past 21 years (figure 1c,d) is due to increased spatial uniformity of weather conditions within years. To further illustrate lack of such an effect, figure 2c,d shows that neither July rainfall, August rainfall nor population growth rate show evidence for decreased (or increased) spatial variance during the study period (linear regression of standard deviation versus year: $p > 0.05$ for all three response variables).

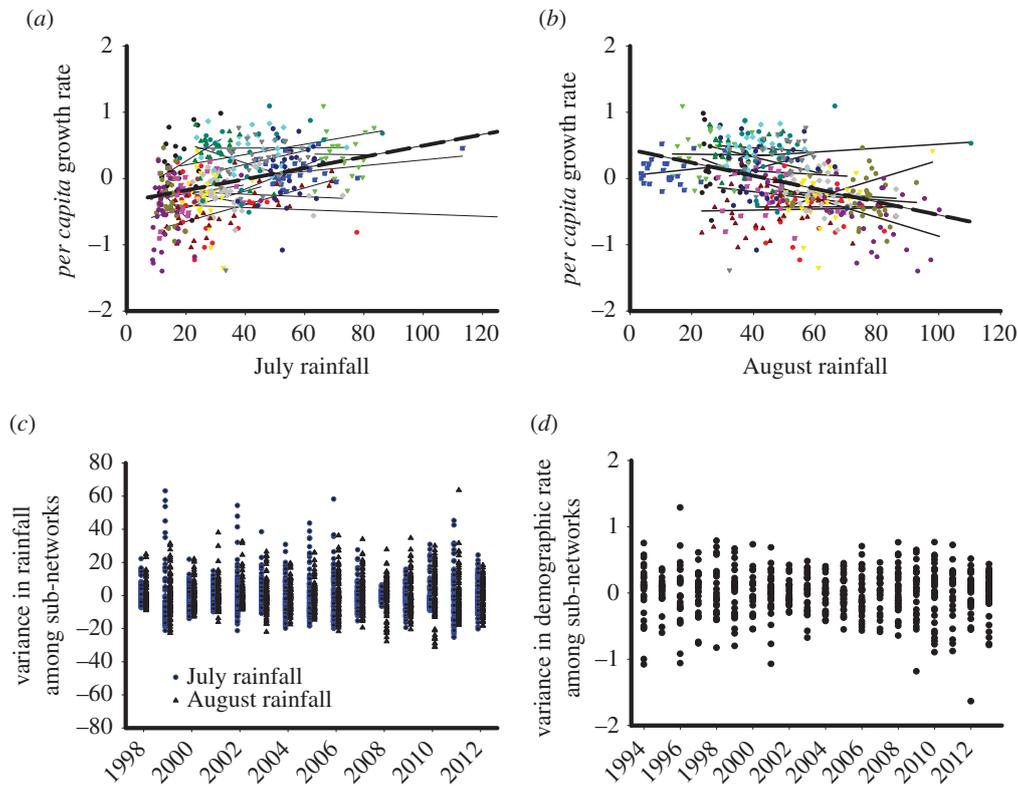


Figure 2. *Per capita* annual growth rate in Glanville fritillary populations and summer rainfall. (a,b) The relationships between *per capita* growth rate and July and August rainfall, respectively, calculated for the 86 sub-networks during the period 1998–2012. The colour and shape of the data points indicate the year. (a,b) Linear regressions fitted to the pooled data (thick dashed lines; $p < 0.0001$ for both regression lines) and year-specific regressions (thin solid lines). (c,d) Spatial variation in July and August rainfall (1998–2012) and *per capita* growth rate (1994–2013) among the 86 sub-networks, respectively. The data are standardized to zero mean in each year. There is no significant trend in the variance (c,d). Two outlier values are off the plot (a,c).

(d) Spatial and temporal variation in plant dryness

The average plant dryness index across the 4000 meadows was high (more than 18% of plants with withering symptoms) in 5 years, otherwise it was low (less than 9% of plants with withering symptoms; electronic supplementary material, figure S2). In the former 5 years, there was substantial variation among the meadows (electronic supplementary material, figure S2; the extreme case was 2002 when 40% of the plants dried out). Annual plant dryness was not correlated with July rainfall ($r^2 = 0.03$), but it was moderately and negatively correlated with August rainfall ($r^2 = 0.41$). Nonetheless, it is apparent that the 5 years with the driest plants were dry either in July or August (electronic supplementary material, figure S3). In the 2 years when high plant dryness coincided with a very dry July, the change in population sizes among the sub-networks was significantly negatively correlated with spatial variation in plant dryness (figure 3d; 2010: $F_{1,32} = 4.91$, $p = 0.034$; 1999: $F_{1,26} = 4.38$, $p = 0.046$), whereas no such correlation was detected for the other years with high plant dryness ($p > 0.79$).

(e) Annual change in metapopulation size

We next analysed the annual change in the size of the metapopulation as a whole. The model with the highest support included density-dependence and rainfall in July, which had the Akaike weights of 0.50 and 0.74 in the full and reduced set of *a priori* models, respectively (table 1 and electronic supplementary material, table S1). The two models including plant dryness received low support (sum of Akaike weights is only 0.01, table 1). The second-best model, based on data

for all the years, included density-dependence, rainfall in July and rainfall in August (Akaike weight = 0.156; electronic supplementary material, table S1). Change in metapopulation size was strongly negatively affected by the number of larval groups in the previous year (figure 3a) and strongly positively affected by July rainfall (figure 3b). The effect of August rainfall was negative (cf. figure 2b).

There has been no temporal change in the mean July and August rainfall during the study period ($F_{1,19} = 0.03$, $p = 0.86$ and $F_{1,19} = 1.43$, $p = 0.25$, respectively). However, in the years when the metapopulation has declined, there has been a significant increase in the intensity of unfavourable weather conditions, characterized by a combination of low July rainfall and high August rainfall (figure 3c; interaction between the month and the year on rainfall: $F_{1,20} = 6.38$, $p = 0.02$). There have been no comparable changes in the years when the metapopulation has increased (interaction between the month and the year on rainfall: $F_{1,12} = 0.65$, $p = 0.43$, respectively).

4. Discussion

We conclude that the increasing spatial synchrony of metapopulation dynamics in 1993–2013 (figure 1c,d), reflected in the increasing amplitude of metapopulation fluctuations (figure 1a), is caused by increasing frequency of dry weather in July (figure 3b,c), which leads to withering of host plants and subsequent larval mortality. We discuss the effect of drought via host plant quality below, but observe meanwhile that, following a steep decline, the metapopulation is largely released from density-dependent regulatory processes

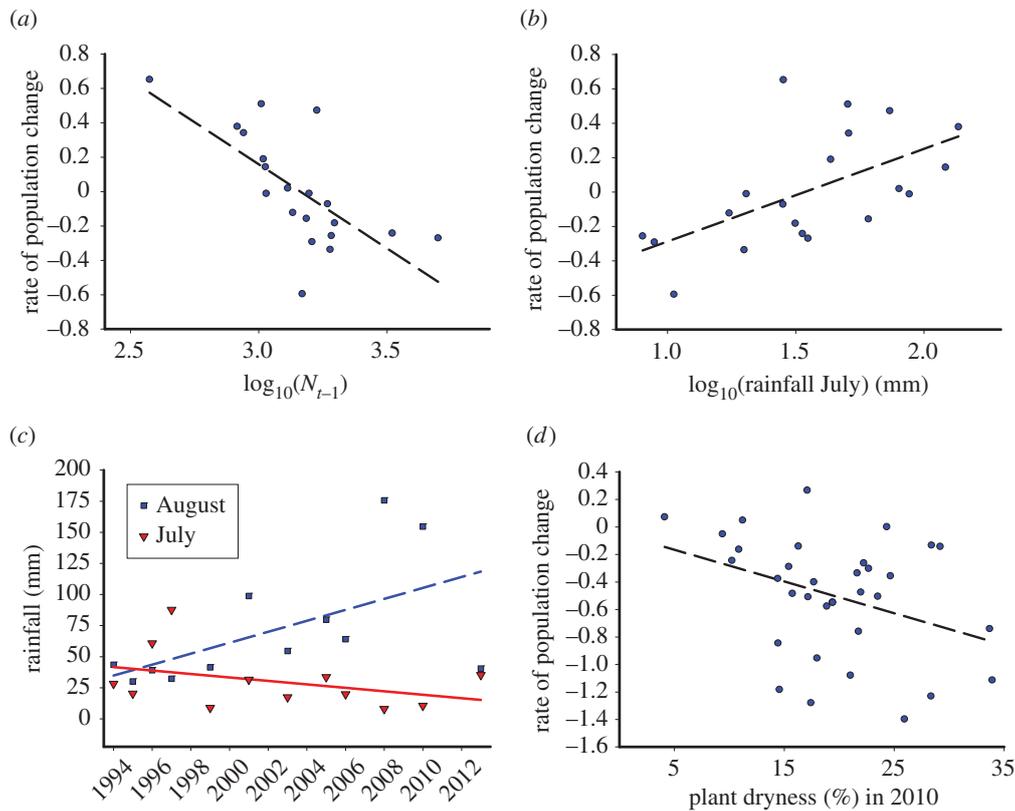


Figure 3. Year-to-year dynamics in the metapopulation of the Glanville fritillary. (a) Strong density-dependence in annual growth rate ($F_{1,18} = 16.24$, $p = 0.0008$). (b) This panel shows how July rainfall affects the growth rate ($F_{1,18} = 9.31$, $p = 0.007$). (c) The temporal decrease and increase in July and August rainfall, respectively, during the years when the metapopulation has declined. The interaction between the month (July versus August) and year in affecting rainfall is significant ($p = 0.02$). (d) Decrease in growth rate with an increasing percentage of withered host plants among the 86 sub-networks in a dry year (2010; $p = 0.03$).

(figure 3a), which has allowed rapid recovery and hence no long-term declining trend in the size of the metapopulation (figure 1a). The maximal fecundity of the Glanville fritillary is very high, as females may lay more than 1000 eggs [42], which allows, when conditions are favourable, rapid population increase. The related and biologically similar species *Euphydryas aurinia* used to exhibit outbreak population dynamics in the UK in the early part of the twentieth century [43], though now the species has declined permanently to low abundance owing to massive habitat loss [44]. In the Åland Islands, in contrast, there has been no substantial change in land-use that could explain changes in spatial synchrony of populations via changes in environmental heterogeneity.

We suggest that little rainfall in July leads to widespread withering of the host plants, which often grow in meadows that have little soil and are hence susceptible to drought. Host plant withering is commonly observed in the field as is the subsequent elevated mortality of larvae. Moreover, even if larvae would not die, poor-quality host plants retard the growth of larvae, which remain small prior to winter diapause with adverse consequences for post-diapause development [45]. Given this hypothesis about the mechanism, it would be preferable to model changes in population size with the plant dryness index instead of July precipitation. We did that, but a model with year-to-year variation in plant dryness was far inferior to a model with July precipitation. This is almost certainly due to our measure of plant dryness reflecting plant condition at the time of the metapopulation survey, in late August to early September, by which time plants have often recovered from a dry July

(I. Hanski 1973–2011, personal observations). We would need a measure of plant dryness in the middle of the summer, but this is not available. However, July precipitation is a good proxy of plant condition in July to early August, during the period when the small larvae feed prior to moulting to the diapause stage from mid-August onwards.

Spatial variation in habitat quality, here susceptibility to drought, would buffer local populations against synchronous changes and would thereby increase metapopulation stability [2,46–48]. In the present case, there is little fixed spatial variation in susceptibility to drought (electronic supplementary material, figure S4), and the observed variation apparently reflects spatial variation in precipitation, which varies from one year to another (see examples in [35]). Nonetheless, a significant spatial relationship between *per capita* growth rate and plant dryness was detected among the 86 sub-networks in some of the years with high overall dryness index. The example in figure 3d is from 2010, a year with a very dry July and the lowest metapopulation size during the entire study period (figure 1a).

Our findings demonstrate increased temporal variability in the dynamics of the butterfly metapopulation, which may threaten its long-term persistence even if the species is still abundant in the study area. In a recent study, Hung *et al.* [49] concluded that drastic fluctuations in the natural populations of the passenger pigeon (*Ectopistes migratorius*) due to ecological and climatic conditions, combined with strong human pressure, resulted in the rapid demise and ultimate extinction in 1914, even if the species had 3–5 billion individuals less than a century before. Likewise, Lockwood & Debrey [50] suggested that the Rocky Mountain grasshopper (*Melanoplus spretus*), once the most serious agricultural pest in the western

United States and Canada, went extinct soon after 1900 due to a combination of a natural population crash in the 1880s coinciding with agricultural destruction of the insect's habitat. Such interactions between natural population fluctuations and human impact are little explored, but will probably become increasingly relevant in the face of habitat fragmentation and changing climate.

Our analysis highlights the generic difficulty of demonstrating the impact of unusual weather events: even though we have two decades of uniquely high-resolution survey data, which unambiguously demonstrate a highly significant pattern of increasing spatial synchrony through time (figure 1*c,d*), it is not easy to pinpoint conclusively the underlying mechanism—which in our case would have required additional long-term data (plant quality in the middle of the summer). Other general difficulties in the study of climate effects on natural populations include nonlinear responses to environmental changes and uncommon situations that have long-lasting consequences for morphology, physiology, behaviour, ecology and evolution of species [51,52]. In-depth ecological knowledge of the focal species is necessary to detect the impact of uncommon climate events, and long time-series are required to gain sufficient statistical power. For example, Harley & Paine [24] showed that extreme weather events, rather than a gradual change in the mean values, determine the vertical distribution of the intertidal red alga *Mazaella parksii* on Tatoosh Island, Washington

State, but the 30 year study included only two punctuated responses to extreme weather events [24]. Similarly, Grant & Grant [53] showed how an extreme drought event radically affected population abundance and character evolution in one of Darwin's finch species (*Geospiza fortis*) in the Galapagos Islands.

Here, we have demonstrated for the Glanville fritillary butterfly that increasing frequency of unfavourable weather conditions during a 21 year period has not affected the long-term average size of the metapopulation but it has affected the magnitude of population fluctuations and the spatial extent of population synchrony. Such complex population dynamic consequences of increasing frequency of unfavourable weather events may represent an unforeseen threat to long-term persistence of species. Given the predictions about the frequency, duration and intensity of climatic variation and extremes [54–59], better understanding of how environmental variability and extreme events affect complex population dynamics remains a key challenge for ecological studies.

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