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RESEARCH PAPER

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European butterfly populations vary in sensitivity to weather across their geographical ranges

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Abstract

Aim: The aim was to assess the sensitivity of butterfly population dynamics to variation in weather conditions across their geographical ranges, relative to sensitivity to density dependence, and determine whether sensitivity is greater towards latitudinal range margins.

Location: Europe.

Time period: 1980–2014.

Major taxa studied: Butterflies.

Methods: We use long-term (35 years) butterfly monitoring data from $>$ 900 sites, ranging from Finland to Spain, grouping sites into 2° latitudinal bands. For 12 univoltine butterfly species with sufficient data from at least four bands, we construct population growth rate models that include density dependence, temperature and precipitation during distinct life-cycle periods, defined to accommodate regional variation in phenology. We use partial R^2 values as indicators of butterfly population dynamics' sensitivity to weather and density dependence, and assess how these vary with latitudinal position within a species' distribution.

Results: Population growth rates appear uniformly sensitive to density dependence across species' geographical distributions, and sensitivity to density dependence is typically greater than sensitivity to weather. Sensitivity to weather is greatest towards range edges, with symmetry in northern and southern parts of the range. This pattern is not driven by variation in the magnitude of weather variability across the range, topographic heterogeneity, latitudinal range extent or phylogeny. Significant weather variables in population growth rate models appear evenly distributed across the life cycle and across temperature and precipitation, with substantial intraspecific variation across the geographical ranges in the associations between population dynamics and specific weather variables.

Main conclusions: Range-edge populations appear more sensitive to changes in weather than those nearer the centre of species' distributions, but density dependence does not exhibit this pattern. Precipitation is as important as temperature in driving butterfly population dynamics. Intraspecific variation in the form and strength of sensitivity to weather suggests that there may be important geographical variation in populations' responses to climate change.

KEYWORDS

adaptation, biogeography, climate, climate change, density dependence, long-term monitoring, population dynamics, population growth, range edge

1 | INTRODUCTION

Understanding how environmental factors regulate population dynamics is a fundamental question in ecology, and one of particular importance in the context of climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Establishing the importance of climatic factors in driving population dynamics, relative to others such as density dependence, is crucial for predicting how populations will be affected by climate change. Climate appears to play a role in regulating populations, as both occupancy and distribution limits are often well explained by climate (Boucher-Lalonde, Morin, & Currie, 2014; Gaston, 2003), and recent distributional shifts are often associated with changing climatic conditions (e.g., Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Poloczanska et al., 2013). These relationships are frequently used to project the impacts of climate change on species' distributions and community structure (Urban et al., 2016). Shifts in phenology, associated changes in biotic interactions, and direct effects also suggest that many species' population dynamics are responding to climate change (CaraDonna, Iler, & Inouye, 2014).

Despite these general arguments supporting the role of climate in driving coarse-scale population distributions and dynamics, studies that attempt directly to link relatively shorter-term weather to inter-annual population dynamics have generated variable conclusions. The ability of weather to explain variation in vital rates, as well as the strength of these effects, has ranged from strongly regulating (Boggs & Inouye, 2012; Forchhammer, Stenseth, Post, & Landvatn, 1998; Gullett, Evans, Robinson, & Hatchwell, 2014) through to being of relatively limited importance relative to other factors, such as density dependence, with weather variables sometimes having negligible explanatory power (Băncilă, Ozgul, Hartel, Sos, & Schmidt, 2016; Nowicki, Bonelli, Barbero, & Balletto, 2009). The reasons for these differences in sensitivity remain unclear. One potential explanation is systematic spatial variation in the relative importance of weather in regulating populations (Sandvik, Coulson, & Sæther, 2008). Population dynamics are driven by many factors that act at varying spatial and temporal scales and involve different processes in different portions of the species' range (Beale, Brewer, & Lennon, 2014; Gaston, 2003). If climatic factors limit species distributions, then one might expect that weather variables are more important determinants of population growth rates at range edges than elsewhere in a species' distribution (Garcia et al., 2000), especially if there is a rapid decline in the suitability of conditions towards the edge of a species' fundamental niche. In contrast, towards the range centre, factors such as intra- and interspecific competition may be of relatively greater importance, overriding the influence of weather effects (Bjørnstad & Grenfell, 2001). Position within the species' range may thus be an important determinant of a given population's sensitivity to weather events. Conversely, if populations across a species' range are highly adapted to local weather regimes then all populations, regardless of their range position, will exhibit similar sensitivity to local weather fluctuations (Myers-Smith et al., 2015).

A number of studies have found latitudinal gradients in sensitivity to weather, but these include positive latitudinal gradients (Chen, Welsh, & Hamann, 2010; Forchhammer, Post, Stenseth, & Boertmann, 2002; Sæther et al., 2003), negative gradients (Forchhammer et al., 2002; Sæther et al., 2008) and a mix of the two (Sandvik et al., 2008; Sæther et al., 2008). The biological basis for this variation in latitudinal trends in sensitivity to weather is unclear (Chen et al., 2010), but could arise through a given latitude meaning different things for different species. A given latitude will be close to the range edge for some species but closer to the range centre for others, and by failing to place the latitudinal position in the context of the species' overall range, this is overlooked. Consequently, variation in latitudinal patterns in weather sensitivity may still be consistent with the hypothesis that range position is associated with sensitivity to weather conditions. To date, few studies have directly examined whether sensitivity to weather is greater in populations at range margins relative to those closer to the range centre. Those studies that have been conducted have, however, primarily found heightened sensitivity towards northern range edges and high altitudes (Ettinger, Ford, & HilleRisLambers, 2011; Myers-Smith et al., 2015).

Variation in organism fitness over environmental gradients is not necessarily symmetrical. Species' performance typically declines more steeply above the thermal optimum than below (e.g., Araújo et al., 2013; Deutsch et al., 2008). Additionally, Sunday et al. (2014) found that upper thermal tolerances are frequently exceeded at the warm range edge, whereas at the cool range edge a larger thermal safety margin exists between lower thermal tolerances and environmental temperatures. As a consequence, at the trailing range margin, temperature may be a relatively more important determinant of population dynamics than at the leading range edge. Alternatively, range-wide patterns of sensitivity may be more complex, with weather effects displaying strong context dependence (Keith et al., 2008) or being masked by different mechanisms, including differential responses to temperature and precipitation, operating in different parts of the range (Beale et al., 2014).

Variation in weather sensitivity across a species' range has important implications. Firstly, weather associations observed in a single or a few population(s) are unlikely to be representative of the overall species' response, which limits the ability of single population studies to generate general conclusions about the species' response across its entire range. Secondly, It further suggests that the response to climate change will not be uniform across the range and, if sensitivity does indeed increase towards range margins, responses will be greater in peripheral regions than in the range centre. Failing to account for these influences therefore limits our ability to understand and predict species persistence and range dynamics under climate change. This suggests a need for additional empirical studies assessing how sensitivity of population growth rates to weather varies across species' distributions.

Here, we assess how population growth rates of 12 univoltine butterfly species vary in sensitivity to weather across their European distributions. We use data from five long-term European butterfly monitoring schemes from 987 sites over five countries along a latitudinal gradient from Spain to Finland, running from 1980 to 2014. Specifically, we model how population growth rate varies as a function of temperature and precipitation variables measured over periods corresponding to different life stages, in order to capture spatiotemporal variation in phenology, and assess how the sensitivity of population growth rates to these weather terms changes with latitudinal position within the species' range. We compare and contrast this with the latitudinal pattern in strength of density dependence to assess whether apparent patterns in weather sensitivity are associated with converse patterns in sensitivity to density dependence. Our central hypothesis is that sensitivity to weather increases towards species' geographical latitudinal range edges, and we further ask whether there is evidence of asymmetry in sensitivity across this range.

2 | METHODS

2.1 | Butterfly and climate datasets

We use annual site-level indices of abundance gathered from the butterfly monitoring schemes of five European Countries: Finland, Germany, the U.K., The Netherlands and Spain. The duration of coverage for each scheme varies: Finland (1999), Germany (2005), the U.K. (1976), The Netherlands (1990) and Spain (1994). Annual site-level abundance indices are calculated from counts made at weekly intervals over the course of the season using a standardized Pollard-walk methodology. Owing to the pronounced patterns of abundance seen in butterfly numbers over the course of a season, abundance indices are derived from these weekly counts by fitting a general additive model (GAM) and generating a measure of the area under the curve (Dennis, Freeman, Brereton, & Roy, 2013). Where counts are missing, the GAM provides an interpolated estimate based on counts made at other sites in the same bioclimatic zone (Metzger et al., 2013; Schmucki et al., 2016). This method has been demonstrated to generate unbiased abundance estimates and to outperform a simple linear interpolation method, which would be the alternative to our chosen approach (Schmucki et al., 2016). To prevent spurious estimates, sites with $>$ 50% observations missing were removed before analysis (Schmucki et al., 2016). To model inter-annual changes in abundance, an index of population growth was calculated from the relative change in abundance between two consecutive years, $\ln(N_t + 1) - \ln(N_{t-1} + 1)$, which is hereafter referred to as relative growth rate. Sites with $<$ 5 years of non-zero data were removed before further analysis.

We obtained climate data from the European Climate and Assessment Dataset project (ECAD; Haylock et al., 2008). This dataset is a gridded dataset of daily temperature (in degrees Celsius) and precipitation (in millimetres) since 1950 at a 25 km resolution (0.22° rotated grid, Version 12.0; Haylock et al., 2008). This spatial resolution is fairly coarse, but it is the only available European climatic dataset with the required temporal resolution. Sites for which there were no climate data, typically because they fell in coastal grid cells that were not covered by the climate surface, were removed. To ensure that climatic data matched as closely as possible the conditions at the monitoring site, we used the 7.5 arc-second ($\sim$250 m) resolution Global Multi-resolution Terrain Elevation Data map (GMTED) to exclude sites whose elevation differed by $>$ 150 m from the mean elevation within a 25 km cell.

The influence of climatic variables on population growth rates can vary between different life stages (Radchuk, Turlure, & Schtickzelle, 2013), the timing of which can vary across the species' range (Schmucki et al., 2016). To accommodate this regional and temporal variation, we used information about the flight period of each species, defined at the level of the bioclimatic zone (Metzger et al., 2013), to tailor climatic indices to specific periods of the butterfly's life cycle. For each species in each latitudinal band (see Section 2.2), we first obtained an average flight curve from relative abundances over the course of the season, following the methodology of Schmucki et al. (2016). We then extracted daily temperature and precipitation variables for each 25 km grid cell, using four time periods that reflect different life stages occurring in an annual cycle: the post-flight, over-wintering, pre-flight and flight periods (Figure 1), and standardized these to unit standard deviation. Flight-period temperature and precipitation were then defined as the mean of the daily temperature and precipitation indices falling between the 10th and 90th percentiles of this flight-period distribution. We used the same process to define the pre-flight and post-flight

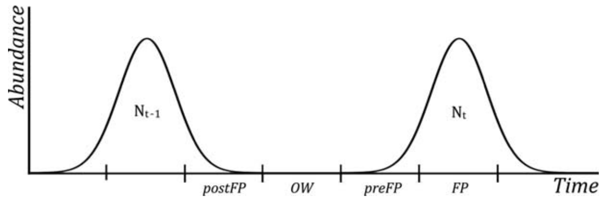

FIGURE 1 Schematic diagram of life-cycle periods and their correspondence to two annual abundance indices, N_t and N_{t-1}. Life-cycle periods are as follows: post flight-period (postFP), over-wintering period (OW), pre-flight period (preFP) and flight period (FP)

periods as the 3 months before and after the flight period. The overwinter period was defined as November–January for all species in all zones (Figure 1). Although over-winter periods could be defined over different time periods, for example December–February, this results in substantial overlap between over-winter and adjacent time periods for some species in some regions. This particular definition was therefore chosen on the basis that it minimizes such overlaps, and these are marginal where they do occur. Analyses are restricted to univoltine species, for which our methods of defining life-cycle periods are most appropriate.

2.2 | Process model of population growth rates

To model the influence of weather variables on population growth rate in different portions of each species range, the range was subdivided into latitudinal sections. Models were constructed at this regional level rather than at the site level because individual sites typically had too few data to reliably fit the climate models (the longest time series was 33 years, and on average a site had data from 9 years), necessitating a higher level of grouping. Latitudinal bands were constructed at 2° intervals on the basis that this maximized the number of models we could construct with reasonable sample sizes, with population growth rate then modelled as a function of weather variables within each latitudinal band. Models were constructed for each latitudinal band with $>$ 150 data points (species/site/year combinations). Supporting Information Figure S1 displays the spatial distribution of sites for each species. For each species, in each latitudinal band, population dynamics were modelled on the logarithmic scale using the stochastic Gompertz model of population growth,

$$N_{it} = N_{it-1}\exp(\alpha_i + \log N_{it-1} + W_{1it} + \ldots + W_{8it} + \varepsilon_{it-1}) \tag{1}$$

where N_{it} is abundance at the ith site at time t, α_i *is* a varying site intercept, W_{jit} is the jth weather variable at site i at time t, and ε_{t-1} is a normally distributed error term. Taking logs and rearranging to express in terms of relative growth rate this becomes,

$$y_{it} = x_{it} - x_{it-1} = \alpha_i + x_{it-1} + W_{1it-1} + \ldots + W_{8it-1} + \varepsilon_{it-1} \tag{2}$$

where x_{it} and x_{it-1} are the logarithmic abundances at site i and times t and time $t-1$, respectively, and y_{it} is thus the relative population growth rate at site i in year t. To confirm that the weather terms included in these models had significance for the population dynamics of the species modelled, we used *F*-tests to compare each model with a reduced model containing no weather terms. Collinearity of weather variables in each model was assessed using pairwise Pearson correlation coefficients. Only 2.4% (43 of 1,792) of pairwise comparisons had absolute correlation coefficients $>$ .7, and therefore the vast majority of individual parameter estimates were considered robust to collinearity.

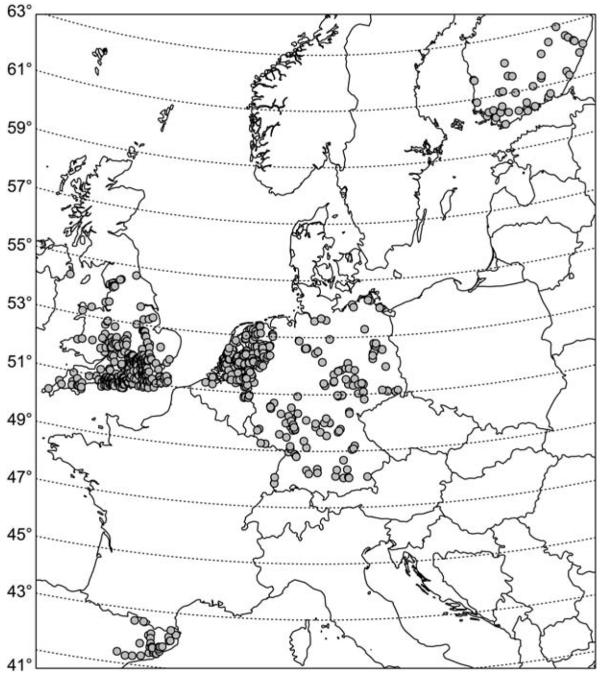

FIGURE 2 Sites retained after exclusion based on criteria outlined in the text, with 2° latitudinal bands overlaid (dotted lines)

2.3 | Butterfly species inclusion

Twelve univoltine species were sufficiently well represented across at least four latitudinal bands to be included in analyses (at least 150 data points in a latitudinal band; Figure 2 and Supporting Information Figure S1), with a total of 52 species/latitudinal band combinations. The 12 species were as follows: orange tip, *Anthocharis cardamines*; ringlet, *Aphantopus hyperantus*; dark-green fritillary, *Argynnis aglaja*; silver-washed fritillary, *Argynnis paphia*; pearl-bordered tritillary, *Boloria euphrosyne*; green hairstreak, *Callophrys rubi*; purple hairstreak, *Favonius quercus*; brimstone, *Gonepteryx rhamni*; meadow brown, *Maniola jurtina*; gatekeeper, *Pyronia tithonus*; Essex skipper, *Thymelicus lineola*; and small skipper, *Thymelicus sylvestris*. One species, brimstone, over-winters as an adult, and we are consequently unable to distinguish between over-wintering individuals and those that emerged that year. To check that this did not alter our conclusions, we therefore also ran the analyses excluding this species. These did not qualitatively affect our results and we therefore report only the full analysis with this species included. Although the distributions of our focal species vary, they all have a pan-European distribution, with some extending slightly into north Africa (which was taken into account when defining range edges; see Section 2.4.1).

2.4 | Assessing variation in sensitivity to weather

2.4.1 | Measuring range position

In order to establish how population sensitivity to weather varies across the latitudinal range of each species, we constructed a measure of relative north–south geographical range position of the data for each latitudinal band, defined along a vector from each species' northern and southern latitudinal range edges. To do this we first calculated, for each latitudinal band, the average latitude of all data points in the model, $\text{lat}_{\text{average}}$, weighted by the number of data points from each site. This was then expressed as a proportional range position, through the following conversion:

$$\text{Relative range position, RRP} = \frac{\text{lat}_{\text{average}} - \text{lat}_{\text{min}}}{\text{lat}_{\text{max}} - \text{lat}_{\text{min}}} \tag{3}$$

where lat_{max} and lat_{min} are the latitudes of the species' northern and southern range extents defined from the European butterfly atlas (Kudrna et al., 2011), and from Tennent (1996) for species whose distributions extended into north Africa (i.e., the relative range position metric does not impose an artificial boundary at the southern European range edge). Thus, our measure of relative range position scales between zero (southern range edge) and one (northern range edge).

Owing to the predominantly European global distribution of all species modelled here, absolute latitude and the derived relative range position are highly correlated (Pearson correlation coefficient of .80). Consequently, it is not possible to distinguish between the effects of absolute latitude and relative latitude. We continue to report results in terms of relative latitude, but this opens up the possibility that patterns of sensitivity may be driven by alternative factors associated with absolute latitude, rather than distance from the range edge per se. We discuss alternative explanations in the Discussion section.

2.4.2 | Assessing sensitivity to weather in relationship to relative range position

We measured climatic sensitivity as the partial R^2 value for the suite of all weather terms in each model (i.e., the difference in R^2 compared with a model containing only site and density dependence terms; Myers-Smith et al., 2015). Increasing partial R^2 values reflect increasing sensitivity to weather. Likewise, the importance of density dependence was measured as the partial R^2 value for the density dependence term in each model. Our approach of using a metric derived from one set of models as response variables in other models is equivalent to that used in a number of other papers assessing spatial variation in population dynamics (e.g., Morrison, Robinson, & Pearce-Higgins, 2016; Myers-Smith et al., 2015).

Latitudinal variation in partial R^2 measures was analysed using mixed-effects models, with a random Gaussian intercept on species, using the *lme4* package in R (Bates, Mächler, Bolker, & Walker, 2015). Three models of increasing complexity were fitted (Equations 4–6). Model improvement through adding latitudinal predictors was tested with an *F*-test with the Kenward–Rogers correction for estimating d.f. in a mixed-modelling framework (Bolker et al., 2009) using the *pbkrtest* package in R (Halekoh & Højsgaard, 2014). We calculated mixed-effect R^2 values for these models based on the framework outlined by Nakagawa and Schielzeth (2013).

$$\text{Sensitivity} = s_j + \varepsilon \tag{4}$$

$$\text{Sensitivity} = s_j + \text{RRP} + \varepsilon \tag{5}$$

$$\text{Sensitivity} = s_j + \text{RRP} + \text{RRP}^2 + \varepsilon \tag{6}$$

where s_j is a random species intercept, RRP is the relative range position for each model, and ε is a normally distributed error term. To check whether phylogenetic relationships between the modelled species could influence our conclusions, we constructed a second model that incorporated the phylogeny of Brooks et al. (2017) into the random effects structure using the MCMCglmm package (Hadfield, 2010). We found that the phylogenetic variance terms approached zero and the model fit was almost identical (Supporting Information Appendix S1 and Figure S2). We therefore report models that do not incorporate phylogeny in the main manuscript.

Sensitivity of butterfly population dynamics to weather could, in principle, be driven partly by either (a) variation in weather variability across the range (i.e., increased exposure rather than increased sensitivity) or (b) through heightened topographic heterogeneity buffering populations from weather effects. We recognize that it may also be possible that habitat may modify response, but this is difficult to quantify formally, and we expect its influence to be minimal (see Discussion). To assess the influence of points (a) and (b), we quantified (a) weather variability for each species/latitudinal band combination (measured as standard deviations, averaged across weather variables), and (b) the average topographic heterogeneity (*SD*) within 500 m of each site (using the GMTED raster), including each of these as additional predictors in models. As a final robustness check, we also included total latitudinal range size ($\text{lat}_{\text{max}} - \text{lat}_{\text{min}}$) as a predictor in models. These additional predictors had a negligible influence on overall model fit and do not qualitatively affect our results (see Supporting Information Appendix S1).

2.4.3 | Testing for asymmetry in climatic sensitivity between northern and southern portions of range

We further set out to assess whether there was any evidence of asymmetry in the latitudinal relationship by assessing whether the rate of change in climatic sensitivity with latitude varied between the northern and southern halves of the range. To do this, we defined the relative range position in terms of distance from the range centre (i.e., difference between the relative range position and the range centre, .5) and allowed the slope to vary depending on whether the relative position was in the northern or southern half of the range:

$$\text{Sensitivity} = s_j + \text{distance} + I(\text{RRP} < 0.5) + \text{distance} \times I(\text{RRP} < 0.5) + \varepsilon \tag{7}$$

where s_j is a random species intercept, 'distance' is the distance from the range centre (scaling between zero at the range centre and .5 at a range edge), and I is an indicator function for range position (i.e., one in the southern half of the range and zero in the northern half). If there is no asymmetry in latitudinal pattern, both halves of the range should display similar slopes, with no interaction term between slope and range portion. Degrees of freedom were estimated using the Satterthwaite approximation (Bates et al., 2015).

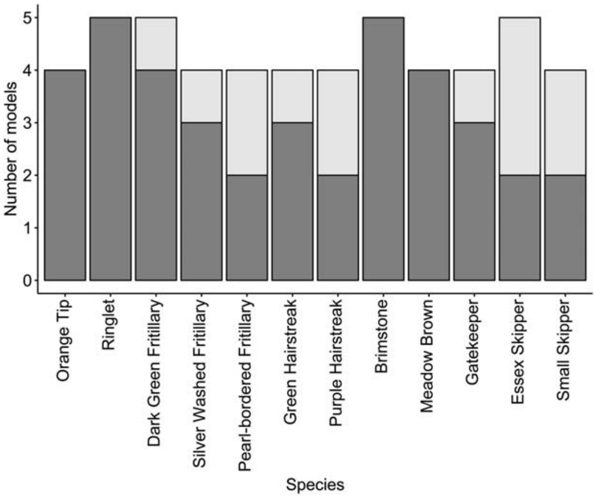

FIGURE 3 Number of models by species, where each model for each species is for a different latitudinal band. Darker shading indicates that inclusion of climate terms resulted in significant model improvement (*F*-test; $p \leq .05$)

3 | RESULTS

Population dynamics were frequently associated with weather, with *F*-tests demonstrating that the inclusion of weather terms significantly improved 75% of models (39 out of 52; Supporting Information Table S1), and for each species this was the case in at least two regions (Figure 3). Individual parameter estimates for weather terms vary in magnitude and direction, with 31% being significant across the 52 models ($p \leq .05$; Supporting Information Table S2). The precise form of the relationships between butterfly population growth rate and weather is highly variable across life stages, both within and across species, but significant parameter estimates are distributed in a fairly even manner across life stages and weather variables (Supporting Information Table S2). Models typically explained *c*. 40% of variation in population dynamics (mean $R^2 = 0.39$; Supporting Information Table S3), with variable contributions from weather terms in these (partial R^2 values range from 1 to 22%, with a mean value of 5%). Negative density dependence was ubiquitous, with all models containing significant negative parameter estimates for log-density ($p < .05$; Supporting Information Table S2). Partial R^2 values for density dependence terms were uniformly larger than those for weather terms, with a mean partial R^2 of 29% (range, 1–52%; Supporting Information Table S3). Although the inclusion of weather terms significantly improved model performance, the ability of the final models to predict relative growth rate remained highly variable, and a large amount of residual variation remained unexplained (mean residual root mean squared error = 0.69; Supporting Information Table S3).

There was support for latitudinal variation in sensitivity to weather, with the partial R^2 values for weather terms in butterfly population dynamic models displaying curvature across the gradient of relative range position, with lowest sensitivity to weather in populations closer to the centre of the species' European distribution (Figure 4). The explanatory capacity of weather variables, as measured by partial R^2, displays a distinct latitudinal pattern, with the model containing quadratic terms performing better than both intercept-only (*F*-test for difference between these two models: $F_{2,44.4} = 8.46$, $p < .001$) and linear-slope models ($F_{1,42.62} = 16.08$, $p < .001$). For the quadratic model, the curve inflection point (minima) is at a relative range position of .52 (i.e., close to the centre of species' latitudinal range). Latitudinal terms explained a reasonable proportion of the variation in partial R^2 values, with a marginal R^2 of 24%. Conversely, there were no statistically significant patterns of latitudinal variation in density dependence when measured by partial R^2 values (linear model: $F_{1,46.13} = 0.28$, $p = .602$; quadratic model: $F_{2,42.94} = 0.19$, $p = .830$; Figure 5).

Measures of climatic sensitivity were tested for asymmetry in the change in sensitivity across the latitudinal gradient using a break-point at the range centre (RPP = 0.5). These indicate an average increase of .20 units partial R^2 per .1 increase in distance from the range centre ($t = 3.87$, d.f. = 46.9, $p > .001$), but no significant difference in slope between the upper and lower range halves ($t = 0.57$, d.f. = 44.0, $p = .570$; Figure 6).

4 | DISCUSSION

Modelling population dynamics of regional populations of 12 univoltine butterfly species suggests that populations towards species' range edges are relatively more sensitive to weather than those in the range centre. This pattern contrasts with the uniform strength of density dependence across species' latitudinal distributions. There was limited evidence of asymmetry in sensitivity, with the amount of variation in population dynamics driven by weather variables being similar at northern and southern range boundaries.

Our analyses focus on populations' relative position within a species range, because ecological theory predicts that range-edge populations will be more sensitive to weather conditions because of inhospitable conditions at the edge of species' fundamental niche space (Oliver, Roy, Brereton, & Thomas, 2012). Our results appear to be robust to a range of potential alternative explanations, including the effects of phylogeny, latitudinal extent of species' distributions and variation in inter-annual variation in weather conditions across the range. Given that we focus on widely distributed species whose ranges are centred on a single region there is, however, an inevitable strong correlation between a population's relative range position and absolute latitude. Consequently, it is difficult to tease apart the effects of relative and absolute range position, with most of our range-edge populations being located in Spain and Finland. It is thus possible that butterfly populations in these two countries display heightened sensitivity to weather for reasons that are unrelated to range position. This seems unlikely, however, given that there are no systematic differences in site selection across schemes, nor did we find any influence of topographic heterogeneity on butterfly populations' sensitivity to weather. In principle, higher habitat quality or connectivity could also partly buffer butterfly populations from adverse conditions, thus reducing their apparent sensitivity to weather (e.g., Oliver et al., 2012); however, our focal countries in central Europe typically have greater agricultural

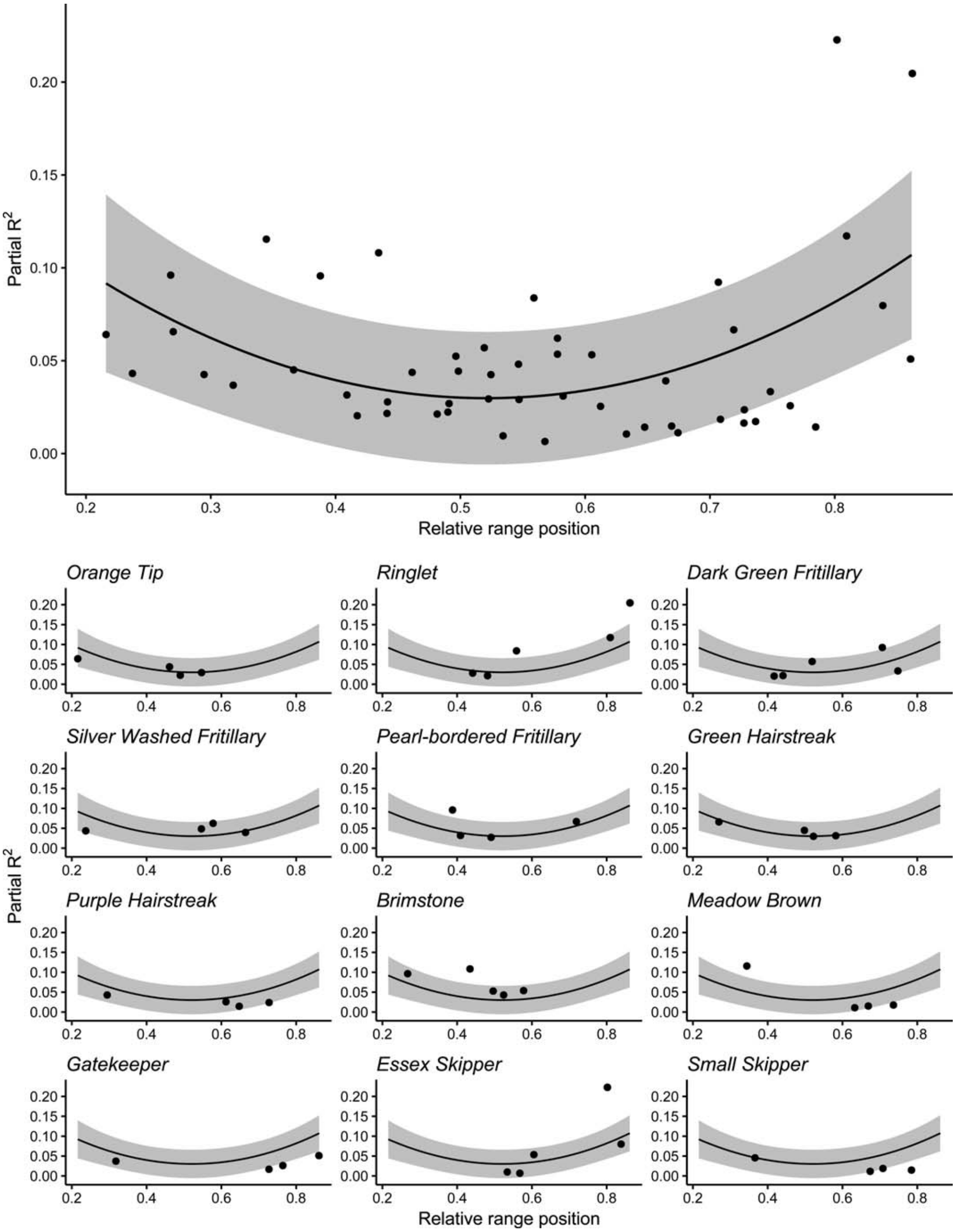

FIGURE 4 Partial R^2 values for the weather terms in each model by their relative position within the geographical range (i.e., each point is a species/latitudinal band combination). The upper panel displays partial R^2 values for all species; the lower panel displays same results, split by species. The fitted curve displays the quadratic model (best supported of the three alternative models), with 95% confidence band overlaid

intensification and habitat fragmentation and lower quality habitats than in Spain and Finland (EEA, 2016), which would act in opposition to the observed pattern.

One mechanism that could drive heightened sensitivity to weather at range edges is if species' range margins coincide with climatic tolerances (i.e., range limits are determined by climatic factors), as heightened sensitivity would then be expected in more peripheral regions of the species' range (Myers-Smith et al., 2015; Oliver et al., 2012). This may arise as a result of conditions towards the range edge becoming increasingly sub-optimal, resulting in relatively larger changes in organism performance as weather conditions vary. For example, if the 'performance curve' (Deutsch et al., 2008) that relates species' performance to weather is unimodal, with declines to either side of this optimum, the rate of change in fitness is relatively larger in more peripheral regions than in the range centre (Vasseur et al., 2014).

Importantly, if species displayed a strong degree of adaptation to local climate, we would not observe range-wide patterns in weather sensitivity, as species would be uniformly sensitive to local climatic

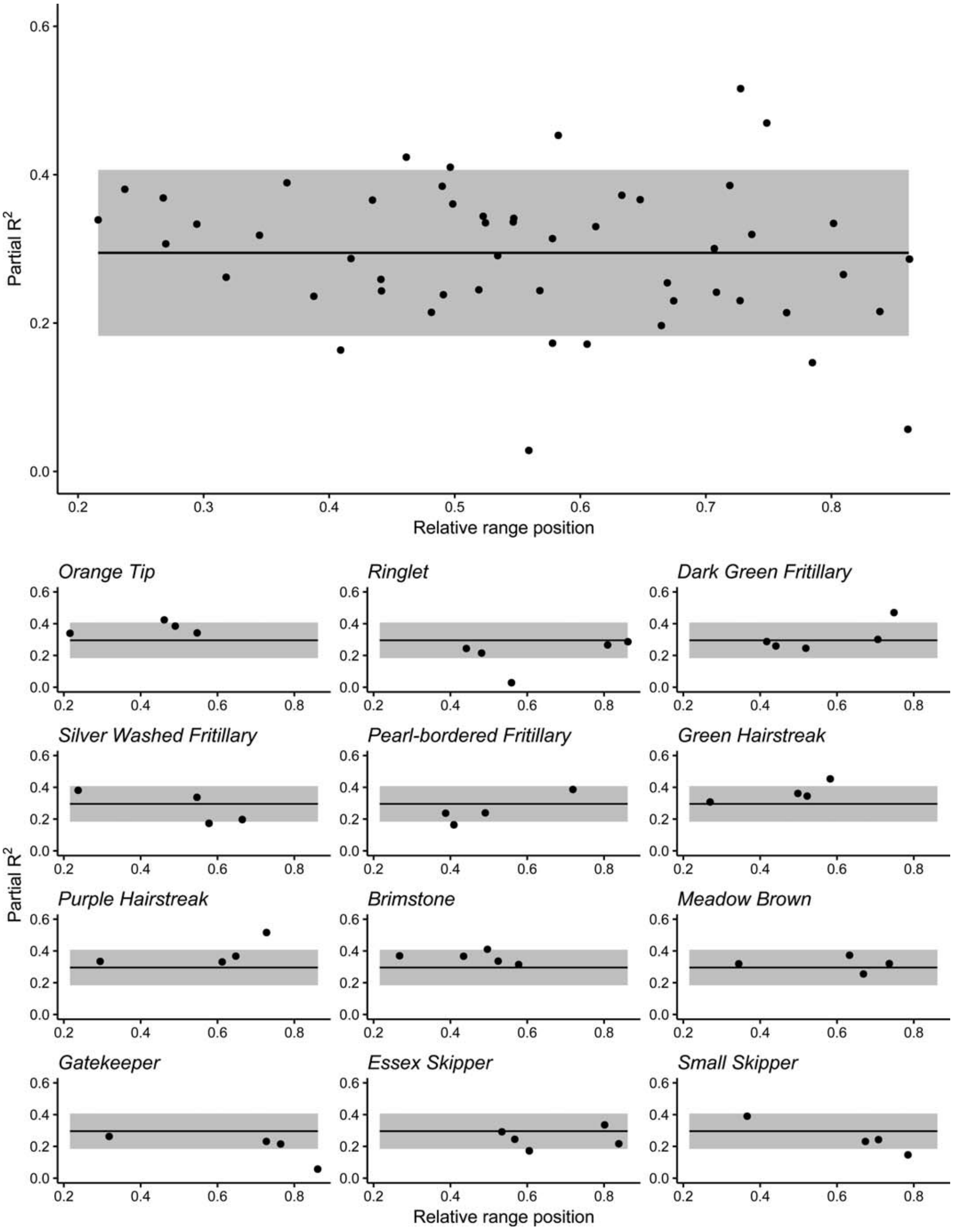

FIGURE 5 Partial R^2 values for the density dependence terms in each model by their relative position within the geographical range (i.e., each point is a species/latitudinal band combination). The upper panel displays partial R^2 values for all species; the lower panel displays the same results, split by species. The fitted line displays the intercept-only model (best supported of the three alternative models), with the 95% confidence band overlaid

conditions (Bennett, Wernberg, Joy, de Bettignies, & Campbell, 2015; Myers-Smith et al., 2015). Adaptation could arise as a result of intraspecific variation in tolerance (Fischer & Karl, 2010) or through behavioural plasticity, for example, behavioural thermoregulation (Buckley, Ehrenberger, & Angilletta, 2015). Our finding that increased sensitivity is observed towards the range edges thus suggests general limitations to these mechanisms of climatic adaptation and supports the hypothesis that latitudinal range limits are at least partly explained by climate. This complements previous results that document elevational range contraction for several European butterfly species in Spain (Wilson et al., 2005) and recent northern range-edge expansions as a result of climate change (Mair et al., 2012).

An alternative mechanism that could drive the observed increase in sensitivity towards range edges is a reverse density dependence effect. If factors such as density dependence are relatively more important in the species' range core than at the edges (i.e., show a reverse pattern to climatic sensitivity), these could mask climatic influences towards the range centre (Sæther et al., 2008). This could potentially

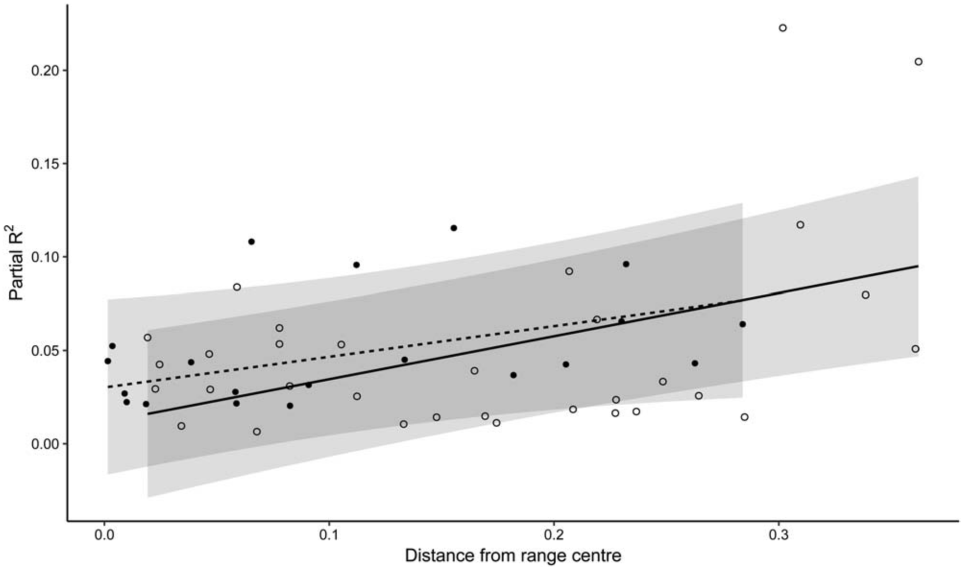

FIGURE 6 Model fits for asymmetry analysis. Plotted is each model's partial R_2 for the suite of weather terms against the distance from the range centre. Filled circles indicate points that lie in the southern range half [i.e., relative range position (RRP) < 0.5], whereas open circles indicate points that lie in the northern range half (i.e., RRP > 0.5). The modelled latitudinal relationship (outlined in the Methods) is illustrated with a dotted line for the southern range half and a continuous line for the northern part of the range (grey shading indicates the 95% confidence bands)

arise as a result of lower population densities towards the range edge or through variation in the importance of intra- or interspecific competition across the range (e.g., Leisnham, Lounibos, O'Meara, & Juliano, 2009). However, the lack of relationship in our results between latitudinal position within a species' range and density dependence effects suggests that the observed latitudinal gradient in climatic sensitivity exists independently of variation in the strength of density dependence.

The overall pattern that we find is one of heightened sensitivity to weather towards southern and northern range limits. Models of species' presence/absence data at coarse spatial scales typically indicate Gaussian response curves in relationship to long-term climate averages (Boucher-Lalonde et al., 2014), whereas species response curves that model changes in individual performance in relationship to short-term temperature are typically asymmetrical, with steeper declines above optima than below (e.g., Araújo et al., 2013; Deutsch et al., 2008). These respective relationships generate divergent expectations; the former suggests that range-wide sensitivities to weather conditions might be symmetrical, with weather being equally important at both range edges, whereas the latter suggests that asymmetry is likely to be observed. Asymmetry could also arise as a consequence of recent rapid climate change, with improving climatic conditions at northern range edges, combined with lagged response rates in northward range expansion (Devictor, Julliard, Couvet, & Jiguet, 2008), bringing northern populations closer to their optimal conditions and thus reducing sensitivity to local weather conditions (Oliver et al., 2012). In contrast, climatic degradation in southern Europe (warming and drying trends; Hartmann et al., 2013) may push populations at trailing range edges more frequently into peripheral regions of their performance curves, in which performance is more strongly affected by weather variation. Our ability to discern between these two competing hypotheses is somewhat limited, but our results fail to support the longstanding theory that abiotic limitation is relatively more important at northern range limits (Gaston, 2003).

Density dependence consistently appears to be a more important driver of population dynamics than weather, even in regions where sensitivity to weather is greatest. This suggests that, for many populations, fluctuations in weather conditions will be partly compensated for by density dependence effects, unless there are a large number of climatically adverse years in close succession (Oliver et al., 2015) or adverse conditions coincide with additional environmental change. It is unclear what the specific drivers of density dependence might be, but it is possibly caused in part by host plant resource availability and responses to natural enemies (e.g., Boggs & Inouye, 2012). Although our density dependence estimates are in line with other studies that use similar methodologies and/or datasets (e.g., Nowicki et al., 2009; Roy, Rothery, Moss, Pollard, & Thomas, 2001), observation error is known to inflate the strength of negative density dependence (Freckleton, Watkinson, Green, & Sutherland, 2006). A caveat that therefore applies to our results (and others, such as the cited studies) is that, owing to the imperfect correspondence between true and measured abundance, our estimates of density dependence may be overestimates (Freckleton et al., 2006). However, as the abundance measures used here are informed by many observations collected over the course of the season (Dennis et al., 2013), we expect any biases arising from observational error to be relatively small.

Both temperature and precipitation appeared to have important effects on butterfly population dynamics, with no clear distinction between the two in terms of either their coefficient estimates or statistical significance (Supporting Information Table S2). Although temperature is often assumed to be a key driver of organism performance, these results suggest that it is important to consider the role of precipitation in addition to temperature, which has particular relevance for forming accurate forecasts of population performance under climate change (McDermott Long et al., 2016; Sinclair et al., 2016). There also appears to be substantial intraspecific variation in the precise form of the weather associations across the range, which many species distribution modelling approaches explicitly assume is not the case. Further exploration of this intraspecific spatial variation in population dynamics in response to weather is thus an important area of future study.

The size of the datasets used here necessitated the pooling of observations both within latitudinal bands and across species (in the mixed-effects framework). Although the overall pattern is one of increased sensitivity towards range margins, this result is tempered by the typically weaker within-species pattern and the limited number of observations for any single species. Future work to investigate range-wide patterns of sensitivity to various environmental drivers at a finer spatial grain for individual species would thus be of considerable interest.

The observation that heightened sensitivities to weather occur towards the latitudinal limits of butterflies adds to previous work documenting directional patterns of sensitivity across climatic gradients (e.g., Ettinger et al., 2011; Myers-Smith et al., 2015). In particular, we were able to extend previous work by investigating patterns that occur towards both range edges simultaneously, rather than one in isolation. There are two key implications of this work. Firstly, the existence of heightened sensitivity at range edges suggests that population-level responses to ongoing climatic change will not be uniform across the range, but are likely to be greatest at species' range boundaries where population dynamics are most strongly determined by weather. Secondly, because sensitivity to weather varies across species' latitudinal range extent, caution is required when extrapolating from studies conducted in part of a species' range or when using projection methodologies that do not take intraspecific variation in responses to weather into account.

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DATA ACCESSIBLITY

Elevation data are available from https://lta.cr.usgs.gov/GMTED2010. Weather data are available through the ECAD project (http://www.ecad.eu/). Butterfly data are available on request through national scheme co-ordinators (http://www.butterfly-monitoring.net/ebms).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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