

Grizzled Skippers stuck in the south: Population-level responses of an early-successional specialist butterfly to climate across its UK range over 40 years

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Abstract

Aim: Climate change has been predicted to facilitate poleward expansion of many early-successional specialist invertebrates. The Grizzled Skipper, *Pyrgus malvae*, is a threatened butterfly in long-term decline that has not met expectations of northern expansion in Britain, possibly indicating that climate change has not improved northern habitat suitability or that another driver (e.g. land use change) is masking its effects. Here, we explore the effect of climate on population size trends over four decades, and whether any regions show an improving population trend that may be a precursor to northern expansion. Examining detailed spatio-temporal abundance data can reveal unexpected limitations to population growth that would not be detectable in widely used climate envelope models.

Location: Central and southern England.

Methods: Mixed models were used to investigate *P. malvae* population size in relation to time and monthly climate measures across its UK range since 1976, based on repeated transect walks.

Results: We found that *P. malvae* population size declined more over time in the north and west of its UK range than in the south and east, and was negatively related to high December temperature and summer rainfall. However, the effect sizes of temperature and rainfall were minimal.

Main Conclusions: The last 40 years of climate change have not ameliorated climate suitability for *P. malvae* at its range edge, contrary to expectations from spatial-only climate envelope models. The clear long-term downward trends in population size are independent of climate change and we propose probably due to habitat deterioration. Our findings highlight potential hazards in predicting species range expansions from spatial models alone. Although some climate variables may be associated with a species' distribution, other factors may be more dominant drivers of trends and therefore more useful predictors of range changes.

KEYWORDS

climate change, conservation, lepidoptera, modelling, range changes

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1 | INTRODUCTION

Temperatures have been increasing globally since the mid-20th century (Intergovernmental Panel on Climate Change, 2014; Met Office, 2019), with increasing regularity of extreme heat and drought summer events, and longer growing seasons (Met Menzel et al., 2020; Office, 2019). It has been predicted that in a scenario of ambient warming, species' geographical ranges may shift in order to track their climate envelopes, predominantly polewards and to higher altitudes (Parmesan et al., 1999; Root et al., 2003). For early-successional specialists that frequently require warmer microclimates within their range, range changes may result from an ability to occupy later seral stages under warming conditions, hereby becoming less specialized and less reliant on early-successional habitats (Komonen et al., 2004; O'Connor et al., 2014; Thomas et al., 1999). Less specialized habitat requirements may enable species to expand their cover within and beyond current population boundaries (Settele et al., 2008; Thomas et al., 2001). Some early-successional species, such as the Brown Argus butterfly (*Aricia agestis*), appear to have already broadened their habitat niche as a result of warmer summers, and expanded polewards (Pateman et al., 2012). However, one early-successional specialist that has not responded to climate change as expected is *Pyrgus malvae*, the Grizzled Skipper butterfly, that has declined in the UK by 55% between 1976 and 2018 (Brereton et al., 2019).

Expectations of range expansions and shifts are not unique to early-successional specialists (Chen et al., 2011; Davis & Shaw, 2001), but in particular *P. malvae*, like other southern restricted and warm-preferring species, is expected to benefit from warming temperatures in large part due to its requirements for warm microclimates for oviposition and development during temperature-sensitive immature stages (Krämer et al., 2012; Weiss et al., 1988). As early-successional specialists like *P. malvae* often rely on the presence of warm microclimates to persist in cooler areas, such as at higher altitudes or more poleward locations, their habitat breadth in those cooler locations may be narrower than in warmer areas in southern Europe (van Swaay et al., 2006). Therefore, an increase in temperature in the northern parts of *P. malvae*'s range may increase breeding habitat availability and facilitate increases in abundance and subsequent range expansions. However, contrary to predictions of poleward expansion under a warming climate, no indication of natural northern expansion has been observed in *P. malvae* (National Biodiversity Network 2020), and declines have been observed that on average do not appear to have slowed in the last decade, despite warming conditions (Brereton et al., 2019; Fox et al., 2015). Similar observations of species not fully tracking their expanding range limits have been made across several taxonomic groups and countries (Bertrand et al., 2016; Devictor et al., 2012; Vanderwal et al., 2013; Warren et al., 2001).

Although there has not yet been evidence of northern expansion by way of colonizations beyond the current north range edge, investigating changes in abundances of northern populations could provide insight into the likelihood of imminent expansion. Increasing

abundances close to the range edge of *Pyrgus malvae* have been found previously to represent an intermediate step prior to colonization (Maggini et al., 2011). Therefore, investigating whether *P. malvae* abundance is showing increases at poleward range limits over time could provide an early indication of increasing climate suitability as would be expected from spatial-based predictions. Spatial-based predictions alone may not be able to fully capture limitations to expansion, such as dispersal capacity and biotic habitat requirements, so assessing trends over time and space may offer a more accurate reflection of potential range changes. In addition, exploring the effects of climate variables on population abundance could provide further insight into the role that climate plays in influencing long-term trends, and differences in regional trends if they are found.

1.1 | Aims

Here, we aim to explore the effect of climate on long-term population size trends, and whether UK Butterfly Monitoring Scheme (UKBMS) indices of population size at UKBMS sites are decreasing at differing rates between regions. Population size trends differing with latitude/longitude is of interest as relatively positive trends in population size may be a precursor to northern expansion (Maggini et al., 2011; Mair et al., 2014).

We hypothesize that if climate change is ameliorating declines in *P. malvae* in the UK, climate predictors will account for a large portion of variation in abundance otherwise explained by time, thereby emerging as a dominant driver of long-term trends. In addition, if climate is the limiting factor for northern range expansion, but range edge conditions are becoming more suitable under climate change, abundance will have relatively positive long-term trends at higher latitudes.

2 | METHODS

Pyrgus malvae is found in early seral stages of grassland, woodland and brownfield habitats (Brereton et al., 1998) in the UK. However, its range has contracted, having lost its northern most population in York in the 1990s and having gone locally extinct in several counties, including in Derbyshire in 2007, where it is currently the focus of reintroduction efforts (Butterfly Conservation, 2018). Another reintroduction was attempted at Gait Barrows in Lancashire in 2002 (geographical locations shown for reference in Figure 1), where it had occupied habitat in the early 20th century, but the population is believed to have gone extinct in 2007 (Coleman, 2017).

The UK Butterfly Monitoring Scheme is a long-term coordinated recording scheme for butterflies in which a core component is a network of more than 2000 sites at which adult butterflies are counted weekly over the flight season between April and September (Brereton et al., 2019; Pollard & Yates, 1993). The weekly butterfly counts are used to produce annual indices that account for missing weeks, and this index can be used as a proxy for a species' population

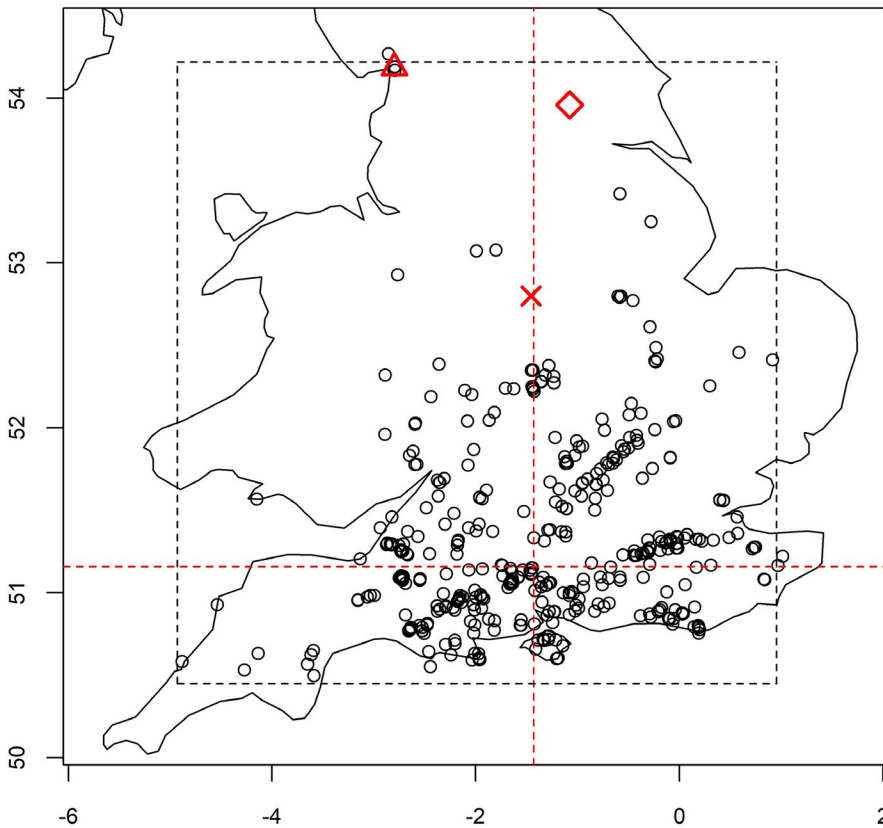


FIGURE 1 Map showing the geographical distribution of UKBMS sites included within analyses, where each site is represented by a black circle. The black dashed lines depict the total range of all UKBMS sites with Grizzled Skipper records. The red dashed lines depict the median latitude and longitude of all records used in analyses. Locations of *P. malvae* extinctions and reintroductions are shown as red symbols; the Derbyshire reintroduction site (cross), Lancashire reintroduction site (triangle), Yorkshire extinction site (diamond)

size at a site (Rothery & Roy, 2001). Henceforth, “Population Index” is used to mean the *P. malvae* annual abundance index at a given UKBMS transect site, which is calculated from a generalized additive model (Rothery & Roy, 2001). Mixed models were used to investigate *P. malvae* population size in relation to year and relevant monthly climate measures across its UK range in the survey period of 1976–2016.

Climate data were obtained from Met Office data at 5×5 km resolution, as monthly mean temperature, and monthly rainfall values (mm) (Perry, 2005). Each population index value was matched to the climate data from its own 5 km square, for the months from June of the previous year to May of the year of the record (inclusive). This time window was chosen to span the life stages of a single generation from the larval period to the following flight period. Mean monthly temperature and rainfall were chosen for ease of interpretation and generality (Palmer et al., 2015; Pollard, 1988). Preliminary investigation of three-month pooled climate values did not produce notably different or more significant effects on population index than monthly mean temperature and rainfall (Appendix S1).

A total of 483 sites, mapped in Figure 1, were available that had at least one year with sufficient data to produce an annual population index during the survey period, and fell within a 5 km grid square with Met Office data. Year-site combinations with *P. malvae* presence but with too few visits to estimate a population index (according to UKBMS criteria) were omitted.

Generalized linear mixed effects models were run using the R package “lme4” (Bates et al., 2015). The error family used was negative binomial to account for a high proportion of zeros in the

population index data (38%). To prevent convergence issues, all predictor variables were standardized by subtracting the mean of each variable, and dividing by the standard deviation.

In all models, to account for pseudoreplication, as sites were visited repeatedly, and for stochastic variation between years and regions across the country, year, site number and 50×50 km grid squares (Total: 59) were introduced as random factors. Our approach did not account for population size in the previous year, because of the limited number of UKBMS records with visits to the same site the prior year. 50×50 km square was selected as the appropriate size in order to minimize the number of grid squares with very few sites, and at a high enough resolution to isolate geographic aggregations of sites with unusually high residual errors from the model when 50×50 km square is not included as a random effect. Model fit was evaluated using AIC comparisons, and validated by assessing heterogeneity in residuals.

We ran three sets of statistical models to elucidate the effects of climate versus potentially co-varying effects of geography. The final minimum adequate model was then used to explore the impact of climate on long-term population index trends.

2.1 | Non-climate predictors

To assess how population size has changed over time across the UK geographical range, irrespective of climate, models were first run containing only year, latitude and longitude as fixed effects. A model was run for each of these fixed effects independently, and then with

all effects, and two-way interactions, with AIC stepwise regression to obtain the minimum adequate model (MAM01).

The initial maximal model (MM01) therefore can be described as:

$$\begin{aligned} \text{Population index} \sim & \text{Year} + \text{Longitude} + \text{Latitude} + \text{Year} \times \text{Longitude} \\ & + \text{Year} \times \text{Latitude} + \text{Longitude} \times \text{Latitude} \\ & + (1|50 \text{ km grid square/Site}) + (1|\text{Year}) \end{aligned}$$

Upon running the final model, we observed a large difference between the real and predicted population index values at the beginning of the recording period in the north-west of the study area. As we believed this to be due to data scarcity for this space and time, we reran a model omitting data prior to 1990, and the outputs were qualitatively unchanged (Appendix S2).

2.2 | Climate predictors

To explore the effect of climate in each month independently, and to avoid auto-correlation between months, individual models were run for each monthly climate value as the only fixed effect, for both temperature and rainfall (24 total models).

An example of one such model can be described as:

$$\begin{aligned} \text{Population index} \sim & \text{Previous July Temperature} \\ & + (1|50 \text{ km grid - square/Site}) + (1|\text{Year}) \end{aligned}$$

All variables found to have a significant effect were included in a single model, with no interactions, to better identify variables that may be accounting for similar variation in population index. The least significant fixed effect was removed in a stepwise manner to minimize AIC and arrive at the minimum adequate model for climate effects (MAM02).

2.3 | All predictors

To assess how much of the trends over time and geography observed in MAM01 (Section i.) can be explained by climate effects, all monthly climate measures included in MAM02 were added to model MAM01, to create the third maximal model MM03. Stepwise AIC regression was used subsequently to determine the final minimum adequate model, with both climate and non-climate predictions (MAM03).

The initial maximal model (MM03) can be described as:

$$\begin{aligned} \text{Population index} \sim & \text{Year} + \text{Longitude} + \text{Latitude} \\ & + \text{Year} \times \text{Longitude} + \text{Year} \times \text{Latitude} \\ & + \text{Previous December Temperature} \\ & + \text{Previous June Rainfall} \\ & + \text{Previous July Rainfall} \\ & + \text{February Rainfall} \\ & + (1|50 \text{ km grid - square/Site}) + (1|\text{Year}) \end{aligned}$$

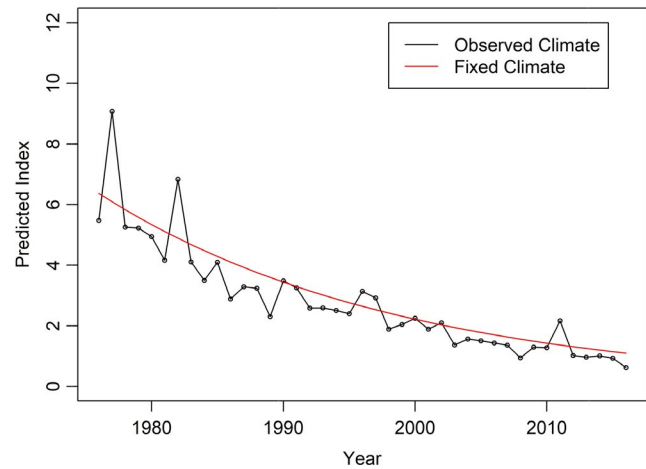


FIGURE 2 Temporal trend in modelled *P. malvae* UKBMS index at a centrally located UKBMS site between 1976 and 2016 under scenarios of fixed and changing climate conditions. Indices are predicted from the minimal adequate model of climate and non-climate effects (MAM03), without including random effects. Modelled index values when climate parameters are kept fixed at mean values from 1976 to 1980 are shown by the red line, while modelled index values when climate parameters represent actual climate data for the focal 5 × 5 km square are shown by the black line

2.4 | Predicting indices under different climate conditions

Having established the minimum adequate model containing both climate and non-climate predictors (MAM03), we explored the extent to which fixing local (5 × 5 km) climate conditions at the mean climate values for the first five years of the study (1976–1980) would have hypothetically altered temporal trends, and population indices in the longer term. A comparison of trends under observed and fixed climate conditions was made for a subset of sites at a range of latitude and longitude values within the *P. malvae* UK range (Figure 2, Appendix S3).

In addition, to further investigate possible trends in climate suitability for *P. malvae* over space and time, we estimated climate suitability using just climate effect coefficients from MAM03 and mean climate values for four regions within the study area, the dimensions of which are presented in Figure 1. The outputs are presented in Appendix S4.

3 | RESULTS

Population index henceforth refers to the *P. malvae* annual abundance index at a given UKBMS transect site. For models involving only non-climate predictors (Methods Section i.), year, in isolation, had a significant negative effect on population index (Est. coef = -0.16, Std. error = 0.05, $p = .001$), but no effect was observed of latitude (Est. coef = -0.19, Std. error = 0.11, $p = .088$) or longitude (Est. coef = 0.06, Std. error = 0.11, $p = .588$) in isolation. The

minimum adequate model MAM01 included interactions between year and latitude, and year and longitude (ΔAIC from the next best fitting model (Year only) = -31.6).

The interaction of longitude and year was positive (Est. coef = 0.12, Std. error = 0.03, $p = <0.001$), and latitude and year was negative (Est. coef = -0.14 , Std. error = 0.03, $p = <0.001$). These interactions suggest, in the absence of other unknown variables correlated with spatial gradients, that trends in population index over time are more negative in the north and west (Table 1, geographical differences illustrated in Figure 3).

When considering effects of climate one by one (Methods Section ii.), we found significant negative effects of December and January temperature, and previous June and previous July rainfall, and a positive effect of February rainfall (Appendix S1). Not all of these effects remained significant when added to a single model; the effects of January temperature, February rainfall and previous July rainfall were the least robust (Appendix S1; Table 1).

The fit of the minimal adequate non-climate model (MAM01) was improved by the inclusion of December temperature, and February, June, and July rainfall effects (ΔAIC from MAM01 = -20.2 , Table 1). Interestingly, neither July nor February rainfall effect was significant when both were included in the model, but when either variable was singly removed, the remaining variable became significant, and the fit of the model was slightly improved (Table 1). However, neither resultant model was a notably better fit than the other ($\Delta\text{AIC} = 0.4$; Table 1), and there was little change in the effect size or significance of other variables. For the purposes of reporting, the final model (MAM03) included climate effects of December temperature, February and June rainfall.

The inclusion of climate slightly reduced the effect size of longitude and latitude on trends over time (Table 1), but the effect size of climate itself remained small overall (Figure 2). In the final model (MAM03), a one degree increase in December temperature was estimated to account for a log decrease of 0.08 in population index (Table 1). Similarly, a 5cm increase in June rainfall accounted for a log decrease of 0.09 in population index. In contrast, a 5cm increase in

February rainfall accounted for a log increase of 0.08 in population index (Table 1).

The effect size of climate is shown in Figure 2 for one site centrally located within *P. malvae*'s UK range (Site Number 2345), but equivalent figures for a group of sites across the range can be found in Appendix S3. Comparing modelled population indices based on either observed annual climatic values, or fixed climatic conditions from 1976 to 1980 revealed a minimal effect of climate in long-term population index trends. Climate's small effect size suggests that climate trends in isolation explain very little of the index declines observed over time (Figure 2). Correspondingly, there are similar trajectories of modelled index values regardless of whether climate parameters are fixed or change as observed. Also, when we plot combined climate suitability based on MAM03, we found no significant trends over time in any of the four regions mapped (Appendix S4).

No patterns in residuals were immediately observable when plotting model residuals against year, latitude, longitude or climate values not included in that model, so no evidence was found for a change in the nature or size of the effect of temperature at different rainfall levels, or vice versa, or over time and space.

4 | DISCUSSION

In this investigation, we explored spatial, temporal and climatic effects at a 5-km resolution on *P. malvae* population size at monitored UKBMS sites, in order to increase understanding of the role of geography and climate in the long-term trends of the declining butterfly. We used a mixed-model approach to control for increasing survey effort over time, and stochastic variation between years and regions. We observed no significant positive effects of temperature on population index; population index henceforth refers to the *P. malvae* annual abundance index at a given UKBMS transect site. In the best fitting model, December temperature and June rainfall had significant negative effects on population index, while February rainfall had a positive effect on population index. However, the effect sizes of all climate variables were very small

TABLE 1 The coefficients of fixed effects, and model weightings from a subset of models run with the same response data

Model	Intercept	Longitude	Latitude	Year	Long:Year	Lat:Year	Feb Rain	July Rain	June Rain	Dec Temp	df	AICc	Delta AIC
MM03	0.95	0.05	-0.21	-0.17	0.11	-0.13	0.07	-0.06	-0.08	-0.17	14	23,921.1	0
MAM03	0.95	0.06	-0.22	-0.18	0.11	-0.13	0.08		-0.09	-0.17	13	23,922.3	1.16
(i)	0.95	0.03	-0.22	-0.16	0.11	-0.13		-0.07	-0.10	-0.17	13	23,922.7	1.51
(ii)	0.95	0.06	-0.22	-0.17	0.11	-0.13	0.09	-0.08		-0.18	13	23,923.7	2.58
(iii)	0.94	0.07	-0.19	-0.18	0.11	-0.13	0.08	-0.06	-0.09		13	23,927.9	6.75
MAM01	0.94	0.06	-0.20	-0.19	0.12	-0.14					10	23,941.3	20.14
MAM02	0.93						0.09	-0.09	-0.09	-0.18	9	23,954.6	33.44

Note: Each row shows the outputs of a model using a unique combination of fixed effects. Models included are (a) MAM01 minimal adequate model with only non-climate effects, (b) MAM02 minimal adequate model with only significant climate effects and (c) MM03 maximal model with non-climate and significant climate effects, and subsequent models with a singular climate effect removed (i–iii). Models ordered in table by AICc weighting.

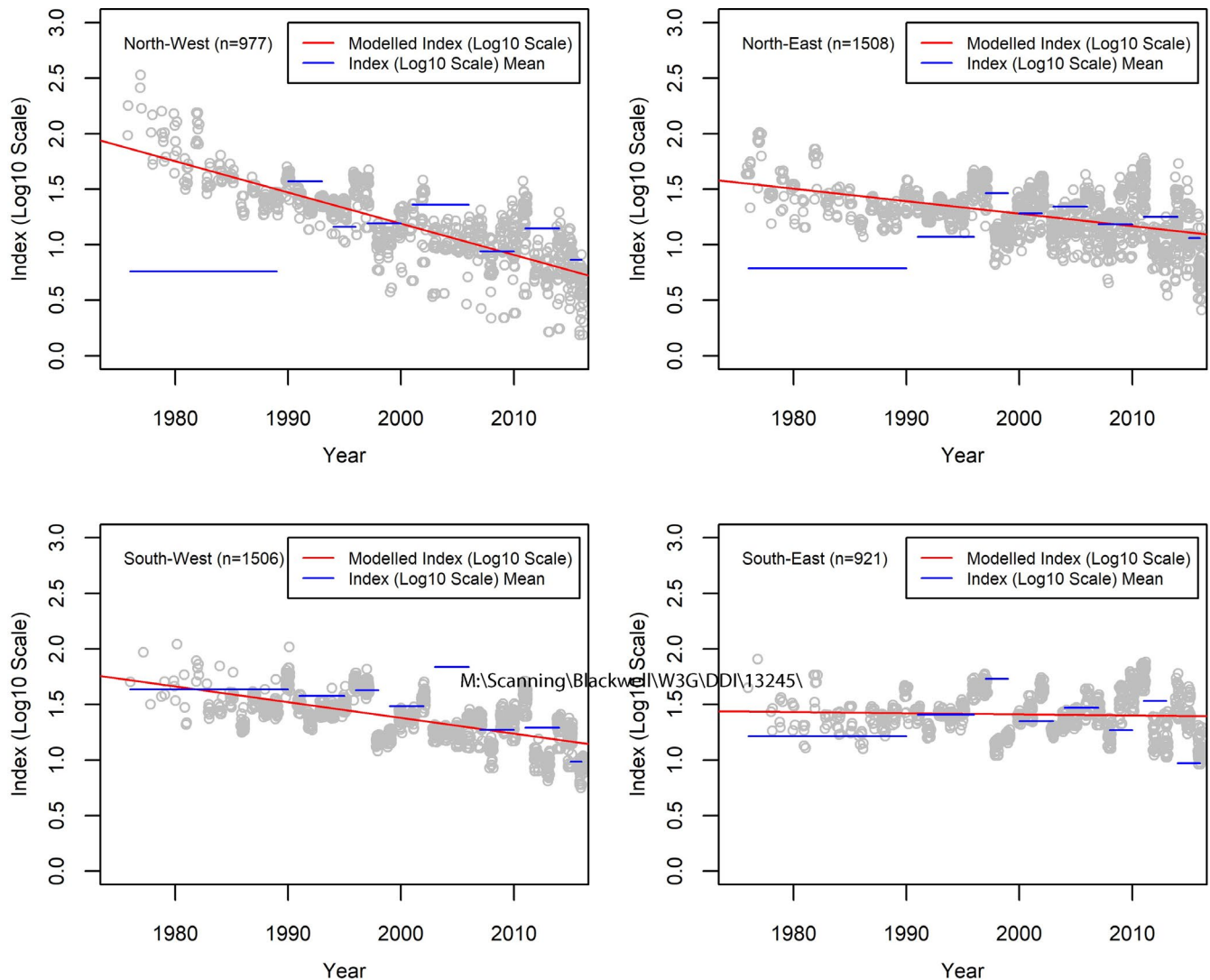


FIGURE 3 Modelled temporal trends of *P. malvae* index divided into north-west, north-east, south-west and south-east regions by the median latitude (51.16) and longitude (−1.43) values of UKBMS sites with records. The modelled log index values for each UKBMS record are shown by grey circles, with jitter of ± 0.2 so points can be more clearly seen. These indices are fitted values (before including random effects) from the minimal adequate model of non-climate and climate effects (MAM03), including year, latitude, longitude and climate effects. Blue lines show the logarithmic mean of observed indices for eight time slices in each region, each covering one of eight quantiles of the data. To clarify modelled trends, linear regression between predicted log index values and year are shown by the red lines. Number of UKBMS records (n) in each region is displayed in each graph

(Table 1). Climate effects manifested between years and across space, but there was little, if any, long-term trend in any of the above climate variables (Appendix S5). In addition, when modelling population index purely as the product of climate effects from the final model, climate suitability did not significantly change over time, which was a consistent finding in all four regions shown in Figure 3 (Appendix 4). As such, the climate effects were largely independent of overall declines in population size which occurred more steeply in the north and west of the range than in the south and east. Our result contradicts predictions of northern expansion for this warm-preferring invertebrate species based on a climate envelope approach (Settele et al., 2008), but is consistent with reports of southward constrictions in *P. malvae*'s range over time (Mair et al., 2012).

4.1 | Climate effects

We found no significant positive impacts of temperature on population index in any month (Appendix S1), which would not suggest that the *P. malvae* is overall benefitting from climate warming during its temperature-sensitive life stages.

To the contrary, we observed a negative effect of December temperatures on population index, which corroborated established detrimental effects of warm winters on a variety of invertebrates (McDermott Long et al., 2017; WallisDeVries & van Swaay, 2006). Suggested mechanisms for which include higher fungal infection rates (Harvell et al., 2002; Radchuk et al., 2013), and phenological asynchrony (Parmesan, 2007) at higher temperatures. One study posited that warmer winters impacted Lepidoptera species

overwintering in temperature-sensitive immature life stages more negatively than those overwintering as adults (WallisDeVries & van Swaay, 2006). WallisDeVries & van Swaay theorized that warmer winters result in reduced vegetation die-back, and earlier and longer growing seasons. Consequently, as live vegetation generates cooler microclimates than bare ground or dead vegetation (Stoutjesdijk & Barkman, 1993), species with life stages restricted to warm microclimates during the spring may be negatively impacted by warm winters through this indirect mechanism.

However, early-successional specialists, such as *P. malvae*, frequently rely on warm microclimates even when immature life stages occur after spring (Brereton *et al.*, 1998; de Schaetzen *et al.*, 2018; Asher *et al.*, 2001), particularly in cooler locations (e.g. at cool range margins). Early-successional specialists may therefore also be impacted by greater total vegetative biomass, and cooler microclimates, resulting from longer and earlier growing seasons following warmer winters. Similarly, populations of temperature-sensitive species in general at their cool range edges could be affected by cooling of microclimates relied upon for refuge from cooler ambient conditions (Oliver *et al.*, 2009).

Lusher vegetation growth may also be a potential mechanism underlying the observed negative effects of June rainfall on *P. malvae* abundance (Appendix S1), because late instar caterpillars are feeding in June; similar effects have been observed previously in *P. malvae* (Pollard, 1988; Roy *et al.*, 2001; WallisDeVries *et al.*, 2011). Given that a model not including the effect of February rainfall was of a similar fit to the minimal adequate model with February rainfall (MAM03), we are cautious about the implications of this effect. The reported effect of February rainfall may be an artefact of its correlation with July rainfall in this data set, given a negative effect of summer rainfall on *P. malvae* abundance having precedence in the literature (Pollard, 1988; Roy *et al.*, 2001; WallisDeVries *et al.*, 2011).

4.2 | Role of climate in declines

While the climate effects were significant, the effect sizes were small, and they did not account for long-term trends in population index, or for geographical differences in those trends. Modelling population index over time revealed similar long-term trends in both unchanging, and observed climate scenarios (Figure 2). Climate's limited role in long-term trends may result from an absence of significant trends in combined climate suitability between 1976 and 2016 in *P. malvae*'s UK range (Appendix S4). Climate did appear to play a larger role in short term yearly variation (Figure 2). Similar findings regarding climate driving short-term variation in abundance between years in a related species, *Pyrgus armoricanus*, were also recently reported, in conjunction with a limited effect of temperature on colonization and extinction dynamics relative to the effects of connectivity and host plant density (Fourcade *et al.*, 2017).

Furthermore, inclusion of climate predictors in the final model did not qualitatively change the effects of interactions between

geography and time on *P. malvae* population index (Table 1), suggesting the climate effects are not the drivers of steeper temporal declines in the north and west than the south and east, respectively. Correspondingly, climate suitability does not show differing temporal trends in any of the geographic subsets shown in Figure 3 (Appendix S4).

Although this study's scope does not extend to estimating *P. malvae* population sizes under future climate scenarios, Met Office predictions (Met Office, 2019) of generally dryer summers may lead to increases in population sizes, while warmer winters may lead to decreases. Some multispecies studies have reported *P. malvae* as "a climate change loser" (Brereton *et al.* In submission), but our results suggest that *P. malvae* is neither a winner nor loser from recent climate change. It is possible that simple temporal correlations could mis-attribute a species' long-term declines to any climate variable that also has a strong trend; this underlines that both space-only and time-only analyses have potential pitfalls.

4.3 | Drivers of decline

We show strong evidence of long-term abundance declines between 1976 and 2016, especially in the northern and western parts of the UK range. We argue that any simple climate mechanism behind these declines would have been identified with our statistical tests and therefore are left with the conclusion that a non-climatic driver is behind the declines, most likely habitat loss and degradation (Brereton *et al.*, 1998).

Early-successional semi-natural habitats (e.g. chalk downland, coppice woodlands), once widespread across the UK and central Europe (Fuller & Warren, 1993; Green, 1990; Wesche *et al.*, 2012), have undergone large-scale losses resulting from agricultural intensification (Bonari *et al.*, 2017; Ridding *et al.*, 2015; Walker *et al.*, 2009), especially since the Second World War (Green, 1990; Robinson & Sutherland, 2002). Corresponding declines have been observed in specialist invertebrates (Kuussaari *et al.*, 2007; Wenzel *et al.*, 2006), including southern restricted butterfly species (Thomas *et al.*, 2015). Furthermore, the quality of remaining habitat has deteriorated in places due to abandonment and changes in natural grazing pressure, such as those resulting from losses of rabbit populations to myxomatosis (Sumption & Flowerdew, 1985; Travers *et al.*, 2019).

In recent decades, some semi-natural grasslands have been restored or improved through rabbit population recoveries (Thomas *et al.*, 2011), and agri-environment scheme introductions, with some proven benefits to butterflies (Brereton *et al.*, 2011; Davies *et al.*, 2005). However, early-successional deciduous woodland habitat quality continues to show an overall decline in the UK, owing to management costs and logistic difficulties. (Atkinson & Townsend, 2011; Keith *et al.*, 2009; Kirby *et al.*, 2017). Contrastingly, coppiced woodland status varies between regions of Central Europe, as a result of silvicultural intensification and abandonment (Bergmeier *et al.*, 2010), leaving the future status of *P. malvae*'s habitat availability uncertain.

Additionally, north-west populations may have been more sensitive to changes in habitat quality than those in the south-east, particularly at the historical northern cool range margin. Populations at cool range margins can be more reliant on warm microclimates than those in the centre (Hodgson et al., 2015; Suggitt et al., 2018), so shifts to later successional stages may be more detrimental to cool range edge-based populations. *P. malvae* has also been shown to have higher habitat specificity at sites with higher rainfall, potentially amplifying detrimental effects of succession (Mair et al., 2012).

This brings us back to the idea that climate warming (in general, but especially in winter and spring) can lead to accelerated vegetation growth in temperate climates and reduce bare ground availability, essentially accelerating succession (Zhou et al., 2001). Some early-successional species may be affected more by this than by the opposing effect that ambient warming makes even tall vegetation warmer. This makes it particularly difficult to plan for the conservation of early-successional habitat specialists, which tend to be threatened across Europe (Kuussaari et al., 2007; van Swaay et al., 2006) as well as in the UK (Thomas, 1993; Thomas et al., 2015). We might expect each species to respond idiosyncratically to climate change at its cool range margin, depending on the precise balance of the opposing effects.

Habitat availability and climate suitability interact, so for species like *P. malvae*, it is a conservation priority to boost populations by improving habitat condition, both for the direct benefits obtained, and to indirectly allow the species to track climate if and when suitability improves. There is increasing empirical evidence that climate-driven range shifts are slower or impossible if there is insufficient habitat availability (Devictor et al., 2012; Platts et al., 2019). For *P. malvae*, overall declines in population size over time, and more negative trends in the north than the south, as was observed (Figure 3), suggest a low likelihood of poleward expansion in the near future (Maggini et al., 2011). Nevertheless, alleviating the non-climatic threats to the species could lead to an expansion of range as well as abundance. This could be important for the global status of the species because as the entirety of the UK is still northerly within *P. malvae*'s overall range, and it may be suffering from heatwaves or droughts at its extreme southern limits.

The complex interactions between habitat and climate discussed so far complicate predictions of habitat suitability when considering range shifts. Species distribution models based only on spatial data (e.g. occurrence) may not fully account for other habitat requirements that limit the potential for a species to exploit opportunities in otherwise climatically suitable habitats. Predictions of range shifts/expansions are particularly vulnerable in a non-equilibrium system, such as one undergoing changes in climate and land management as is the case in many systems across the globe (Elith & Leathwick, 2009). The findings of this study reinforce the need to consider other key habitat requirements and dispersal/colonization limitations when planning conservation actions that attempt to consider the effects of climate change on range changes (Devictor et al., 2012; Greiser et al., 2020; Oliver et al., 2012; Platts et al., 2019).

DATA ACCESSIBILITY STATEMENT

The data that support the findings of this study are available upon request from the Natural Environment Research Council's Data Repository for Atmospheric Science and Earth Observation (climate data)¹, and Centre for Ecology and Hydrology (UKBMS data)². Restrictions apply to the availability of these data, which were used under licence for this study. 1: <https://catalogue.ceda.ac.uk/uuid/94f757d9b28846b5ac810a277a916fa7>. 2: <https://www.ukbms.org/obtaining>

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PEER REVIEW

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BIOSKETCH

Fiona Bell's current research focus is on climate change, land use change, the interactions of drivers of decline, and the conservation of threatened species, with a particular interest in lepidoptera, that is the Grizzled Skipper (*Pyrgus malvae*), which is the focal species of her ongoing PhD.

SUPPORTING INFORMATION

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

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