


RESEARCH ARTICLE

Testing space-for-time transferability of climate effects on occupancy and abundance

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Abstract

1. Species distribution models (SDMs) are frequently used to project species' ranges under future climate conditions. Such space-for-time substitutions rely on the assumptions that spatial climate-distribution relationships are causal and that relationships are equivalent over space and time. These assumptions have rarely been tested.
2. Using UK populations of the Orange-tip butterfly (*Anthocharis cardamines*) as a case study, we demonstrate an approach to test whether these key assumptions are met. First, we identified the seasonal periods over which temperature and precipitation variables best explained the Orange-tip butterfly's abundance. Then, we compared the effects of climate variables on both occupancy and abundance over space versus time.
3. We found that, over both space and time, temperature in the previous year's flight period has a positive effect on the occupancy (i.e. presence) and abundance of the Orange-tip butterfly, whereas precipitation appeared not to have a causal effect. We found that temporal effects of temperature on abundance did not differ from spatial effects at colder sites, but at warmer UK sites, the magnitude of these effects significantly differed. Conversely, spatial and temporal effects of temperature on occupancy did not differ at warmer (mid-range) sites, with effect magnitudes significantly differing at colder sites.
4. Our results demonstrate the importance of identifying causal climate-distribution relationships before making projections. We also show that the reliability of SDM projections over time can be highly context dependent, even when considering a single species. Therefore, where data are available over space and time, the space versus time modelling approach presented here should be incorporated into the SDM statistical repertoire to improve the reliability of projections.

KEYWORDS

abundance, climate change, occupancy, Orange-tip butterfly, precipitation, space-for-time substitution, species distribution modelling, temperature

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1 | INTRODUCTION

Rapid anthropogenic climate change is driving major ecological changes (IPCC, 2022). Among the most widely documented impacts of climate change are changes in species' geographic distributions—including range contractions and expansions, as well as shifts to higher latitudes, altitudes and deeper waters (Chen et al., 2011; Lenoir & Svenning, 2015; Poloczanska et al., 2013). It is vitally important for ecologists and policymakers to understand, predict and mitigate these impacts, and so a major focus of ecological research is on developing and applying tools to predict how species' distributions will change in response to global change drivers.

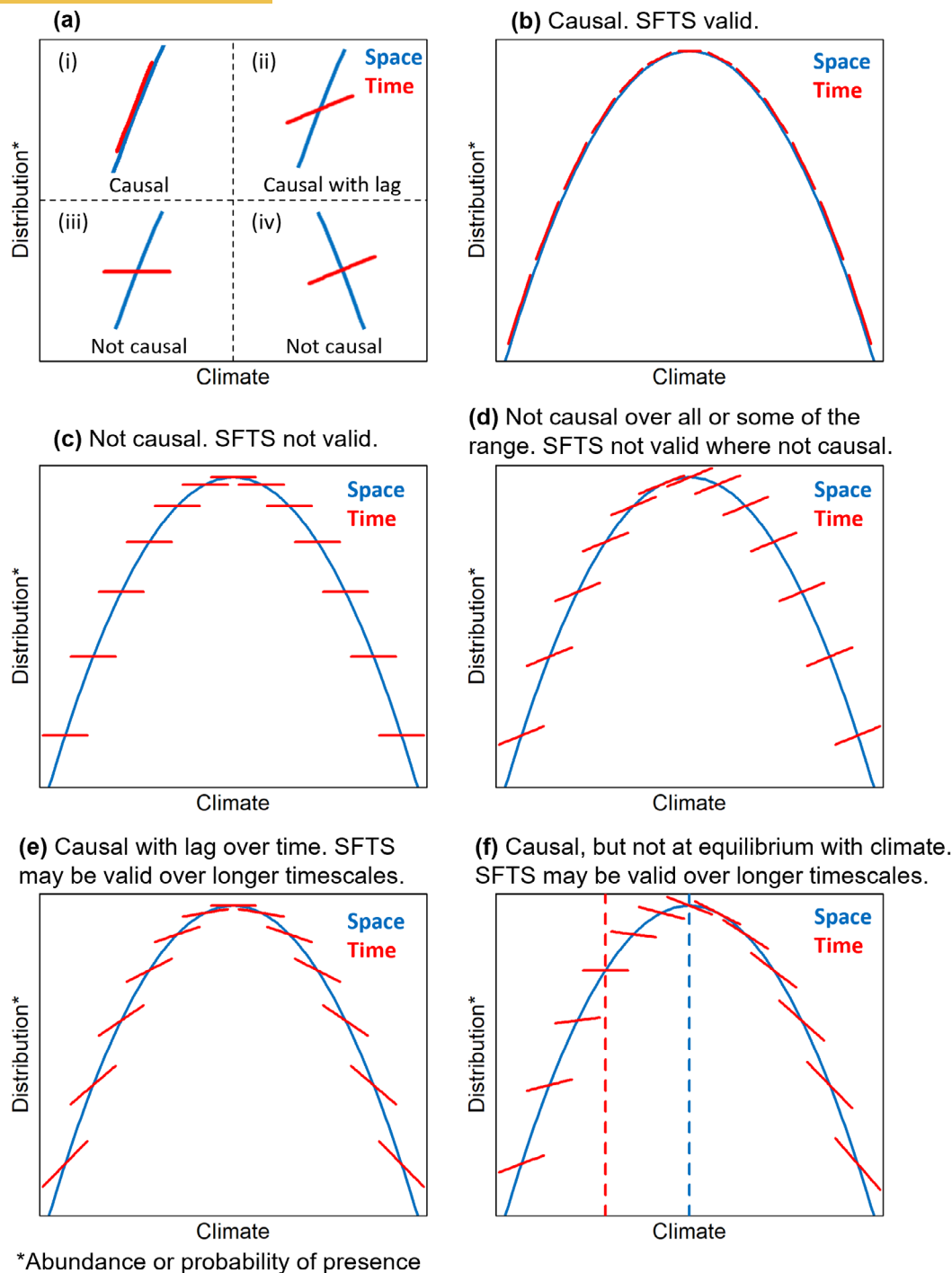
The most extensively used approach for modelling the effects of climate variables on species' distributions are correlational 'species distribution models' (SDMs; also termed ecological niche models; Elith & Leathwick, 2009). A common application of these models involves projecting areas of environmental suitability for a species under future conditions (Kharouba & Williams, 2024; Pearson & Dawson, 2003), allowing a broad range of inferences to be made, such as about changes in species' distributions (Berry et al., 2002); extinction risk (Thuiller et al., 2005); suitability of areas for assisted migration (Willis et al., 2009) and crop growth (Ramirez-Cabral et al., 2017); and the spread of pests (Early et al., 2022), disease vectors (Barker & MacIsaac, 2022) and invasive species (Srivastava et al., 2019). The SDM approach is very widely applied to project species' responses to future climate change, and so ensuring the robustness of these models is vital (Kharouba & Williams, 2024; Lovell et al., 2023).

A climate-focussed SDM typically involves estimating relationships between climate data and a species' contemporary spatial distribution, specifically occupancy (presence/absence) or abundance. Typically, SDMs estimate climate-distribution relationships across geographic space, and these relationships can then be transferred over time to predict the landscape suitability for a species under projected future climate conditions (Kharouba & Williams, 2024). As such, SDMs involve a 'space-for-time substitution', where spatial relationships are used as a proxy for temporal relationships (Figure S1; Kharouba & Williams, 2024; Lovell et al., 2023; Pickett, 1989). As space-for-time substitutions, SDMs rely on two often-implicit assumptions. Firstly, space-for-time substitutions assume that the modelled spatial climate-distribution relationships capture causal effects (Figure S1a; Kharouba & Williams, 2024; Lovell et al., 2023). However, many SDMs use a standard set of annual/seasonal temperature and precipitation metrics, averaged over a 30-year period (WorldClim, Fick & Hijmans, 2017), whereas in reality, species' distributions are likely responding to climate drivers acting over a relatively narrow timescale, such as a seasonal period corresponding to a specific life stage. Yet, there has been very little focus on identifying these precise time periods of climate sensitivity (Mills et al., 2017; Pollard, 1988; Roy et al., 2001). Secondly, space-for-time substitutions assume that relationships identified over space are transferable over time ('space-time equivalence'; Figure S1b; Kharouba & Williams, 2024; Lovell et al., 2023). However, this assumption has

rarely been tested (Bradter et al., 2022; Oedekoven et al., 2017), and the extent to which spatial climate-distribution relationships hold over time is largely unclear.

Despite the widespread use of SDMs, the critical assumption of space-time equivalence (Figure S1b) has rarely been tested for species' distributions (Kharouba & Williams, 2024; Lovell et al., 2023); while there have been some studies comparing spatial and temporal climate effects on phenotypes (e.g. Kharouba et al., 2014; Klesse et al., 2020; Perret et al., 2024; Phillimore et al., 2010; Wu et al., 2022) and communities (e.g. Adler & Levine, 2007; Elmendorf et al., 2015; La Sorte et al., 2009; Sandel, 2019), we are aware of few directly testing for equivalence between spatial and temporal climate-distribution relationships (Bradter et al., 2022; Oedekoven et al., 2017), and none directly considering both occupancy and abundance or the variation in the degree of agreement between spatial and temporal relationships within a species' range. Instead, most SDM validation is conducted over space alone, testing the causality of spatial climate-distribution relationships rather than their transferability over time (Sequeira et al., 2018). Spatial validation often involves data that are not truly independent (Roberts et al., 2017; Santini et al., 2021), but sometimes uses spatial data from different regions or new data (Early & Sax, 2014; Greiser et al., 2020; Randin et al., 2006). Testing the transferability of SDMs over time (Kharouba & Williams, 2024; Lovell et al., 2023) typically involves comparing SDM predictions and observed data at a specific time point to test predictive accuracy (Dobrowski et al., 2011; Rapacciuolo et al., 2012). For instance, SDM predictions have been tested against historic observations (Dobrowski et al., 2011; Morán-Ordóñez et al., 2017), paleodata (Pearman et al., 2008; Veloz et al., 2012), simulated data (Santini et al., 2021) and time-series projections (Isaac et al., 2011). However, the transferability of SDMs over time has been found to be mixed, with predictive performance ranging from good to poor, and varying across taxa and timescales (Dobrowski et al., 2011; Morán-Ordóñez et al., 2017; Pearman et al., 2008; Rapacciuolo et al., 2012; Wogan, 2016).

While predictive validations can inform as to the accuracy of projections for particular points in time, in isolation they provide little insight into the processes that generate spatial and temporal patterns (Lovell et al., 2023). In contrast, directly comparing the slopes of spatial and temporal climate-distribution relationships (hereon, 'slopes') has the potential to provide further insights into whether the same processes are operating in space and time, and thus how predictive accuracy may vary across timescales (Bradter et al., 2022; Phillimore et al., 2010). For instance, if the temporal climate-distribution relationship is smaller in magnitude than the spatial relationship, this could suggest that there is a lag in the response over time and that spatial patterns may be driven by slower acting processes which may only manifest over longer timescales (Phillimore et al., 2010, Figure 1a_{ii}). While some studies have applied this type of 'space-time comparison' approach to phenotypes (e.g. Kharouba et al., 2014; Klesse et al., 2020; Phillimore et al., 2010) and community composition (e.g. Adler & Levine, 2007; La Sorte et al., 2009;



Sandel, 2019), very few studies have conducted space-time comparisons on species' distribution data (but see Bradter et al., 2022; Oedekoven et al., 2017).

Extensive spatiotemporally replicated species' abundance and climate datasets are a largely unrealised opportunity for estimating and comparing spatial and temporal climate-distribution relationships (Lovell et al., 2023; Phillimore et al., 2010). We are only aware of two previous studies directly comparing the slopes of spatial and temporal climate effects on species' abundances, both of which are focused on birds (Bradter et al., 2022; Oedekoven et al., 2017). These studies separated spatiotemporal climate

variation into (i) spatial values averaged across years, (ii) temporal (yearly) values averaged across sites and (iii) spatiotemporal values of the remaining variation. These derived variables were then used to estimate linear spatial, temporal and spatiotemporal climate effects on abundance (Bradter et al., 2022; Oedekoven et al., 2017). However, usually when we consider climate-distribution relationships across a range of climate values spanning the species climatic niche, we anticipate a hump-shaped relationship, where the probability of presence or the abundance is maximised at an intermediate (optimum) climate value (Martínez-Meyer et al., 2013; Shelford, 1911). We therefore suggest that it makes sense to allow

FIGURE 1 Hypothetical spatial (blue) and temporal (red) climate-distribution relationships, the processes that may generate them and implications for space-for-time substitutions (SFTS). Spatial climate variation is defined by the mean climate values at each site across years. Across a species' entire climatic range, the climate-distribution relationship is assumed to follow a humped form (but within the United Kingdom, we may only observe a section of this curve). Temporal climate variation is defined as each year's deviation from the site's average climate. Several possible scenarios are shown, each of which has different implications for space-for-time substitution. (a) Responses in a localised area under different scenarios: (ai) Spatial and temporal slopes are equivalent in direction and magnitude (temporal responses are jittered here for visual clarity), consistent with the relationships being causal and meaning that space can substitute for time; (aii) Slopes in space and time are in the same direction but the temporal slope is shallower, consistent with a causal effect of the climate variable but a lag in the response over time. Under this scenario space-for-time substitution may be valid over longer timescales if slower acting processes allow the lag to be closed; (aiii, iv) the spatial climate-distribution relationship is not consistent with causality because (aiii) no response is seen over time (i.e. slope of zero; note that this could correspond to an extreme lag, but this is unlikely over longer timescales) or space (not illustrated) or (aiv) temporal and spatial slopes are in opposite directions. (b–f) Patterns that may be seen across a range of climate values: (b) Spatial and temporal slopes are equivalent (see ai) across the range, and space can substitute for time (temporal responses are jittered here for visual clarity); (c) No response is seen over time (see aiii), suggesting that the spatial climate-distribution relationship is not consistent with causality across the species' range and space-for-time substitutions will not be valid over any timescale; (d) The temporal slope is of consistent direction and magnitude across climate values, suggesting the climate variable is not consistent with causality across all or some of the range, and where it does not appear to be causal space-for-time substitutions will not be valid over any timescale; (e) Slopes in space and time are in the same direction but the temporal slope is shallower than the local spatial slope across climate values (see aii), consistent with a causal effect of the climate variable but a lag in the response over time. Note that different slopes in space and time could also arise via a third variable that correlates differently with climate and distribution over space versus time. (f) Different climate optima over space and time (dashed lines), wherein the temporal slope changes direction at a different point to the spatial slope. This may arise if the climate has shifted over time and the spatial relationship between climate and abundance lags behind the equilibrium relationship. For (e) and (f), space-for-time substitution may only be valid over longer timescales if slower acting processes can manifest and this allows the lag to be recovered. *Abundance or probability of presence.

a quadratic spatial climate-distribution relationship, with temporal climate effects considered as deviations from the local spatial values (Figure 1). Using estimates derived from this model permits a test of whether temporal climate effects differ from local spatial effects across a species' range. We identify several distinct patterns of spatial and temporal relationships that may arise, with different inferences into the processes at play (Figure 1).

Here, we focused on Lepidoptera, ectothermic organisms known to be highly sensitive to changes in temperature and precipitation, which directly influence their activity levels (Hill et al., 2021; Pollard, 1988; Roy et al., 2001). This means that climate variables may be expected to have a causal effect on their distributions. Furthermore, Lepidoptera have been subject to long term and spatially structured monitoring programmes, such as the UK Butterfly Monitoring Scheme (UKBMS; Botham et al., 2022), with high levels of replication that increases statistical power to detect population responses to climate variables over space and time. We here focused on the Orange-tip butterfly (*Anthocharis cardamines*) a species that is widely distributed across the United Kingdom and known to be sensitive to climate variables (Roy et al., 2001). For instance, the Orange-tip's range has been expanding northwards as the climate warms (Thomas, 2010) and its phenology has been found to advance with increased spring temperatures (Phillimore et al., 2012). We here used the Orange-tip as a test case of our approach, with the aim of testing the space-for-time transferability assumption that commonly underpins SDMs. First, we identified the seasonal periods over which temperature and precipitation variables best predict spatiotemporal variation in Orange-tip abundance in the United Kingdom. We then compared the spatial and temporal effects of climate variables on Orange-tip populations across the species range.

2 | MATERIALS AND METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Populations	Populations	Total of 14,830 site-year combinations, including 2130 sites across the United Kingdom for the years 1977–2021

An overview of the methods used is given in Figure S2.

2.2 | Butterfly abundance data

We used abundance data from the UK Butterfly Monitoring Scheme (UKBMS), which has been recording the abundance of butterfly species across the United Kingdom since 1976 (Botham et al., 2022). The UKBMS data consists of counts of the number of individual butterflies observed on transect walks (mean transect length = 2.01 km, SD = 1.08), with surveys conducted weekly between the 1 April and 30 September at each site in each year. Weekly counts are used to produce 'site indices' as a measure of a species' relative abundance at each transect site in each year—these are calculated as the area underneath a generalised additive model fitted to each species' data from each site-year (Botham et al., 2022). Note that although we refer to the site indices as 'abundance', they are not a measure of true population size, but rather an estimate of sampled abundance that is comparable across sites and years.

For the Orange-tip butterfly (*Anthocharis cardamines*), we obtained UKBMS site index data for the years 1976–2021, assigning zero counts to site-years that were surveyed but where the Orange-tip was not seen. We excluded site-years where the species was observed but monitoring was not sufficient to generate a site index value. Since one year's abundance is likely to influence the next year's population size, the previous year's site index was included as a predictor in our models (Pollard & Lakhani, 1985; Roy et al., 2001). We therefore also excluded site-years for which the previous year's abundance was unavailable. This resulted in a total of 14,830 site-year combinations for use in our analyses, spanning the years 1977–2021 and 2130 sites across the United Kingdom (note that not all transects have counts in all years; Figure S3). To partially account for spatial pseudoreplication of transect sites, each UKBMS site was mapped to a 50 km grid cell which was included as a random effect in our models.

2.3 | Climate variables

Historical UK climate data were obtained from the HadUK-Grid, which consists of daily data from climate stations, interpolated to a 1 km grid (Hollis et al., 2019). For each transect site in each year (1976–2021), we extracted daily maximum temperature (°C, which is highly correlated with daily minimum and mean temperatures) and precipitation (mm) values for the 1 km grid cell that the beginning of the site's transect is found in.

In order to explore the effects of climate on Orange-tip abundance/occupancy across space and time, we first decomposed climate variation into spatial and temporal components (Bradter et al., 2022; Brodie et al., 2021; Oedekoven et al., 2017; Phillimore et al., 2010). We used a within-subject centring approach to separate between-site (i.e. spatial) and within-site (i.e. temporal) variation in the climate variables of interest (van de Pol & Wright, 2009). Under this approach, spatial variation in a climate variable was captured by the mean climate value at each site across multiple years (the spatial average), and the local temporal variation in a climate variable was each year's deviation from the site's spatial average. We calculated the spatial average across the $n=15$ years spanning 1976–1990, treating this period as the climate baseline. We used this baseline period rather than the entire duration of our data because substantial climate change occurred in the period after 1990 (Figure S3d), and so we expect this period to better capture the historical climate conditions that populations may be in equilibrium with over space (Lovell et al., 2023).

2.4 | Model structure

All analyses were conducted in R version 4.3.1 (R Core Team, 2021).

Our models are based on Poisson family generalised linear mixed models, with Orange-tip abundance, A , at site i in year y modelled as:

$$\log(A_{i,y}) = \beta_0 + \beta_S \bar{X}_i + \beta_{S^2} \bar{X}_i^2 + \beta_T (X_{i,y} - \bar{X}_i) + \beta_{ST} (\bar{X}_i) (X_{i,y} - \bar{X}_i) + \beta_A A_{T_{i,y-1}} + u_i + u_y + u_g + u_{g:y} + \varepsilon_{i,y} \quad (1)$$

where β_0 is the intercept, and the fixed and random effects are as follows.

A climate variable, X , is the average temperature or precipitation value over a given seasonal window (see Section 2.5). For each climate variable, X , included in a model (one or both of a temperature variable and a precipitation variable), we included four fixed effect terms. We separated the spatial (S) and temporal (T) climate effects using the within-site centring approach described above (van de Pol & Wright, 2009). Spatial climate variation, the spatial average \bar{X}_i , was the average climate value at site i between 1976 and 1990. As described by Fay et al. (2022), we also included a spatial quadratic term \bar{X}_i^2 , to allow for the scenario where climate-abundance relationships have an optimal climate value, beyond which abundance declines. The inclusion of this quadratic term was supported by AIC and marginal R^2 values (Supplementary Methods; Table S2). The temporal climate variation was the deviation of the climate in each year y from the site's average climate value, $X_{i,y} - \bar{X}_i$. Finally, we included the interaction between spatial and temporal climate variation, to allow the temporal effect to change depending on the spatial climate value, thereby allowing the temporal climate effect to follow the quadratic curve and vary across the specie's range (Figure 1). We also included abundance at site i in the previous year ($y-1$) as a fixed effect because the previous year's abundance is likely to influence the current year's abundance (Pollard & Lakhani, 1985; Roy et al., 2001). To ensure that this is only considering a temporal effect, and not capturing spatial patterns in abundance, the previous year's abundance was included as a deviation from the site's average abundance across all years (i.e. calculated in the same way as temporal climate variation), where $A_{T_{i,y-1}} = \log(1 + A_{i,y-1}) - \log(1 + \bar{A}_{i,y-1})$; see Figure S4 for further exploration of this term and its effect. To account for pseudoreplication, random effects, u , were included for site i , year y , 50 km grid cell g and the grid:year interaction $g:y$. We also included an observation-level random effect $\varepsilon_{i,y}$ to account for overdispersion; since there is only one observation for each site-year, this is equivalent to a site:year random effect.

2.5 | Sliding windows

We used a sliding window approach to identify the seasonal periods over which temperature and precipitation variables best explain variation in Orange-tip abundance (van de Pol et al., 2016; see Supplementary Methods for further details). In short, using the lme4 R package (Bates et al., 2015), we fitted a series of maximum likelihood Poisson mixed effects models (Equation 1) including climate predictors averaged over different 'windows' with varying durations and timings. We searched for one temperature window followed by one precipitation window, identifying the climate windows that best described Orange-tip abundance based on the models with the lowest AICs (Supplementary Methods). We hereon use 'temperature window' and 'precipitation window' to refer to these identified periods of time over which the climate variables are most important. We also ran space-only and time-only windows searches to determine whether similar seasonal

periods were important in space and time, as is expected if the climate variable has a causal effect ([Supplementary Methods](#)).

2.6 | Comparing climate-distribution relationships in space and time

Having identified the climate variables important for predicting spatiotemporal variation in Orange-tip abundance, we then compared spatial and temporal climate-distribution relationships at different climate values experienced within the species' range. We used a Bayesian model, fitted using the MCMCglmm R package (Hadfield, 2010), to derive posterior distributions for the differences between spatial and temporal climate-abundance/occupancy slopes across climate values. This allowed us to determine whether spatial and temporal effects of the climate variable significantly differ across the species' climate range.

We found the Poisson model to be zero inflated ([Supplementary Methods](#)), and so we fitted a hurdle-Poisson mixed model (Equation S1). This model involved modelling the response in two parts: a binomial part that modelled occupancy (presence/absence, the probability that an observation is zero), and a truncated-Poisson part that modelled the positive (non-zero) abundance values. We had a similar model structure for the Binomial and truncated-Poisson parts of the model, with the only difference being that the previous year's abundance term ($A_{T_{iy-1}}$) was only included in the Poisson part. Random effects were modelled with an unstructured covariance structure to allow covariance between their effects in the two parts of the model. Residual variances ($\epsilon_{i,y}$) were allowed to differ between the two parts of the model, but with no covariance between them. Since the binomial part of the model is binary, a residual variance cannot be estimated for this part of the model and is fixed at 1. The model was run for 5,000,000 iterations, with a burn-in of 1,000,000 and thinning interval of 100, ensuring that the majority of effective sample sizes exceeded 1000, though in a minority of instances were only over 400 ([Table S3](#)). We used default flat normal priors ($\mu=0$, $\text{var.}=10^8$) for fixed effects, parameter-expanded priors for random effects ($\nu=2$, $V=1$, $\alpha.\mu=0$, $\alpha.V=1000$), an inverse Wishart prior ($\nu=0.002$, $V=1$) for the truncated-Poisson residual term and the residual prior for the binomial was fixed at 1. Traceplots were examined to ensure adequate mixing and convergence.

To test whether spatial and temporal slopes differed at particular points along the spatial temperature/precipitation gradient, we took the following approach. For each of the truncated Poisson and Binomial parts of the model, and for values spanning the observed range of each climate variable (0.1°C or mm intervals between 13.0°C and 20.6°C for temperature and 1.1 and 6.3 mm for precipitation), we estimated (i) the posterior of the spatial climate-abundance/occupancy slope (the tangent of the quadratic curve at that climate value) and (ii) the posterior of the temporal climate-abundance/occupancy slope (i.e. the slope of the deviation from the spatial curve). We then derived the posterior distribution of the slope difference (space minus time) across these climate values and found the 95% credible interval of these differences. Where these did not overlap zero, the

effects of the climate variable in space and time were considered significantly different (Phillimore et al., 2010, 2016). This allowed us to draw inferences about the causality of climate-distribution relationships, the presence of lags in the responses over time and the speed of processes giving rise to these spatial and temporal patterns ([Figure 1](#)).

We note that the credible intervals on the spatial and temporal slope estimates ([Figure S6](#)) are wider at more extreme temperatures, resulting in lower power to reject the null expectation of no difference between slopes.

3 | RESULTS

3.1 | Climate signals

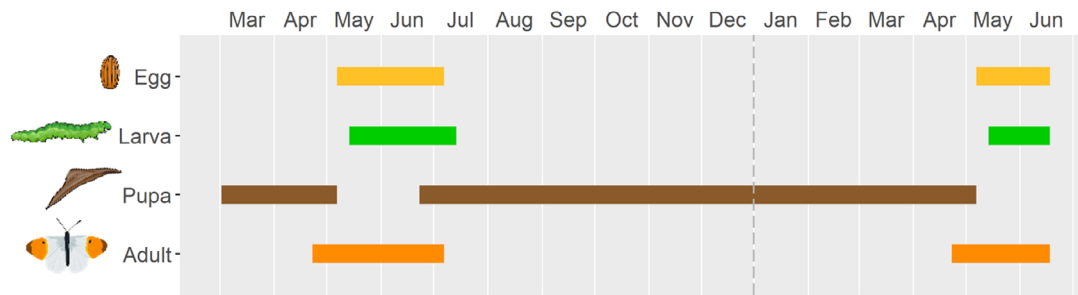
3.1.1 | Maximum temperature

We identified the most important temperature window for Orange-tip abundance as the average daily maximum value between ordinal days 136 and 195 (16th May–14th July) in the previous year (marginal pseudo- $R^2=0.15$; [Figure 2b](#), [Table S1a](#)). The average maximum temperature within this window increased by an estimated 1.14°C between 1976 and 2021 (averaged across sites; [Figure S3d](#)) and across the latitudinal extent of our data it was estimated to differ by 4.06°C (averaged across years; [Figure S3e](#)). This window falls within the previous year's flight period and also coincides with egg and larval life stages ([Figure 2a,b](#)). The model including our best temperature window had an AIC that was 171.2 lower than a null model with no climate predictors, and 1.8 lower than the model containing the next best temperature window ([Figure 2b](#); see [Table S1a](#) for full model comparison). All windows within 20 AIC of the best model included overlapping windows within roughly the same time period ([Figure 2b](#)), increasing confidence that temperature during this window may have a causal effect on abundance. Further evidence that temperature in this period may have a causal effect on Orange-tip populations over both space and time came from the fact that windows overlapping this period were identified using spatial data only (ordinal days 176 (25 June)–195 (14 July) in the previous year; [Figure S5](#)) and temporal data only (ordinal days 136 (16 May)–195 (14 July) in the previous year; [Figure S5](#)).

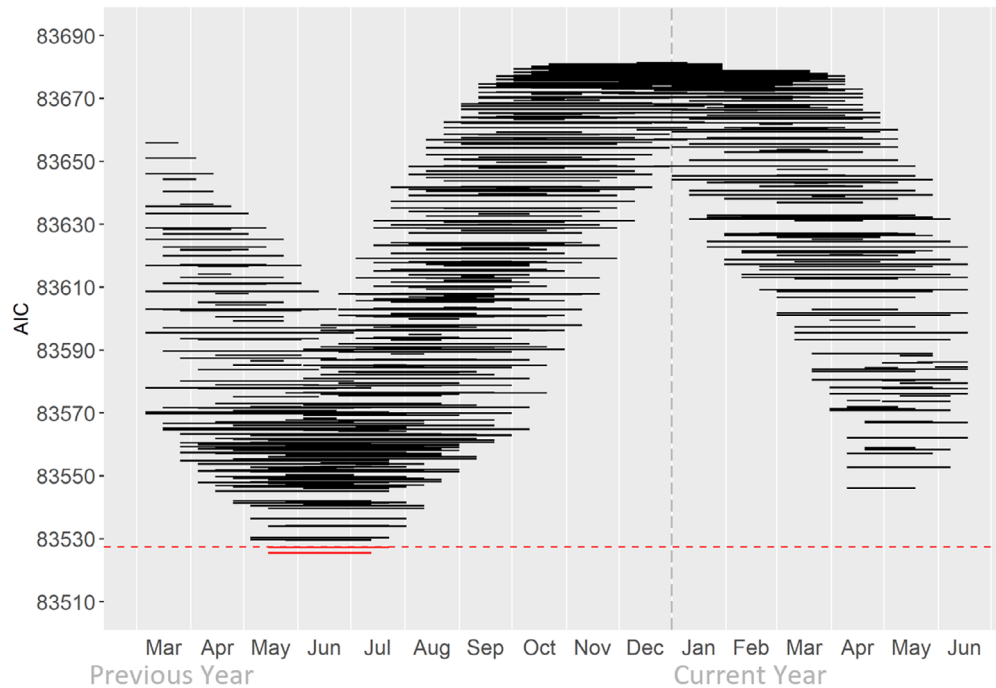
3.1.2 | Precipitation

The precipitation window that best explained Orange-tip abundance was identified as between ordinal days 131 and 150 (11 May–30 May) in the current year (marginal pseudo- $R^2=0.19$; [Figure 2c](#); [Table S1b](#)). On average across sites, average precipitation in this time window increased by an estimated 0.52 mm between 1976 and 2021 ([Figure S3f](#)), and on average across years, the daily mean precipitation across latitudes had an estimated range of only 0.27 mm ([Figure S3g](#)). The selected precipitation window falls just after the

(a) Orange-tip lifecycle



(b) Temperature



(c) Precipitation

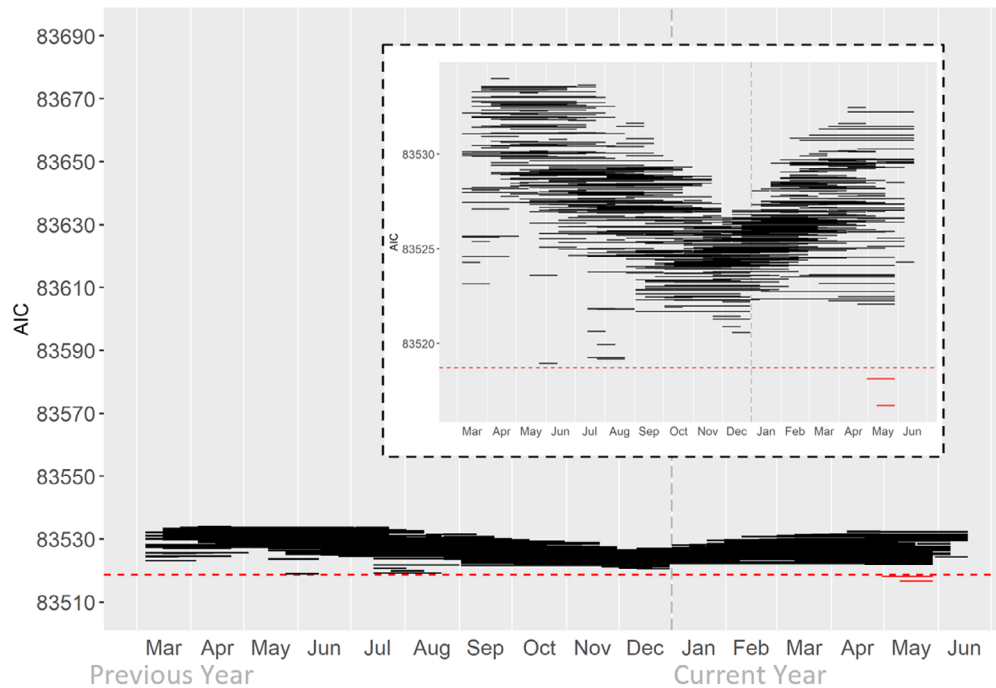


FIGURE 2 The Orange-tip butterfly's lifecycle and the AICs of the models including different climate windows as predictors of abundance. Poisson mixed effects models (Equation 1) were fitted using different climate windows as predictors of the Orange-tip butterfly's abundance. The windows explored fell between ordinal day 61 in the previous year and 170 in the current year, with different timings and durations explored. See Section 2 for further details. (a) Approximation of the Orange-tip butterfly's lifecycle during the window search period. (b, c) AICs of models fitted with different climate windows for (b) temperature and (c) precipitation. Bars in red indicated windows within 2 AIC of the best window (that with the lowest AIC). The insert in (c) shows the same information across a reduced AIC range.

previous year's flight period, when pupae are present (Figure 2a,c). Including our precipitation window decreased AIC by 8.7 compared to the temperature-only model (see Table S1b for full model comparison). The time-only window search identified a precipitation window overlapping that of the full model: between ordinal days 121 and 150 (1 May–30 May) in the current year (Figure S5). However, in contrast to the full and time-only models, the space-only precipitation window fell between ordinal days 206 and 225 (25 July–13 August) in the previous year (Figure S5). This discrepancy between space and time suggests that the precipitation window identified by the full model may not be causal.

3.1.3 | Model validation

Models including climate variables had considerably higher marginal pseudo- R^2 values and lower AIC values compared to the null model, with the model including both temperature and precipitation variables better supported than the temperature-only model. We also found support for including quadratic spatial climate terms: Models including the quadratic term had consistently higher marginal pseudo- R^2 values and lower AICs than the equivalent model excluding this quadratic term (Table S2).

3.2 | Space versus time

For the best temperature and precipitation windows, we compared climate-distribution relationships in space and time using a Bayesian hurdle-Poisson mixed model (after finding that a non-hurdle model was zero inflated, Figure S7). Model outputs quoted in-text for temperature are the derived spatial or temporal slope estimates at the midpoint of the spatial temperature values (16.79°C), averaged across all iterations. These estimates are on the link scales (logit for occupancy and log for abundance). Raw model outputs are in Table S3.

We found that at sites which were warmer between 16 May and 14 July in the previous year, the Orange-tip was more likely to be present (Binomial spatial slope mean = -1.439 , CIs = -1.767 to -1.112 ; Figure 3a, Table S3) and had higher abundance (truncated-Poisson spatial slope mean = 0.376 , CIs = 0.244 – 0.508 ; Figure 3b, Table S3).

We found a quadratic effect of spatial temperature on occupancy, with the spatial effect declining towards zero as temperature increased (Figure 3a, Table S3). Similarly, over time, the Orange-tip

was more likely to be present at warmer sites (Binomial temporal slope mean = -0.247 , CIs = -0.432 to -0.056 ; Figure 3a, Table S3), with the temporal slope decreasing towards zero as the spatial temperature increased (Figure 3a, Table S3). The credible intervals of the difference between the spatial and temporal slopes on occupancy only overlapped zero at 19.7°C and above, indicating that these slopes were not significantly different at higher temperature sites (Figure 3c). Below this, effects in space and time were significantly different, with temporal slopes lower in magnitude than local spatial slopes.

The quadratic effect of spatial temperature on abundance was minimal (Figure 3b, Table S3). There was an interaction between spatial and temporal temperature effects on abundance (Figure 3b, Table S3), meaning that the effect of temperature change over time depended on the position in the species' climatic range: temperature had a positive effect on abundance up until 20.25°C, beyond which increasing temperatures were associated with decreases in abundance (truncated-Poisson temporal slope mean = 0.192 , CIs = 0.147 to 0.236 ; Figure 3b, Table S3). The credible intervals of the difference between spatial and temporal slopes overlapped zero up to 16.4°C, but departed from zero beyond this, indicating that the temperature-abundance slopes were significantly different at higher temperature sites (Figure 3d). As higher temperatures were approached, the temporal slope began to have a lower magnitude than the local spatial slope, and was even in the opposite direction at the highest temperatures (Figure 3b,d).

Across the United Kingdom, we found that spatial and temporal temperature-occupancy slopes significantly differed at more northern (cooler) sites, whereas temperature-abundance slopes differed in the more southern (warmer) sites (Figure 4). As a result, abundance and occupancy projections based on spatial and temporal climate variables differed (Figure S8). For instance, at a low temperature site (14.91°C), increasing temperature by 1°C over space is predicted to increase probability of presence by 0.18 (from 0.05 to 0.23), whereas over time, a 1°C increase is only predicted to increase by 0.02 (from 0.05 to 0.07; Figure S8). Similarly, at a high temperature site (18.67°C), increasing temperature by 1°C over space is predicted to increase abundance by a factor of 1.41, whereas over time, it is predicted to increase it by a factor of 1.09 (Figure S8).

We found a quadratic relationship between precipitation in the period 11 May–30 May in the current year and both occupancy and abundance (Table S3, Figure S9). With increased rainfall over space, the Orange-tip was more likely to be present up until 2.25 mm/day, beyond which increased rainfall decreased its probability of

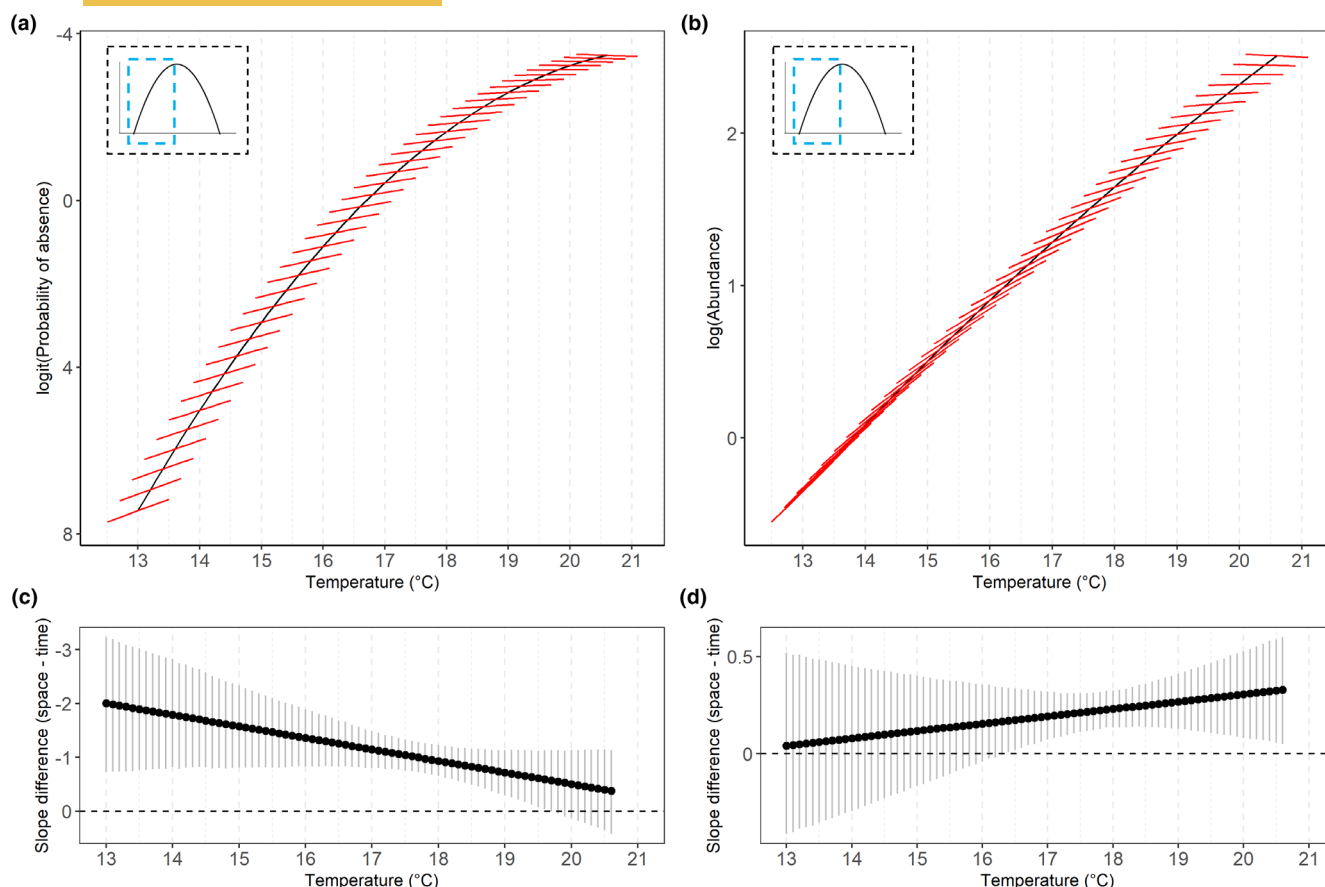


FIGURE 3 Effect of temperature on the Orange-tip butterfly's distribution in space versus time. A Bayesian hurdle-Poisson mixed model (Equation S1) was used to model the spatial and temporal effects of temperature and precipitation on the Orange-tip's abundance and occupancy (see Section 2). (a, b) The spatial (black) and temporal (red) relationships between maximum temperature (averaged over 16 May and 14 July in the previous year) and Orange-tip (a) probability of absence (Binomial part, logit scale, note reversed y axis) and (b) abundance (conditional on presence; truncated-Poisson part, log scale). Note that if we looked across the species' entire distribution, we would expect the spatial curves in (a) and (b) to be hump-shaped (as in the insert). (c, d) The difference between the latent scale spatial and temporal slopes at different temperature values for (c) probability of absence and (d) abundance. Grey bars indicate the 95% credible intervals of these differences; where these do not overlap zero, slopes in space and time can be considered significantly different. Note that in (a, b) temporal slopes are plotted at 0.2°C spatial temperature intervals for visual clarity, but slope differences in (c, d) are at 0.1°C intervals.

presence (Figure S9, Table S3). Similarly, the spatial effect of precipitation on abundance was positive up until 1.7 mm/day, beyond which it was negative (Figure S9, Table S3). However, for both occupancy and abundance, the credible intervals of the temporal relationship overlapped zero for the majority of precipitation values (Figure S9). Given the lack of response to precipitation over time, we lacked confidence that this association was causal and so our comparisons of spatial and temporal slopes focus on the temperature window.

We found that the temporal variation in the previous year's abundance (calculated as a deviation from the site's average abundance) was associated with a higher abundance in the current year (Table S3).

4 | DISCUSSION

Two critical assumptions underlying SDMs projections of species' responses to climate change are that (i) the climate-distribution

relationships identified across space are causal and (ii) the effects that climate variables have on the species' distribution are equivalent over space and time (Elith & Leathwick, 2009; Kharouba & Williams, 2024; Lovell et al., 2023). For UK populations of the Orange-tip butterfly, we found that the causality assumption appears to be met for temperature but not for precipitation, and showed that Orange-tip populations are sensitive to temperature during a specific window of time in the previous year (Figure 2b), highlighting the importance of using carefully selected climate predictors (Da Re et al., 2024; Kharouba & Williams, 2024; Lovell et al., 2023). The second assumption—that of space–time equivalence—held in different parts of the Orange-tip's range for temperature effects on occupancy versus abundance (conditional on presence; Figure 4). This suggests that the reliability of SDM projections will vary across distribution metrics and regions. Previous work has reported that space–time equivalence differs across species (Bradter et al., 2022; Oedekoven et al., 2017) and here we extend these insights by demonstrating that variation in space–time equivalence is also found

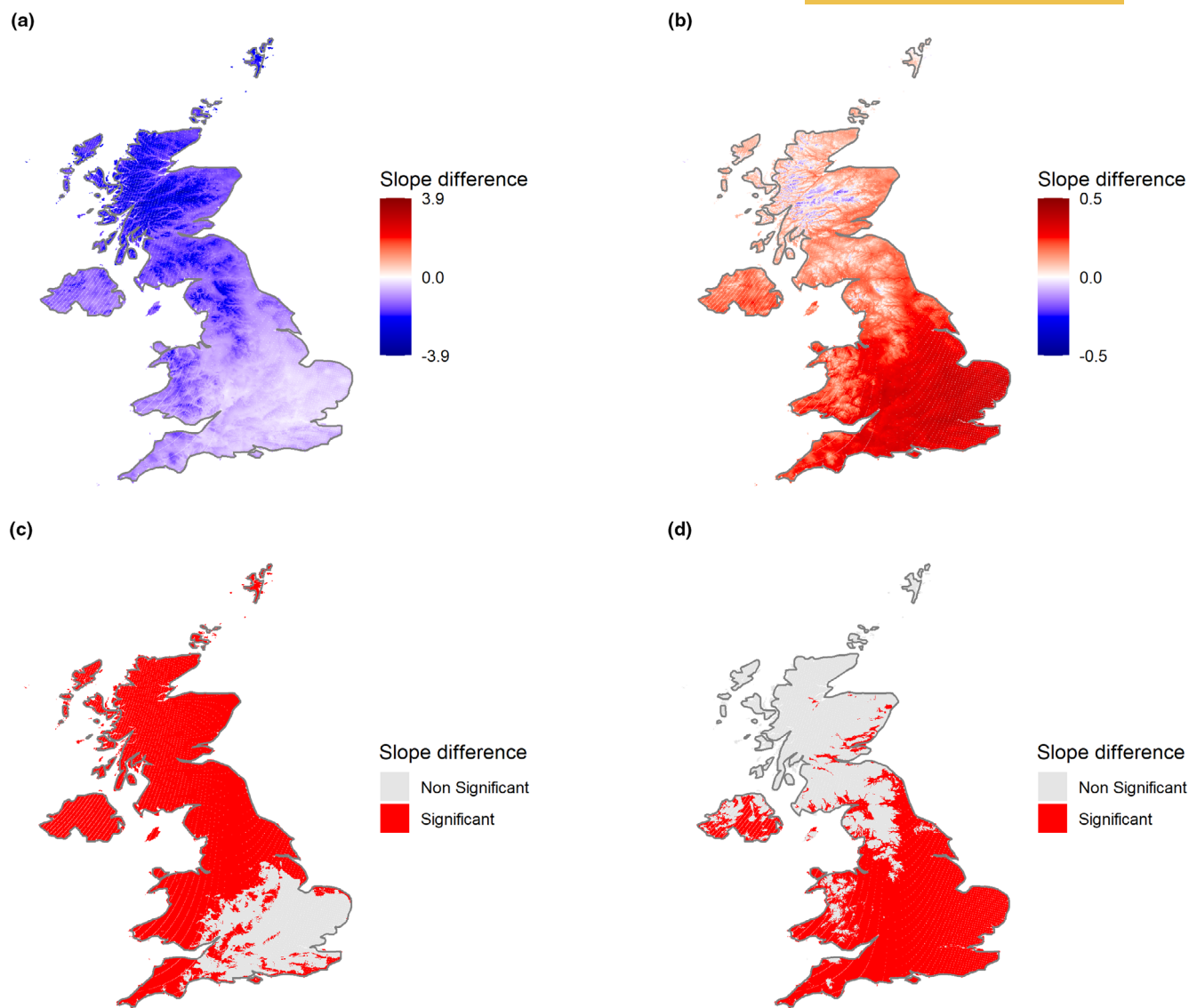


FIGURE 4 Geographical variation in space-time equivalence for the effect of temperature on Orange-tip occupancy and abundance. A Bayesian hurdle-Poisson mixed model (Equation S1; see Section 2) was used to predict the spatial and temporal effects of the maximum temperature (averaged between 16 May and 14 July in the previous year) on Orange-tip abundance and occupancy at different temperature values observed across the United Kingdom at a 1 km grid resolution. Maps indicate the difference between the effect of temperature on (a, c) occupancy (probability of absence) and (b, d) abundance in space and time. (a, b) The mean differences between slopes in space and time. (c, d) Whether the slopes in space and time are significantly different from each other (Figure 3c,d).

within a single species' range and between different distribution metrics (occupancy vs abundance). Overall, our results demonstrate how SDM projections parameterised solely from species' responses to climate variation in space have the potential to be misleading, and highlight the complexities that arise when relying on space-for-time substitutions.

The United Kingdom is towards the northern (cold) edge of the Orange-tip's range, and so our data includes northern (leading-edge) to mid-range sites. This may explain why the spatial temperature-distribution relationships for this species do not show a peak abundance or probability of presence within the range of our temperature data (Figure 3a,b). Across the Orange-tip's UK range, both temperature-abundance and temperature-occupancy relationships

were usually in the same direction over space and time, and overlapping climate windows were identified over both space and time (Figure S5), consistent with a causal positive effect of temperatures on probability of presence and on abundance (Figure 3a,b). This suggests that spatial temperature-distribution relationships may be somewhat transferable over time. However, we discovered complexities in patterns of space-time equivalence that highlight the context-dependence of the validity of space-for-time substitutions: The response in time was often shallower than that in space, and patterns of space-time equivalence varied across the species' range and across response variables (occupancy versus abundance; Figure 3). As a result, predicted changes based on spatial and temporal climate variation can differ (Figure S8).

The varying geographical patterns of space–time equivalence (Figure 4) present an opportunity to examine the mechanisms by which temperature affects occupancy and abundance. At lower temperatures nearer to the cold edge of the Orange-tip's thermal niche, temperature changes over time had an immediate effect on *abundance* that tracked the local spatial temperature effect (Figure 3b), consistent with a causal and limiting effect of temperature. However, in colder regions, the *occupancy* response over time was shallower than that seen over space (Figure 3a). This slope difference could be due to the range-limiting effects of other variables such as habitat type and availability (Platts et al., 2019), biotic interactions (HilleRisLambers et al., 2013) or availability of microclimate refugia (Suggitt et al., 2018). Alternatively, this slope difference may arise because colonisations and/or extinctions at the range margins take time to manifest after a temperature change (i.e. there is lag in the response over time; Alexander et al., 2018; Ash et al., 2017; Lovell et al., 2023). For instance, increasing temperatures may render a site newly suitable for the species, but colonisation of this unoccupied site relies on the presence of a nearby source population (i.e. there is an effect of spatial autocorrelation in occupancies).

At higher temperatures closer to the range core, different patterns were seen. Here, the temporal temperature–*abundance* slope was shallower than the local spatial slope (Figure 3b). One explanation for a shallower temporal slope is that stochasticity in annual temperature variation may limit the extent to which demographic processes (i.e. births and deaths) allow populations to track annual fluctuations in equilibrium population sizes (Figure 1e). Similarly, a lag in time may also arise if spatial relationships are shaped by slower acting processes, such as local adaptation, that only manifest over longer timescales (Adler et al., 2020). The observed pattern with the temporal slope becoming increasingly shallow compared to the local spatial slope as the spatial temperature increases (Figure 3b) could also arise if population sizes in *space* are lagging behind the equilibrium expectation; this would manifest as abundance peaking at a higher temperature in space than in time (Figure 1f). However, testing this hypothesis rigorously would require consideration of the full thermal niche for the species. Alternatively, diverging spatial and temporal temperature–abundance slopes may occur if temperature is non-causal at higher temperatures. Under this scenario, the species is more sensitive to temperature towards the edge of its thermal niche (MacArthur, 1984), with other variables (e.g. density dependence) assuming greater importance in limiting abundance towards the species' range centre and thermal optima (as found by Mills et al., 2017 for European butterflies including the Orange-tip). The spatial and temporal temperature–*occupancy* relationships did not differ at higher temperature sites. Both the spatial and temporal slopes declined towards zero as the temperature increases (Figure S6a,d; Figure 3a); this is likely to be because changes in occupancy will be rarer towards the centre of the species' range, and so temperature may also be most important for generating variation in occupancy towards the range edge compared to the range centre (MacArthur, 1984).

The fact that we found different—largely opposite—patterns of space–time equivalence for the effect of temperature on occupancy versus abundance (Figures 3c,d and 4) highlights that different processes are likely to be driving these two responses, with implications for the accuracy of space-for-time projections. Indeed, while occupancy and abundance are related aspects of species' distributions, they may exhibit differing responses to climate variables (Billman et al., 2021; Dallas & Hastings, 2018; Fox et al., 2023). Patterns in occupancy are likely to be the result of slower acting processes—such as colonisations beyond the range limits and extinctions—and thus reflect longer term suitability of environmental conditions (Billman et al., 2021; Schulz et al., 2020). In contrast, abundance may respond more rapidly to environmental changes, with a greater contribution of faster acting processes (such as changes in population growth rates), and so patterns of abundance may be more reflective of shorter term environmental variation (Billman et al., 2021; Schulz et al., 2020). Although, slower acting processes such as local adaptation may also influence abundance trends and could prevent tracking of environmental change in the near-term. Failure to separate these two facets of species' distributions could mask the complexity of how species' distributions respond to climate change (Dibner et al., 2017; Schulz et al., 2020). For instance, when we fitted a (non-hurdle) Poisson mixed model to our data (Figure S7)—that is, considering both occupancy and abundance as a single variable—we found patterns of space–time equivalence for temperature effects that were similar to those that we see for occupancy (Figure 3a,c). Therefore, such an estimate would overlook the impact of temperature on abundance (conditional on presence; Figure 3b,d). However, SDMs often focus on occupancy alone and rarely consider both occupancy and abundance (Waldock et al., 2022). A hurdle model represents a useful tool to model these two responses simultaneously, even where data are not zero inflated (Schulz et al., 2020). Furthermore, the distinction between the trends observed for abundance versus occupancy highlights that the accuracy of space-for-time SDM projections over different timescales will be dependent on both the response variable used and the position within the species' range.

The time window over which we found that average temperature best predicted the Orange-tip's distribution (16 May–14 July) spans a period in the previous year when Orange-tip adults, eggs and larvae are all present (Figure 2a,b). The positive spatial relationship that we found between temperature in this window and both abundance and probability of presence agreed with the direction of the May–July trends identified by Roy et al. (2001), although they only found May to be statistically significant. Warmer temperatures during this period of the previous year may affect the next year's abundance by increasing adult survival, oviposition and/or larval survival, resulting increased population size in the subsequent year (Pollard & Lakhani, 1985; Radchuk et al., 2013; Turner et al., 1987). The precipitation window that we identified (11 May–30 May) falls in the current year over a period where adults, eggs and larvae are all present (Figure 2a,c). The negative spatial effect of precipitation on abundance and probability of presence above approximately 1.7 and 2.25 mm/day, respectively, is consistent with the

expectation that increased precipitation will negatively affect survival (Pollard, 1988). This inference agrees with the negative effect of precipitation in the current May identified by Roy et al. (2001), although they did not find this effect to be significant. Additionally, the minimal effect of precipitation on Orange-tip populations over time suggests a lack of causality (Figure S9). Overall, this gives us confidence that our temperature window is causal, but raises doubt over the precipitation window.

Our results highlight the importance of carefully selecting climate predictors over fine temporal scales before making space-for-time SDM projections (Da Re et al., 2024; Lovell et al., 2023). The temperature window that we identified was a significantly better predictor of the Orange-tip's abundance than other windows of the year (Figure 2b), and represents a period that would not be captured by the standard set of bioclimatic variables that are commonly used in SDMs (Fick & Hijmans, 2017). Furthermore, our spatial climate values (averaged over the years 1976–1990) are similar to the 30-year climate averages that are commonly used in SDMs (Fick & Hijmans, 2017; although we consider climate variables averaged over a carefully selected seasonal period rather than the standard set of annual and seasonal averages). Our finding that temporal responses to temperature were often shallower than spatial responses (Figure 3) emphasises that the relationships between species distributions and these long-term climate averages may reflect outcomes that arise over longer periods of time and so may not be predictive of temporal changes in the short term.

In this study, we demonstrated that a space–time comparison approach presents an opportunity to explore the contexts under which the causality and equivalence assumptions implicit in using SDMs for projections hold (Figure S1). An important avenue for future work is to apply this approach to other species in order to explore the generality of these inferences across species (Bradter et al., 2022). Our understanding of the contexts under which space-for-time assumptions are most likely to hold, and thus space-for-time substitution is likely to work best, would benefit from further analysis of available spatiotemporal datasets and simulations. In particular, an open question is what timescales projections are valid over (Adler et al., 2020; Brodie et al., 2021). As well as providing an opportunity to test the validity of the space–time equivalence assumption across a species' range, the slope comparison approach also has the potential to detect the presence of lags in the response over time, and thus provide insights into the timescale of projection and how this varies across space (although where slopes are shallower in time than space, we cannot rule out the possibility of a third variable that correlates differently with abundance and climate over space versus time; Tansey et al., 2017). For instance, we found that at lower temperature sites, the response of the Orange-tip's occupancy to temperature was shallower in time than in space (Figure 3a,b). This suggests that there was a lag in the temporal response and that space-for-time projections would overestimate northward range expansion in response to temperature rises over shorter timescales.

Our analyses are also subject to a number of limitations (see Supporting Information for further discussion). Firstly, our UK data

were limited to a northern portion of the Orange-tip's global distribution, and did not include the southern range edge. This means that we could not draw inferences about space–time equivalence at the warm range edge and whether patterns differed from at the cold range edge. Secondly, while we aimed to carefully identify causal climate drivers of the Orange-tip butterfly's UK distribution, some limitations remain. For instance, we did not consider microclimate variation, which could allow a species to persist in areas where macroclimate conditions are unsuitable (Lawson et al., 2014; Suggitt et al., 2018). We also assumed that occupancy and abundance are responding to climate variables in the same seasonal period, and only considered a single window for each climate variable. Finally, due to computational limitations, we assumed that climate windows are a fixed seasonal period over space and time (i.e. do not shift with phenology) and we did not consider an interaction between temperature and precipitation variables.

In this paper, we have presented a new approach that offers the potential to use spatiotemporal abundance data to leverage insights into the causality and transferability of climate–distribution relationships. Applying this approach to the Orange-tip butterfly, we add to an extensive evidence-base suggesting that using SDM to generate projections of species' distributions under future climate conditions should be approached with care. In particular, we highlight the importance of ensuring that spatial relationships are both causal and transferable over time in order to avoid generating misleading projections. We found that the equivalence between spatial and temporal temperature–abundance relationships was variable, even when focussing on a single species and a single climate variable. This suggests that the accuracy of space-for-time projections will be highly context-dependent, and emphasises the need for further exploration of the conditions and timescales under which projections will be most reliable.

AUTHOR CONTRIBUTIONS

Rebecca S. L. Lovell and Albert B. Phillimore conceived the study. Rebecca S. L. Lovell performed the analysis, with input from Albert B. Phillimore and Gary D. Powney. Gary D. Powney and Marc S. Botham provided advice on UKBMS data. Rebecca S. L. Lovell wrote the first draft of the manuscript, with all authors contributing to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are publicly available from the UK Butterfly Monitoring Scheme (<https://catalogue.ceh.ac.uk/documents/6d725dda-b85c-41c3-ae97-5635d736d6d3>; public dataset excludes sensitive sites) and the Met Office (<https://www.metoffice.gov.uk/research/climate/maps-and-data/data/haduk-grid/datasets>). Code used in this analysis is available on Zenodo (Lovell, 2025; <https://doi.org/10.5281/zenodo.14735268>) and GitHub (<https://github.com/RebeccaLovell/OrangeTipAnalyses>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The spatial and temporal steps and assumptions of using a species distribution model to make a projection over time.

Figure S2. Illustration of data and analytical steps.

Figure S3. Spatial and temporal distribution of the butterfly and climate data used.

Figure S4. Effects of including the previous year's abundance as a predictor on parameter estimates and other inferences.

Figure S5. Orange-tip lifecycle and the AICs of models including different climate windows in space or time only as predictors.

Figure S6. Estimates of spatial and temporal temperature-distribution relationships.

Figure S7. Spatial and temporal effects of temperature on abundance, estimated with a Poisson mixed model (non-hurdle model).

Figure S8. Estimated effects of a 1°C increase and a 1°C decrease in temperature on predicted occupancy and proportional change in abundance at high-, mid- and low-temperature sites.

Figure S9. Effect of precipitation on the Orange-tip's distribution in space versus time.

Figure S10. The AICs of the models including different temperature windows as predictors of abundance.

Table S1. Model performance and comparison for temperature and precipitation window searches.

Table S2. Comparison of sliding window models with and without quadratic climate terms.

Table S3. Model output for the hurdle-Poisson mixed model comparing spatial and temporal temperature effects on orange-tip abundance.

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