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Challenges in Modelling Spatio-Temporal Climatic Correlates of Local Losses of Wild Bees Using Dynamic Occupancy Models

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ABSTRACT

Aim: Impacts of climate change on biodiversity are well documented. Much of the evidence linking climate change to species distribution changes derives from studies using long-term climate averages in a correlative spatial framework. While useful, these static species distribution models (SDMs) give little insight into the process behind the correlations. Here, we model changes in wild bee occupancy dynamics as a function of temperature covariates that vary in space and time. We aim to detect fine-scale, climate-associated distribution changes in wild bees beyond those captured by traditional SDMs and aim to assess the challenges of applying dynamic occupancy models to large-scale opportunistic datasets.

Location: Great Britain.

Methods: We use dynamic occupancy models to examine the relationship between temperature and local losses for 106 wild bee species. We focus on one spatial metric (mean long-term temperature average, akin to SDM approaches) and one spatio-temporal metric (the annual temperature anomaly). We use a risk-of-bias assessment to evaluate how data limitations may affect inference in our dynamic occupancy models.

Results: Mean long-term temperature for a site was associated with the probability of local loss for > 60% of species. In general, mean temperature was negatively associated with the probability of local loss for southerly distributed species (meaning a lower probability of loss at warmer sites), while the relationship was reversed for northerly species. The annual temperature anomaly was only influential for one species.

Main Conclusions: Our results mirror the large-scale spatial pattern of SDMs, and although ecologically plausible, we find little signal of fine-scale, climate-associated wild bee distribution changes. We attribute this lack of signal to data-model mismatches as revealed by the detailed risk-of-bias assessment. We conclude that while dynamic occupancy models offer promise for integrating spatio-temporal covariates, their use may be limited when applied to large-scale opportunistic datasets that lack systematic sampling effort.

1 | Introduction

Climate change is a major threat to biodiversity, with a host of studies reporting climate-driven losses across many taxa (Thuiller et al. 2011; Kerr et al. 2015; Díaz et al. 2019; Trisos et al. 2020; Thierry et al. 2022). However, species' responses to changing climatic and environmental conditions (such as warming average annual temperatures) vary. Some show greater vulnerability to climate-driven losses in abundance and distribution, whilst others can thrive under the emerging novel conditions. For example, Chen et al. 2011, found range shift in response to climate change was highly variable between species, while Kerr et al. (2015) consistently found climate-related distribution losses at the warmer range edge of bumblebee species, but inter-specific variation in the extent of these losses. Identifying the variability and uncertainty surrounding species' responses to past climatic changes is crucial for understanding and mitigating potential negative impacts of future change (Outhwaite et al. 2022).

A variety of models have been used to assess the impacts of climate change on species. These models vary in terms of response variable, covariates/input data and their structure (Jentsch and Beierkuhnlein 2008; Stott 2016; Ummenhofer and Meehl 2017; Nicholson and Egan 2020). The studies or approaches generally fall across a correlative-process spectrum, with the position on that spectrum based on the assumptions and the form of the climate-species relationship that is modelled. At the correlative end of the spectrum, traditional species distribution models (SDMs) tend to use broad-scale environmental (climate) averages in a correlative spatial framework to identify species' environmental associations (Elith and Leathwick 2009; Dormann et al. 2012; Blois et al. 2013). These SDMs can estimate probabilities of occurrence and/or relative environmental suitability (Guisan and Thuiller 2005; Booth et al. 2014; Guillera-Arroita et al. 2015; Rasmont et al. 2015) and when combined with climate scenarios, can be used to predict future species distribution patterns (Elith and Leathwick 2009). These predictions rely on a space-for-time assumption, specifically that species-climate relationships are consistent over space and time, also known as 'stationarity' (Elith and Leathwick 2009; Lovell et al. 2022). However, this assumption has been frequently questioned, for example, Oedekoven et al. (2017) and Bradter et al. (2022), used a climate decomposition method to split the spatial, temporal and spatio-temporal components of weather data, revealing inconsistent bird species-climate associations between the components. Bradter et al. (2022) found that the direction and magnitude of species' associations with climate variables frequently differed between the spatial and temporal aspects of the analysis, ultimately questioning the space-for-time equivalence assumption.

Mechanistic models are located at the opposite end of the correlative-process spectrum to the SDMs discussed above, where they capture how demographic and dispersal processes relate to climatic variables (Dormann et al. 2012; Briscoe et al. 2019; Bocedi et al. 2021; Zurell et al. 2022; Uribe-Rivera et al. 2023). For example, the impact of temperature can be modelled at the individual level (based on physiology and behaviour) to characterise links between demographic rates (e.g., reproduction or mortality) and temperature (Chapman et al. 2014; Sibly et al. 2013; Briscoe et al. 2019; Johnston et al. 2019). Essentially, mechanistic models focus on ecological processes, contrasting with the correlative nature of traditional space-for-time approaches (Yates et al. 2018; Bocedi et al. 2021; Zurell et al. 2022). This shift in the ability to capture the underlying ecological process is associated with an increased data requirement, ecological understanding, and computational burden, meaning uptake has been far lower than that of traditional space-for-time approaches (Yates et al. 2018; Zurell et al. 2022).

There are several approaches that sit between mechanistic models and SDMs, one set of approaches involves modelling temporal changes in the biodiversity status of given locations in relation to climate metrics (Kerr et al. 2015; Suggitt et al. 2018; Soroye et al. 2020). While still using correlative methods, these approaches move closer to the desired goal of describing spatio-temporal changes in species' status and associated ecological processes. Occupancy models are one such example, occupying a promising intermediate position along the correlative-process spectrum. In their simplest form (i.e., non-dynamic), occupancy models assess the probability that a given species is present within a given location or set of locations (Guillera-Arroita 2017; Shirey et al. 2023). Dynamic occupancy models are designed to explicitly capture colonisation and (local) extinction processes, making it possible to model changes in occupancy as a function of covariates that vary in space and time. These dynamic models can potentially reveal finer scale environmental associations that may be missed by traditional SDMs. For example, Malinowska et al. (2014) used dynamic occupancy models to examine local loss and colonisation of sites in response to weather variability. A further benefit of occupancy models is that they can be adapted to mitigate for some forms of bias that lead to variation in detectability over time, vital when modelling opportunistic species occurrence data (van Strien et al. 2013; Isaac et al. 2014). Such models have been used to examine the impact of environmental drivers on occupancy dynamics for birds (Lassiter et al. 2021; Kéry et al. 2013; Jones et al. 2016; Rushing et al. 2019), insects (Malinowska et al. 2014; Termaat et al. 2019) and salamanders (Rucker et al. 2022), among others. The ability of dynamic occupancy models to include regional responses to a range of drivers within a spatio-temporal framework makes them particularly desirable for assessing species associations with climatic drivers in both space and time.

However, while dynamic occupancy models are useful for detecting spatio-temporal dynamics, they are data hungry, for example needing within-year repeat visits to the same sites to reliably estimate and account for variation in detectability (MacKenzie et al. 2002; Pescott et al. 2019). This means that the performance of dynamic occupancy models can be undermined by data limitations and biases, commonly found in opportunistic datasets (Altwegg and Nichols 2019). Understanding these limitations is critical if such models are to be reliably used to infer climate-associated distribution change. This raises two key questions: firstly, can dynamic occupancy models detect climate-associated distribution changes at fine spatio-temporal scales beyond what is captured by traditional SDMs? Second, how well do these models perform when applied to large-scale, opportunistic species occurrence datasets?

To explore these questions, we apply dynamic occupancy models with two temperature metrics to 106 wild bee species in Britain. We focus on bee species as pollination is a critically important ecosystem service, valued at up to $577 billion per annum to global agricultural production (Díaz et al. 2019), with bees widely considered one of the most important groups of pollinating insects (Garibaldi et al. 2013; Rader et al. 2013). Furthermore, evidence suggests that climate change is having a negative impact on many bee species (Polce et al. 2014; Settele et al. 2016; Giannini et al. 2020), with a consistent pattern emerging of climate-driven losses, particularly at warmer range margins (southern range edge for northern hemisphere species). Specifically, we ask whether local losses can be explained by (1) the long-term temperature average of the site (a spatial term), akin to the spatial associations that underpin SDMs, and/or (2) a spatio-temporally resolved temperature metric (annual deviation from the long-term mean), which could reveal potential climate-driven losses at a fine scale. We address whether these relationships with temperature can explain interspecific variation in trends over recent decades. Finally, we assess the performance of dynamic occupancy models when applied to a high-quality opportunistic species occurrence dataset, and use a formal risk-of-bias assessment (Boyd et al. 2022) to help understand model performance.

2 | Methods

2.1 | Data Sources

The occupancy dynamics of bee species were examined using biological records collated from a range of sources and recorders and verified by the Bees, Wasps and Ants Recording Society (BWARS: https://www.bwars.com). The data are presence only and are dominated by incidental records collected without systematic survey design. We analysed over 150,000 records across 106 bee species, where each record represents a unique combination of a particular species, date, and 200 × 2 km grid cell. We excluded the honey bee (*Apis mellifera*), as occupancy dynamics for this species are influenced by human management of hives. Our analysis spans the period 1990 to 2015, a period of climate warming during which time the recording intensity of wild bees in Britain was relatively stable (see Appendix S5). Following numerous published studies, we inferred absence when at least one other wild bee species was recorded within the grid cell–date combination, but the target species was not recorded (following van Strien et al. 2013; Powney et al. 2019; Rapacciuolo et al. 2021). Despite being a well-established approach to inferring absence, this is a low threshold to assume a cell has been sampled and infer absence, and means 'targeted sampling' (a visit where a collector seeks a single species) will be used to infer non-detection for non-target species (Shirey et al. 2023). However, as this study applies and assesses an industry standard approach to modelling unstructured data, we follow this method here. Species with significant widespread nomenclatural confusion were omitted following Powney et al. (2019).

We extracted monthly near-surface air temperature data at 1 km grid cell scale between 1990 and 2015 from the Climate, Hydrology and Ecology research Support System (CHESS) (Robinson et al. 2017). Near-surface air temperatures were deemed appropriate as they are frequently associated with insect dynamics (e.g., distribution patterns, range shift and phenological events) and the data were available at the temporal scale of interest (annual) (Terando et al. 2018; Boyd, Harvey, et al. 2023; Boyd, Powney, and Pescott 2023). The temperature data were converted to the 2 × 2 km grid cell scale by calculating the mean temperature across all 1 × 1 km cells within each 2 × 2 km. Annual temperature variables were extracted from months coinciding with the flight period of each bee species, estimated as the mean temperature across all months falling between the upper and lower 95th percentiles of a density curve fitted to the given species' records. Consequently, species with multiple flight periods were excluded from the analysis (25 species). Our final analysis was based on 106 bee species in Britain across 13,750 unique 2 × 2 km grid cells. See Appendix S5 for an in-depth description and map of the occurrence data.

We included two temperature covariates within the species models, both extracted from the annual temperature dataset described above. Firstly, we estimated the spatial temperature term (ST) as the mean temperature between 1990 and 2015 for each 2 × 2 km grid cell; this was calculated separately for each species using temperature data that coincides with the given species' flight period (discussed above). Secondly, we calculated the spatio-temporal term, the local temperature anomaly (TA). TA was calculated as the difference between the annual temperature for the site-year in question and the overall average (across all years) for the given site. In other words, TA captures both spatial and temporal variation, as it is calculated for each unique site-year combination by subtracting the long-term average temperature for that site (across all years) from the annual temperature in a specific year at that same given site. An illustrative example showing the calculation of the two temperature metrics is shown in Appendix S1. TA was calculated separately for each species using the temperature values coinciding with the species' flight period. To bring the two variables onto a similar scale and thereby give equal weight to the analysis, the ST term was standardised to have a mean of 0 and a standard deviation of 1. We used these variables to examine if a local temperature metric (here, TA) shows greater correlation with the probability of local grid cell loss than the equivalent broader spatial temperature metrics (here, ST). We note that as both climate variables and their interaction term are included in the model, here we are estimating partial associations between the climate metrics conditional on the other variables in the model.

2.2 | Modelling Species Response to Temperature

Biological records tend to be collated from a range of sources, with many records collected without a systematic sampling process. This means the records can contain various forms of bias that require attention when modelling species response to environmental drivers (Hill 2012; Powney and Isaac 2015). These biases are discussed in Appendix S5, where we present a risk-of-bias in temporal trends assessment (Boyd et al. 2022) for the data and models used in this study. We used dynamic hierarchical occupancy models fitted within a Bayesian framework to model species colonisation and local loss (often referred to as local extinction). Evidence suggests such occupancy-detection models may be used to deal with a range of common forms of bias associated with biological records (Isaac et al. 2014; Guillera-Arroita et al. 2014). There are two key reasons for using these models. Firstly, the hierarchical component of the model is necessary to attempt to mitigate variation in detectability, specifically using a detection sub-model (the parameters of which are described below). Secondly, the dynamic aspect of the model captures time-varying covariates of species' local loss and colonisation (van Strien et al. 2013; Briscoe et al. 2021). Here, we fit single-species dynamic occupancy models, defined in Equations (1 and 2) below, to assess the strength of the association between ST and TA with local losses of bee species across Britain between 1990 and 2015. We include the temperature terms as covariates of local loss (as opposed to both local loss and colonisation) because we wanted to focus on understanding the greater declines seen in upland species (compared to southern species) in Powney et al. 2019, whilst not over-parameterising the model.

Equation 1: The occupancy (state) sub-model:

For all years (except the first year):

$$Z_{it} \sim \text{Bernoulli}(\psi_{it}); \psi_{it} = Z_{i,t-1} \times (1 - \Phi_{it-1}) + (1 - Z_{i,t-1}) \times \gamma_{t-1}$$

$$\text{logit}(\Phi_{it}) = a + \beta_1.\text{ST}_i + \beta_2.\text{TA}_{i,t} + \beta_3.\text{ST}_i.\text{TA}_{i,t}$$

For the first year:

$$Z_{it=1} \sim \text{Bernoulli}(\psi_{it=1}); \psi_{it=1} = Z_{i,t=1} \times \delta_{it=1}$$

$$\text{logit}(\delta_{i,t=1}) = \phi + \beta_0.\text{ST}_i$$

Equation 2: The detection (observation) sub-model:

$$Y_{itv} \mid Z_{it} \sim \text{Bernoulli}(Z_{it} \times P_{itv}); \text{logit}(P_{itv}) = \alpha_t + \beta_4.\text{DT2}_{itv} + \beta_5.\text{DT3}_{itv}$$

In the occupancy (state) sub-model, the true presence or absence of the species at site i and time t (Z_{it}) is a function of the probability of occupancy (ψ_{it}), which is informed by a colonisation (γ_{t-1}) and a local loss parameter (Φ_{it-1}). For the first year, probability of occupancy ($\delta_{i,t=1}$) is a linear function of the average temperature of the site (ST_i) with an intercept (ϕ) capturing average occupancy of the species in question for the first year. We allow colonisation to vary by year (γ_t).

Assessing the impact of temperature on local grid cell loss forms the main focus of this study. Here, local loss (Φ_{it}) is a linear function of the average temperature of the site ($\beta_1.\text{ST}_i$), and a linear function of the local temperature anomaly for the given year ($\beta_2.\text{TA}_{i,t}$). Local loss (Φ_{it}) is also a function of the interaction between the two temperature parameters ($\beta_3.\text{ST}_i.\text{TA}_{i,t}$), enabling us to examine how the relationship between local loss and local temperature anomaly varies based on the average temperature of the site in question. For example, does local loss tend to show stronger positive associations with warmer years in cooler sites? Thus, the core focus of this analysis is evaluating β_1, (the spatial effect), β_2 (the spatio-temporal effect) and β_3 (the spatio-temporal interaction). Furthermore, we examine how these effects vary across the broad distribution category trait described in Powney et al. (2019), where a clustering algorithm was used to split species into one of four categories based on their distribution patterns. The four categories of Powney et al. (2019) are upland species, southern species, widespread southern species, and widespread species (which was dominated by hoverfly species). Of the 106 bee species in this analysis, a single bee species (*Bombus pascuorum*) was categorised as 'widespread' based on Powney et al. (2019); we therefore included this species in the 'widespread southern' category, meaning we present the β effects across the remaining three categories: upland species, southern species, and widespread southern species.

The detection sub-model (equation 2) aims to capture (and therefore account for) the observation process. Here, the observed/recorded data (Y_{itv}) is a function of the true presence or absence of the species in a given site in a given year (Z_{it}) and the probability that it would be detected on the given visit (P_{itv}). The probability of detection is a function of the year (α_t), thereby allowing detectability to vary temporally, and as a function of the category of list length (the number of species recorded on the visit) ($\beta_4.\text{DT2}_{itv}$ and $\beta_5.\text{DT3}_{itv}$). Visits were grouped into three categories based on the number of species recorded: (1) single species lists, (2) short-day lists, 2 or 3 species recorded (*DT2*), and (3) comprehensive day lists, visits with > 3 species recorded (*DT3*). The list length category is used as a surrogate for recorder effort on a given visit (van Strien et al. 2013; Powney et al. 2019). The detection model requires repeat visits within site-year combinations to parameterise the detectability estimates; this was our primary justification for conducting the analysis at the 2 km grid square scale. Furthermore, the dynamic model requires repeat visits to grid cells across successive years in order to assess colonisation and persistence. Moving to a larger spatial scale will increase both these aspects of the data. However, shifting to broader scales is a trade-off, increasing repeat visits at the potential cost of the ability to detect climate signals (discussed in more detail in the discussion).

Modelling and data manipulation were run in R version 4.1.0 (R Core Team 2021). Dynamic occupancy models were implemented in a Bayesian framework using the *ubms* v1.1.0 R package (Kellner et al. 2022). For each model we ran three chains with 3000 iterations and a warm up (burn in) of 1500 iterations. Model parameter convergence was assessed using the Rhat statistic, with convergence considered adequate where Rhat < 1.1 (Kéry and Schaub 2012). There was a weak positive association between TA and ST across the full dataset (slope = 0.2, $r = 0.41$, $r^2 = 0.17$), suggesting minimal collinearity issues within the models. Again, our inferences are based on the distribution of beta parameters for each species, and we highlight notable parameters in cases where the 95% credible intervals (CI) exclude zero. For clarity, the 95% CIs refer to the range between the 2.5th and 97.5th percentiles of the posterior distribution for the given parameter. Therefore, we consider a parameter as 'notable' if there is at least a 97.5% probability that its true value excludes zero given the model results. This indicates it is overwhelmingly likely to be positive (lower 2.5th percentile above zero) or negative (upper 97.5th percentile below zero) based on the spread of the posterior distribution for the given parameter.

3 | Results

We found substantial species-specific variation in the association between the temperature covariates, ST (the spatial term:

long-term site-specific mean temperature) and TA (the spatio-temporal term: local temperature anomaly) and the probability of local grid cell losses (Figures 1 and 2) and in the relationship between ST and the probability of initial occupancy (Figure 3). The clearest signal was found in the correlation between ST and the probability of local loss (Figure 1), where most species (> 60%) showed notable (95% CI do not span zero) correlations. This is in sharp contrast to the correlation with TA, where only one species (*Bombus soroeensis*) showed a notable (95% CI do not span zero) correlation between TA and the probability of

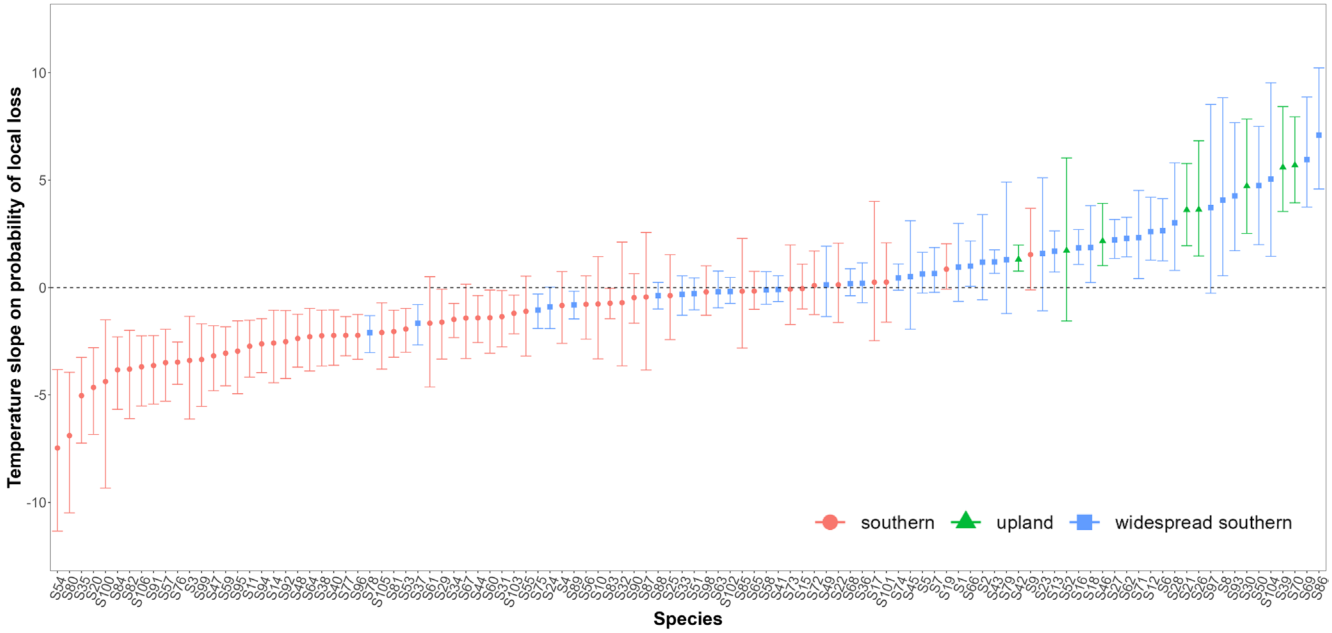

FIGURE 1 | The effect (slope) of mean annual temperature (ST) on probability of local site loss. Data are the mean and 95% credible intervals (CIs) of the slope parameter for each species. Species are arranged from the most negative to most positive mean slope estimate. Species codes are listed on the *x*-axis, the species name and species code look-up table is available in Appendix S6. Colour is used to distinguish species based on the distribution category trait (Powney et al. 2019). Species with negative slopes (left side of the plot), show greater probability of local loss at cooler sites, while species with positive slopes (right side of the plot) experience a greater probability of loss at warmer sites. Slope estimates are considered notable if the spread of the 95% CIs excludes zero.

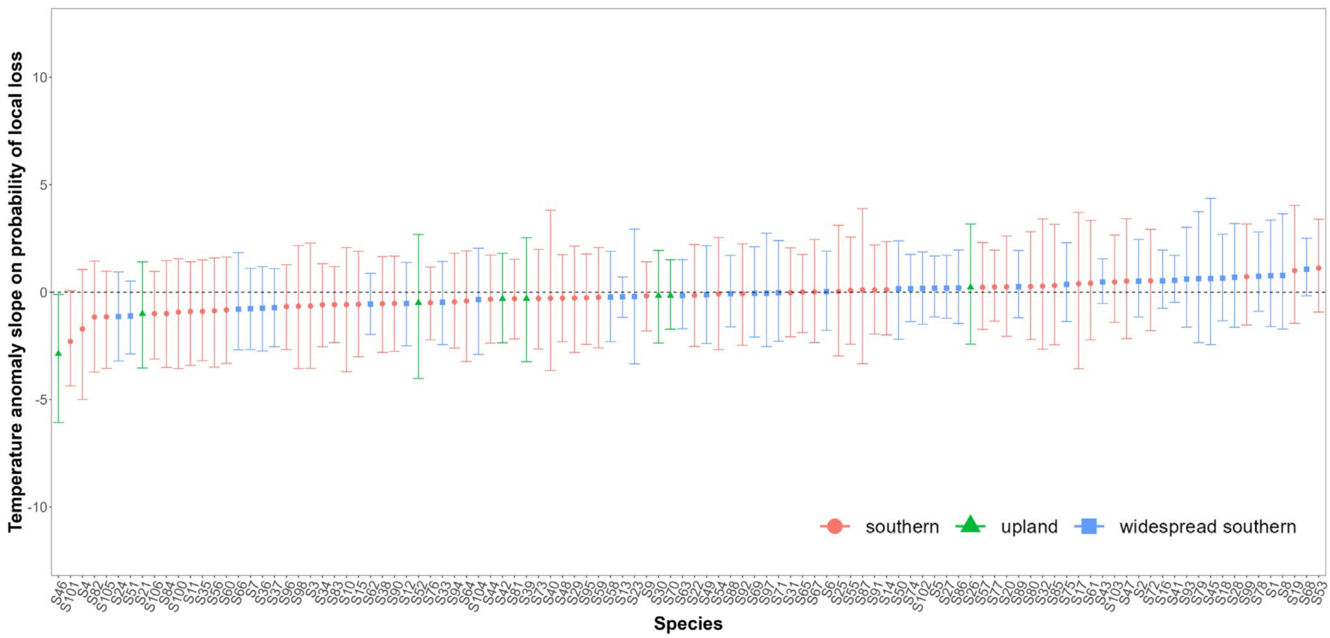

FIGURE 2 | Temperature anomaly (TA) slope on probability of local site loss. Data are the mean and 95% credible intervals (CIs) of the slope parameter for each species. Species are arranged from the most negative to most positive mean slope estimate, and coloured based on the distribution category trait (Powney et al. 2019). Species codes are listed on the *x*-axis, the species name and species code look-up table is available in Appendix S6. Slope estimates are considered notable if the spread of the 95% CIs excludes zero.

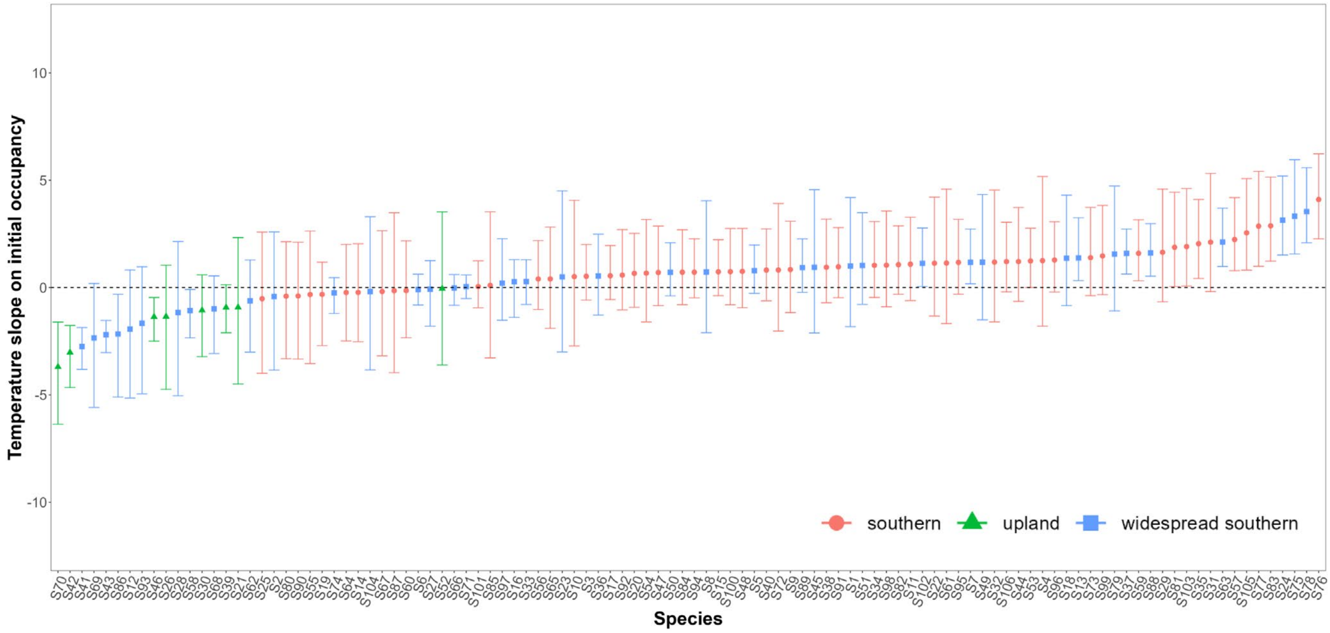

FIGURE 3 | Mean temperature effect (slope) on probability of occupancy in the first year (1990). Data are the mean and 95% credible intervals (CIs) of the slope parameter for each species. Species are arranged from the most negative to most positive mean slope estimate, and coloured based on the distribution category trait (Powney et al. 2019). Species codes are listed on the *x*-axis, the species name and species code look-up table is available in Appendix S6. Slope estimates are considered notable if the spread of the 95% CIs excludes zero.

local loss (Figure 2). A notable relationship between ST and the probability of occupancy in the initial year, 1990 (Figure 3), was revealed for approximately a fifth of species. We found no evidence to support an interaction effect on the probability of local loss between the two temperature terms (Appendix S2).

In Figure 1, we rank species in ascending order of mean β_1 (slope of the ST parameter on probability of local loss). A negative relationship between ST and probability of local loss suggests these species show an increased probability of loss at cooler sites (and lower risk of loss at warmer sites), and we show that 37% of species fall within this group (where the 95% CI do not span zero). By contrast, 23% of species had a notable positive relationship between ST and probability of local loss. As expected, the probability of local loss increased with ST for species that tend to occur in cooler sites, with the reverse pattern seen for southerly distributed species (Figure 1). Interestingly, species belonging to the widespread southern grouping also tended to show positive associations between ST and probability of local loss, meaning a greater probability of loss at warmer sites. Although this was not as clear a distinction as the patterns seen in the southern and upland groupings, (i.e., four widespread southern species showed a negative association between ST and probability of local loss).

We found that the best estimate (posterior mean) of the slope describing the relationship between ST and probability of occupancy in 1990 was negative for all upland species. However, only 38% of these were considered notably negative associations, where the upper bound of the 95% credible interval was below zero, indicating stronger confidence that the true association was negative (Figure 3). Interestingly, the 19% of species that showed a notable positive correlation between ST and initial occupancy in 1990 all fell within the southern or widespread southern trait grouping.

While we found a strong spatial signal in the association between ST and local loss, the slope of this relationship was not related to the species-specific annual trend estimates from Powney et al. (2019) (Appendix S3).

Mean detectability averaged across all species was 0.02, 0.04, and 0.11 for list length categories 1, 2, and 3, respectively. This low level of detectability was broadly consistent across years (see Appendix S4).

4 | Discussion

Results from the dynamic occupancy models revealed a strong spatial climate signal (ST) across many species, but little evidence that the spatio-temporal temperature term (TA) is associated with local loss of wild bee species in Britain. This pattern likely reflects both real ecological dynamics and limitations in model–data sensitivity to detect patterns of change. We cannot definitively state that the lack of spatio-temporal signal genuinely reflects a lack of local temperature influence on the occupancy dynamics of wild bee species. Our use of a detailed risk-of-bias assessment (Appendix S5) revealed a lack of repeat site visits within and between years that is likely inhibiting our ability to account for detection bias in the analyses, in turn influencing our ability to detect species–temperature associations. Furthermore, refinement of the period from which the temperature metrics were derived might improve the climate signal in our model outputs.

The exclusively spatial term, mean temperature (ST), was a notable correlate of the probability of local losses for the majority (> 60%) of species. While the direction and strength of the correlation varied across species, it was consistent with expectations based on their broad distribution patterns (Kerr et al. 2015). For example, the probability of local loss was negatively associated with ST for many southern species, suggesting the risk of loss was highest in the coolest parts of the distribution range for these species. This is the cool range edge (colonisation front) for many of these warm adapted southern species and is likely to contain sites characterised by high levels of interannual occupancy fluctuation. Populations inhabiting sites near the temperature tolerance threshold have limited ability to adapt to other pressures (e.g., populations at the cool range edge may already be restricted to habitats containing the warmest microclimates) and therefore are more likely to undergo local losses in times of perturbation (Oliver et al. 2009). This can be considered an indirect relationship with temperature, as the probability to detect local loss in these regions will be increased due to a vulnerability to a range of other environmental drivers. Evidence to support this indirect impact of temperature can be seen in Oliver et al. (2009), who found southern species of British butterflies were restricted to their most favoured habitats in cooler locations. The correlation we see between the probability of local loss and the spatial temperature term may also be partly explained by standard range edge demographic processes (e.g., lower reproductive rate, increased population variability, etc.) (Thomas et al. 1999; Oliver et al. 2012). Furthermore, species are likely to be less common at their range margin, meaning they are less likely to be observed. Interestingly, we found that mean temperature was positively associated with the probability of local loss for several widespread southern species. This could be an artefact, caused by a known limitation of space-for-time approaches based on correlative modelling: confounding. That is, the trend could reflect a different, spatially correlated driver of the probability of local loss, with land-use or land-cover change a likely candidate (Rowland et al. 2020). Southern Britain has undergone greater land use change and has a greater proportion of agricultural land compared to northern Britain (Tomlinson et al. 2018), these land use characteristics being well-known drivers of biodiversity loss (Díaz et al. 2019; Davison et al. 2021). Increasing the number of environmental predictors, climate metrics, and taxonomic coverage within this modelling framework would help shed light on the key drivers of species occupancy dynamics and is an ideal area for future work.

Below, we discuss potential reasons for the lack of spatio-temporal climate signal detected in our modelling framework. These explanations fall into three categories: (1) a lack of sufficient data for the data-hungry dynamic occupancy model (i.e., the combination of data and modelling framework is insufficient), (2) suboptimal temperature metrics, or (3) a genuine lack of temperature influence on the spatio-temporal dynamics of wild bee species in Britain.

The lack of correlation between the annual temperature anomaly (TA) and probability of local loss suggests that individual warm or cold years are not important in the context of local losses based on our modelling framework. This result is surprising for such thermophilic species and given the body of evidence broadly supporting such trends (Settele et al. 2016; Sirois-Delisle and Kerr 2022; Soroye et al. 2020), although see a response questioning the robustness of the analytical methods of Soroye et al. (2020) and Guzman et al. (2021). For example, a global meta-analysis by Wiens (2016) found 47% of species (covering plants and animals) had experienced climate-related local extinctions, while Román-Palacios and Wiens (2020) found sites with larger increases in maximum temperatures (hot anomalies) had higher levels of local extinction (plants, insects and birds). Our results of weak spatio-temporal temperature signals in bee occupancy dynamics contrasts those climate associations discussed above, but our results do align with those from Malinowska et al. (2014), who also found little evidence of an association between fine-scale spatio-temporal temperature metrics and species' occupancy dynamics of insects and reptiles. It is worth noting that Malinowska et al. (2014) used a similar dynamic occupancy modelling framework and so may have encountered similar modelling issues as discussed below.

B. soroeensis was the only species to show a notable association with the annual temperature anomaly, where we found that the probability of local losses was highest in cooler years. This was not expected given the ecology of the species, which is thought to be habitat restricted (rather than temperature limited). Furthermore, as with most bumblebee species, *B. soroeensis* is adapted to cooler conditions (Maebe et al. 2021). Changes in recorder behaviour over time may have influenced the results here, as this species has been the focus of targeted recording (by activity of the Bumblebee Working Group) in the past but not the present. The occupancy model is likely to struggle with targeted recording and its consequences for model assumptions (such as the generation of inferred absences). Shirey et al. (2023) highlighted this issue, stating that species-specific targeted sampling provides no information on non-target species. Ultimately, Shirey et al. (2023) cite the issue of targeted sampling as a reason for using static occupancy models over dynamic occupancy models. They found dynamic occupancy models performed poorly if the proportion of full lists (full community sampled) was low (i.e., a large proportion of targeted recording visits). This is because inferring non-target species non-detections from targeted records causes an increase in non-detections with little information, leading to unreliable estimates of change in state (colonisation and persistence). Shirey et al. (2023) also recommend restricting the inference of non-detections from non-target species records within the target species likely distribution range.

Some have questioned the value of the detection model if not well-specified or data are limited (van Strien et al. 2010; Welsh et al. 2013; Pescott et al. 2019), and our results lend further support to those concerns. Early applications of these hierarchical dynamic occupancy models used structured survey datasets (such as the country-specific Breeding Bird Survey datasets, see Kéry et al. 2013, although note Briscoe et al. 2021), which tend to suffer fewer issues around spatial and temporal bias, missing data, and variation in detectability. Hierarchical dynamic occupancy models fitted to such structured survey datasets tend to have substantially greater average detectability estimates compared to those seen in this study. For example, in this study, mean detectability across all species was 0.02, 0.04 and 0.11 for list length categories 1, 2 and 3, respectively while Kéry et al. 2013, estimated mean probability of detection at ~0.5, Briscoe et al. 2021, had a median probability of detection of 0.77. See Kellner and Swihart (2014) for a review of detectability estimates across the literature. Applications of dynamic occupancy modelling to opportunistic citizen science data are less frequent than their application to structured survey data (see van Strien et al. 2010 and Bled et al. 2013 as examples of this modelling approach applied to opportunistic data). The inclusion of environmental covariates of colonisation or loss (as is done here) is infrequent. A notable exception to this is Malinowska et al. (2014), discussed above. In the context of building a well-specified detection model, adding additional parameters (e.g., Julian day) to the detection model would be an interesting area for future work. However, given the lack of repeat visits within site-year combinations (discussed in more detailed in the following paragraph), it is likely that the additional parameters would lead to issues with over-parameterisation.

The formalised risk-of-bias assessment that we present in Appendix S5 provides some key insights. The assessment highlights the low average number of within-year repeat visits to grid cells within the analysed data (mean = 2.02), which are also spatially and temporally biased (figures 6 and 7 within Appendix S5). Using simulations, MacKenzie et al. (2002) found that mean detection should be greater than 0.3 if sites are only visited twice; otherwise, precision of the occupancy estimate may be too coarse for any useful inference. Furthermore, Pescott et al. (2019) argued against the use of occupancy models in their study where the average number of repeat visits was 1.4, noting that occupancy models tend to be fit to datasets with greater numbers of repeat visits (generally > 4 repeat visits on average). It is likely that the low number of repeat visits in this study has led to imprecise estimates of detectability. While we were still able to detect broader spatial climate signals using this approach, the imprecise and potentially biased detectability estimates may have inhibited our ability to detect any finer scale spatio-temporal climate signal.

Alongside the low number of repeat visits within years, we also found a general lack of grid cells that were visited in multiple years within the time series of the study, and even fewer grid cells that were visited in adjacent years (figures 1 and 2 within Appendix S5). This may mean it is hard to pin down the year in which a population was lost from a grid cell, thus unambiguously linking the loss to anomalous temperatures. Given that this dynamic model requires visits to the same grid cells in adjacent years, the patterns within the visit maps of figure 2 in Appendix S5, and that most of the records used in this analysis were collected without systematic sampling design, it is likely that there is a non-zero correlation between sample inclusion and occupancy. This correlation means the resulting models will likely contain bias in the estimated parameters (Meng 2018; Boyd, Harvey, et al. 2023; Boyd, Powney, and Pescott 2023). Further evidence of this sample inclusion bias can be seen in the distribution of visited grid cells, which tended to be biased towards the warmer regions of Britain (figures 3 and 4 within Appendix S5). This spatial bias means the temperature-occupancy parameter estimates in our models will be driven by dynamics/patterns of change in those warmer regions. It should be noted that this bias is not necessarily an issue if we acknowledge that results likely reflect the pattern of change in the warmer parts of Britain. Furthermore, we were able to detect a spatial climate signal for many species even with the spatial bias in data. Also, bee richness in Britain is greater in the south, so increased survey effort in these regions may better reflect the true distribution of the focal group.

Despite efforts to extract a temperature metric for the climatically important time-window (mean temperature across month coinciding with the species' flight period), there is potential to refine this approach. For example, using a sliding window focused on time-periods that coincide with the species emergence (as seen in Wyver et al. 2023) may increase the sensitivity of our models. Further refinement options for the climate variables can be seen in Müller et al. (2023), where they found 75% of the variation in temporal changes in insect biomass was explained by a model containing a range of weather metrics (including climate anomalies) alongside habitat metrics. In our study, only 19% of species showed a notable positive relationship between initial occupancy (1990) and mean annual temperature. We would expect this percentage to be greater given the dominance of southern and widespread southern species included in this analysis and given the thermophilic nature of most insects. Again, this could be due to the broad time-window used to estimate the temperature metric, or due to a lack of repeat visits in the early time periods (figure 6 within Appendix S5). As a result, the models struggle to estimate detectability and in turn the true distribution of, and temperature impact on, the species in 1990. Applying these same models to a thermophilic insect group covered by a long-term structured monitoring scheme (e.g., UK butterflies) would be an interesting area for future work. This would help decipher whether the lack of spatio-temporal temperature signal on local loss is genuine (as partly suggested in Malinowska et al. 2014) or due to the combination of modelling approach, temperature metrics and data quality. Furthermore, given the temperature dependence of insect flight activity and the widespread evidence of climate-driven range expansion at species' cooler range edge (Chen et al. 2011; Mason et al. 2015; Platts et al. 2019), we may also expect to detect a spatio-temporal climate signal on site colonisation, another area for future work.

To conclude, while we find strong spatial signals between long-term temperature and the occupancy dynamics of wild bee species in Britain, our ability to detect responses to local temperature anomalies appears limited. This is likely due to data–model structure and detectability challenges inherent when applying dynamic occupancy models to large-scale opportunistic occurrence data. Targeted effort to refine the temperature metrics (e.g., focusing on key phenological windows), increase repeat site visits, and incorporate other drivers (e.g., land use change) will be essential for improving future inference. Finally, we highlight the importance of including clear risk-of-bias assessments in studies of biodiversity trends. These assessments provide a structured way to identify and account for potential sources of bias. Here, they helped identify possible limitations in detecting local temperature effects due to underlying sampling patterns. As the use of opportunistic occurrence datasets increases, we strongly encourage researchers to make risk-of-bias assessments a routine part of their analytical workflows.

Author Contributions

Gary D. Powney: conceptualisation, funding acquisition, data curation, methodology, formal analysis, visualisation, writing – original draft,

writing – review and editing. James M. Bullock: conceptualisation, funding acquisition, methodology, writing – review and editing. Robin J. Boyd: conceptualisation, methodology, writing – review and editing. Claire Carvell: conceptualisation, funding acquisition, methodology, writing – review and editing. Mike Edwards: conceptualisation, data curation, methodology, writing – review and editing. Rowan Edwards: conceptualisation, data curation, methodology, writing – review and editing. Bill William E. Kunin: conceptualisation, funding acquisition, methodology, writing – review and editing. Nick J.B. Isaac: conceptualisation, funding acquisition, methodology, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The underlying temperature data used in this study are available here: https://catalogue.ceh.ac.uk/documents/b745e7b1-626c-4ccc-ac27-56582e77b900. The species occurrence data cannot be redistributed by the authors; however, the data are freely available from the Bees, Wasps and Ants Recording Society (https://bwars.com/content/bwars-data-download).

Peer Review

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Supporting Information

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