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The role of weather in regulating European bird and butterfly populations

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General summary

Understanding the causes of temporal variation in abundance is a fundamental question within population ecology, and one with a number of implications for how we think about and manage our natural systems. In particular, there is much interest in the role of climatic variation, or weather, in determining population processes, due both to the observation that these variables can be substantially involved in regulating demographic and population processes, as well as the current context of climate change, which is forecast to become a major determinant of population change over the course of 21st century. In this thesis, I address the role of weather in determining variation in abundance of European birds and butterflies, using large-scale monitoring datasets from 11 countries across Europe. In chapter II I assess the sensitivity of 12 univoltine butterfly species to climatic variation across their geographic range, finding that weather appears to be relatively more important towards latitudinal range margins. In chapter III I address the extent to which weather variables contribute to observed temporal variation in abundance in 153 species of European bird. I find that, while there is a statistical signal of weather in the population growth rates of the majority of species, explanatory capacities are typically low, with the effect that models that contain large sets of weather variables perform fairly equivalently to those that contain none at all. There are a number of potential causes of this result, which I discuss, as well as make recommendations for further work to discriminate between these. In chapter IV I test whether including information about short-term thermal variation in population growth rate models enhances our ability to explain variation in abundance for 32 species of butterfly in the UK. I find that, for the majority of species, models of population growth are more able to explain variation in abundance when they include information about fine-scale thermal variation. These results suggest that it may be important to consider thermal variation acting at short timescales to understand the temporal dynamics of populations. Looking across the thesis as a whole, my findings indicate that using monitoring scheme datasets to relate inter-annual variation in abundance to weather is not straight forward; future work with these datasets needs to do more to address the measurement process, as well as working to identify the limitations of models that do not contain population detail such as demographic structure.

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Declaration

The work presented herein is my own, but owes substantially to the guidance and intellectual contributions of my supervisors, as well as a wider group of data providers who are included on the resultant manuscripts.

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All writing, analyses, and data preparation were done by me under the guidance of my supervisors, T.H.O, R.B.B., R.D.G., and K.L.E. Other listed coauthors provided the butterfly datasets, and provided input on the resulting manuscript and contributed to subsequent revisions.

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All writing, analyses, and data preparation were done by me under the guidance of my supervisors, T.H.O., R.B.B., R.D.G., and K.L.E. Other authors provided the butterfly datasets, and provided input on the resulting manuscript and contributed to subsequent revisions. Jana Škorpilová contacted all data providers and was heavily involved in accessing the datasets from the eleven scheme coordinators.

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Chapter 1:

General Introduction

One of the most self-evident features of the natural world is its dynamism. The numbers of animals and plants are in constant flux, both over the course of the year, with abundance varying from season to season, as well as across wider temporal scales, with both marked variation between one year and the next and systematic shifts measured at the scale of decades and longer (Oliver *et al.* 2012; Spooner *et al.* 2018). Taking a long-enough perspective, it is further evident that many species are absent from regions in which they were once abundant, while others are now present where once they were not (Gaston 2003). What causes these spatial and temporal dynamics is a question that lies at the heart of population ecology and has innumerable implications for how we think about and manage our natural systems (Turchin 2003).

Early work on population dynamics tended to have a fairly narrow focus on the relative importance of endogeneous vs. exogeneous processes for determining temporal patterns of abundance (e.g. Elton, 1924), and, indeed, this has been a major theme throughout the development of the field (Bjørnstad & Grenfell 2001). Two key features have emerged from these debates. First is the realisation that complex dynamics can occur in the absence of any external forces at all, as a consequence of chaotic dynamics (May 1976) or simply through complex demographic processes (Turchin 2003). Second, many of the population dynamics we observe in the natural world are readily explained in terms of variation in the environment, and explanations that do not involve these factors will therefore tend to be limited (Stenseth *et al.* 2002). Modern population ecology now tends to consider the causes of variation in abundance in a more unified way, with a focus on how to go about adequately capturing various population processes with statistical models (Krebs 1995; Coulson *et al.* 2004).

Alongside this growth in our understanding of how populations behave are two other important developments. The first of these is that there has been a dramatic change in the availability of datasets with which to compare competing models of population dynamics (Turchin 2003). This represents a radical departure from early work, which relied heavily on theoretical models (e.g. Nicholson, 1933), or attempted to discriminate between competing explanations for population dynamics with what we would now consider unfeasibly small sets of observations (e.g. Elton, 1924). The current era of large longitudinal datasets such as the UK butterfly monitoring scheme (Pollard & Yates 1993) or Pan-European Common Bird Monitoring Scheme (Gregory *et al.* 2005), has transformed our capacity to ask questions of the processes that regulate populations, and, indeed, has resolved many of the major debates that marked the early period of population ecology (Turchin 1999).

The second development is that over the course of the last century there has been a growing awareness of the dramatic changes occurring within our populations and ecosystems. Global analyses document systematic shifts towards ecosystems that are both more depauperate (Ceballos *et al.* 2015; Maxwell *et al.* 2016) and defaunated (Dirzo *et al.* 2014; Inger *et al.* 2015), as well as increasingly homogenised (Newbold *et al.* 2015). Some 1/5 of animals and plants are now considered threatened or endangered (Hoffmann *et al.* 2010; Collen *et al.* 2012). Rising threat-status is mirrored in observed rates of extinction, with at least 322 recorded vertebrate extinctions in the last 500 years (Dirzo *et al.* 2014), which corresponds to a 100-fold rise in the risk of extinction in the era of modern humans (Ceballos *et al.* 2015). Population change is further reflected in marked shifts in spatial distribution across many species (Chen *et al.* 2011), as the Earth's biota redistributes according to modern-day pressures (Sunday *et al.* 2012; Wernberg *et al.* 2012).

The magnitude of many of these population changes is substantial cause for concern, particularly given that rates of change appear to have accelerated over the course of the last century (Newbold *et al.* 2015). Questions of population regulation are increasingly of great practical importance, and there is now an intense focus upon resolving the key determinants of abundance and identifying the impacts that anthropogenic activity has upon population processes. Identifying these drivers and developing mitigation strategies is fundamental to the task of managing our natural systems in a way that preserves them for future generations (Mace *et al.* 2018). However, while there are often clear cases where numerical changes in abundance can be unambiguously related to particular drivers, this is frequently not the case, and thus, while we know populations are changing, often the specific drivers of this population change are unclear.

There are a number of different explanations for observed population changes, which can broadly be distinguished as climate-related impacts and non-climate-related impacts, and also their interaction. The latter category includes factors such as habitat-loss and degradation, type of land-use and land-use intensity, and shifting patterns of land-use. The effects of these can be substantial, and, often, may outweigh the effects of climate (Maxwell *et al.* 2016; Newbold 2018). Land-use, for example is estimated to have resulted in average declines of 13.6% in species richness, and 10.7% in total abundance (Newbold *et al.* 2015). Similarly, over-exploitation of habitats is thought to be a major driver of population decline and species threat-status, with ¾ of extinctions since 1500 attributed to either overexploitation, agricultural activity, or both (Maxwell *et al.* 2016). There are thus clear linkages between how landscapes are used and a range of metrics of ecosystem function, including biological and functional diversity, total biomass, and ecosystem resilience (Millenium Ecosystem Assessment, 2005). While habitat loss and degradation have to date arguably been the major causes of many observed population changes, there is now substantial concern about the role of climate change (Pereira *et al.* 2010).

The effects of climate change on populations can be substantial (Parmesan & Yohe 2003), and, moreover, as climate change proceeds, the relative importance of climatic factors in driving population change is likely to shift, with changing climate likely representing a major force of population change over the course of the next century (Newbold 2018). The relative importance of different drivers of contemporary population change is further likely to vary according to a range of other factors. In areas that are experiencing substantial ongoing habitat conversion, for example, factors relating to habitat type and quality are likely to dominate observed changes in abundance. Conversely, in areas that habitat condition is relatively constant from year to year, climatic variation and changing climate is likely to be a relatively more important driver of change. Many regions are experiencing high levels of ongoing habitat conversion and agricultural expansion (for example, the tropics); however, in the context of Europe, contemporary habitat conversion and degradation is relatively minimal. There are however other changes to how we manage landscapes within

Europe that may be important for driving population change. For example, long-term population trend of farmland birds has been linked to shifting agricultural practice in (Doxa *et al.* 2010), and variation in pesticide application is thought to be involved in determining trends of insectivorous bird populations (Hallmann *et al.* 2014).

Resolving the regulatory role of weather and climate (see Box 1 for definition of terms) is increasingly important if we are to understand and forecast population change into the 21st century, and design adaptation and mitigation strategies in response to these (Oliver & Roy 2015). Identifying the effects of weather and climate on populations of European birds and butterflies is the focus of this thesis. I present three chapters (described in section 1.2) that use bird and butterfly monitoring datasets from 11 countries across Europe (described in section 1.3), to understand the role of weather in regulating populations. First, I briefly review the conceptual framework that links population dynamics with climatic variation.

1.1 The role of weather in regulating populations

Most fundamentally, temporal variation in abundance is born from the cumulative effects of four processes, births (B), deaths (D), immigration (I) and emigration (E):

$$N[t+1] = N[t](B - D) + I - E$$

Births and deaths are both per-capita processes, as they must act as a proportion of the population at time *t*, N[t]. By assuming, that immigration and emigration cancel (or that the population is closed), and collapsing the separate *B* and D processes into a single term, *r*, we arrive at the ‘classic’ discrete growth rate equation (Turchin 2003):

$$N[t+1] = rN[t]$$

Where *r* is the population growth rate, or per-capita rate of change (Turchin 1999), and the effects of weather, density, or any other putative driver of population growth act upon this directly. In order to arrive at this latter equation, in which abundance is modelled as a function of *r* alone, we have traded the ability to resolve the individual components *B, D, I,* and *E*, for the opportunity to model variation in *N* in the absence of knowledge about variation in the underlying vital rates. This distinction is an important one, and one that I will return to as I address the linkages between population dynamics and weather.

1.1.1 Weather and individuals

At the most basic level, a population is composed of individuals. Any individual organism does not perform uniformly well across environmental gradients, but rather has regions in which performance is maximised, with declines in performance as conditions increasingly depart from this (Martin & Huey 2008; Vasseur *et al.* 2014). Most well elucidated are thermal performance curves (TPCs), which describe how individual or population performance varies across a thermal gradient. These appear to be characterised by an asymmetric response, with a gradual rise to an optimum with more precipitous declines as temperatures move beyond this (Deutsch *et al.* 2008).

While these curves are often studied in the context of direct physiological responses, these are not the only way in which climatic variables can affect performance, and variation in performance may also arise through varying ability to maintain other important functions across environmental gradients. For example, reproductive capacity is likely to be impaired well before a survival limit is reached (Gaston 2003), but this would similarly contribute towards declining performance. Thus, the TPC can be considered as an integration across all the individual fitness components (Martin & Huey 2008).

The existence of these performance curves suggest a role for climatic regulation in nature, and, indeed, they are often used to forecast how populations and species might respond to changing climatic conditions (e.g. Deutsch *et al.* 2008; Sunday *et al.* 2014; Vasseur *et al.* 2014), as they directly bear on the birth and death components in the population model. However, there are a number of factors that can act to limit their applicability to the real world (Sinclair *et al.* 2016).

Perhaps most importantly, in order to study variation in performance across environmental gradients, *in vitro* studies strip away an organism's ability to behaviourally respond to the environment. However, behavioural response will in many cases form a major component of response to varying environmental conditions

(Buckley *et al.* 2015), and organism function in the real world cannot be understood in the absence of considering the flexibility introduced by this (Sunday *et al.* 2014). A butterfly, for example, can alter its core body temperature by up to 12°C simply though altering its basking behaviour (Barton *et al.* 2014), or, alternatively, selecting for different microhabitats (Suggitt *et al.* 2011; Sunday *et al.* 2014). It is thus not clear how relevant the response to a particular heat-exposure is, given that an individual may readily avoid these exposures through behavioural modification.

Similarly, by shifting the timing of various life history events (i.e. phenology), species are able to minimise their exposure to sub-optimal conditions. In North America for example, despite an average warming in breeding season temperatures of ~1°C, birds have maintained a consistent egg-rearing temperature by shifting breeding phenology forwards by 5-12 days (Socolar *et al.* 2018). Phenological shifts are one of the most readily observed biological responses to ongoing climate change and are well documented in a great many taxa (Root *et al.* 2003). The key implication of these phenological responses is that there is some elasticity in how populations respond to variation in climatic conditions at a particular location, as they can avoid some exposure through concomitant shifts in the timing of life-history events.

Behavioural responses to environmental conditions are, however, not without limits of their own. As conditions increasingly depart from those that are tolerable for a particular species, an organism is increasingly forced to invest in survival responses at the expense of other fitness-generating activities. The accumulating costs of behavioural response then in turn become a limiting factor on organism persistence (Martin & Huey 2008). Phenological changes are similarly limited: though they introduce some flexibility in how a particular species is able to respond to climatic variation *in situ*, they are unlikely to be perfectly compensatory, particularly as conditions start to significantly depart from those that are tolerable. The existence of behavioural regulation is therefore not evidence against the concept of a TPC in general, but rather it is a limitation of TPCs that are observed under simple lab-conditions (Sinclair *et al.* 2016).

Box 1. Defining terms

Climate is the "average weather" for a particular location or region, defined for a particular time-period (IPCC 2014). More specifically, this is the statistical summary of climatic conditions, which might be comprised of a mean and a standard deviation, or potentially other parameters, depending on the complexity of the climatic distribution. *Climate change* is the change in the statistical distribution of climate through time, reflected in any, or all, of its descriptive parameters.

An *Event* is an individual draw from this climatic distribution, the full set of which define the climate for a particular area. Often we might think of an event as *weather* (though this terminology becomes a bit stretched at very small, e.g. minutes, or very large, e.g. annual, temporal scales).

Extreme Climatic Events (ECEs) have been frequently and variably defined (see, for example, Gaines & Denny 1993; Gutschick & BassiriRad 2003, 2010; Jentsch *et al.* 2007; Smith 2011b; Bailey & van de Pol 2016). The number and variety of definitions has had the consequence that it is that it is not clear what the shared features, if any, of ECE research are. My personal synthesis is that such an event would be any event that occurs in the tail of a climatic distribution (and thus is statistically infrequent). I expand on the justification of this, and the effects of events of this form in section 1.2

Finally, *climatic variation* is synonomous with *climatic stochasticity* (which is itself a subset of *environmental stochasticity*), and I use this simply to describe variation in climatic conditions, i.e. variation around some climatic average.

The second important limitation of performance curves built in controlled conditions, is that it is not clear how well these translate to the wider world. *In vivo* performance may be far more affected by factors such as predation (Pitt 1999) or competition (Coulson *et al.* 2004), or the temperature response itself may vary according to other factors such as individual condition (Brett 1971) and developmental stage (Sinclair *et al.* 2016). As a result, TPCs may represent a relatively minor component of overall organism performance. Thus, while there is an abundance of *in vitro* literature documenting the existence of TPCs, and evidence of this form is often used to make inferences about how species and populations in the real world will respond to changing climatic conditions, in order to understand population response in nature this ideally needs to be considered directly.

1.1.2 Weather and demography

The link between how individuals respond to climatic conditions and how the population as a whole responds comes in the form of demography which translates individual responses to a population-level outcome through variation in Births, Deaths, Immigration and Emigration (Merow *et al.* 2014; Griffith *et al.* 2016).

Demographic responses to variation in climatic conditions are well documented across a wide-range of taxa, and indicate that in natural populations climatic conditions can have a significant influence on population vital rates (e.g. Sillett *et al.* 2000; Coulson *et al.* 2001, 2005; Robinson *et al.* 2007; Dybala *et al.* 2013; Cleasby *et al.* 2017). The effects of these responses to climatic variation can be substantial. In the California Song Sparrow *Melospiza melodia*, for example, winter weather (average temperature and precipitation during over-winter period) alone can explain 44% of the variation in adult survival (Dybala *et al.* 2013). Similarly, in Soay sheep, a model that links variation in winter conditions to survival can explain 92% of the observed variation in population size (Coulson *et al.* 2001).

While demographic studies such as those described above indicate that climatic variation can have significant impacts on natural populations, they also raise some substantive issues that are particularly concerning to the would-be modeller of population dynamics. The first of these is that, where applied to age-structured populations, they frequently find substantial divergence in how different age-classes respond to variation in environmental conditions (e.g. Milner *et al.* 1999; Coulson *et al.* 2001; Robinson *et al.* 2007; Dybala *et al.* 2013). In Soay sheep, for example, though the population is strongly regulated by winter weather, its effects can vary markedly between different age- and gender-classes (Milner *et al.* 1999), with the consequence that weather effects are weakly resolved until additional information on this population structure is included into statistical models of population growth (Grenfell *et al.* 1998; Coulson *et al.* 2001).

In the case of the California Song Sparrow, divergent juvenile responses indicate that not only can the action of a particular weather variable be poorly resolved in the absence of knowledge of the population structure, but also that entirely different sets of weather variables act on different population age-components (Dybala *et al.* 2013). Thus, as with the Soay sheep, if a statistical model is unable to resolve vital rates directly, there may be quite serious limitations on its capacity to model variation in abundance through time. A further demonstration of the importance of age-structured variation in vital rate arises due to the fact that the relative frequencies of different age-components is expected to shift through time as a consequence of climate change (Dybala *et al.* 2013). From the perspective of a model that could not resolve the separate contributions of different age-classes to overall population size, population response would appear to shift through time, despite the fact that the direct weather responses are unchanged.

Generally then, demographic studies suggest both that weather plays an important role in regulating populations, but also that these drivers may be difficult to resolve with models that only observe the growth-rate term, r (Knape & de Valpine 2011). This can be understood as the loss of model-flexibility that arises due to collapsing these separate population processes (B, D, I, and E) into a single term. However, the other side of this trade-off is that, due to the high data-requirements required to resolve these fine-resolution processes, in order to model these vital-rate processes directly we have drastically narrowed the data available to understand drivers of population change. The inability to learn from and predict population responses to changing climate from models that cannot resolve vital rates would represent a severe limitation in our capacity to understand how populations will respond to change, and to predict response across the large spatial extents required for conservation.

However, while a model that cannot observe *B, D, I,* and *E*, directly will necessarily incur some cost to its explanatory capacity (Coulson *et al.* 2001), in a range of contexts, population-dynamic models have also displayed substantial capacity to explain inter-annual variation in abundance (e.g. Roy *et al.* 2001; Jiguet *et al.* 2006; Boggs & Inouye 2012; Roland & Matter 2013; Oliver *et al.* 2015). Interestingly, issues related to population structure further suggest a role for taxonomic differences in model performance: species with relatively more simple population structure (or, equivalently, there is no population-structured heterogeneity in response) would be predicted to have population dynamics that are more explicable than those with complex population structure. Indeed, many of the examples that I refer to below are for taxa such as Lepidoptera, which, based on the arguments here, we might *a priori* expect to be more readily explicable in the absence of information on population structure.

This issue of population structure relates to a more fundamental tension within ecology between explanations that are sufficiently nuanced to recognise the important idiosyncracies of a system, while sufficiently general that they do not simply become a unique case (Lawton 1999; Bjørnstad & Grenfell 2001). This distinction can be framed as a difference between models that are sufficiently generic that they can be applied across wide taxonomic and spatial extents, and models that are highly-case specific but can explain the behaviour of a particular focal system well (Godfray & Rees 2002). This is a point I return to throughout this thesis, and one that I discuss below.

1.1.3 Weather and populations

The population dynamics of the mormon fritillary *Speyeria mormonia* are in large part due to just a single weather driver, date of snow melt, with some 84% of the temporal variation in abundance attributed to this factor alone (Boggs & Inouye 2012). Though population abundance can be understood in terms of a single driver, its action is quite complex, and is mediated both via the direct effects of snow-melt date, and also by the indirect effects of flowering of the preferred nectar resource, which is in turn determined by snow-melt. This example identifies that a simple population growth rate model can explain variation in abundance remarkably well, but also suggests that there may be strong context dependencies in the factors that modify abundance in this system. For example, this species is found in montane habitats spread across much of north America (Sims 2017). How well does this mechanism transfer to other populations of butterfly found in other portions of the range? Moreover, how well would this mechanism translate to other butterfly species; would it translate to closely related species? Most importantly, would a more generic model that knew nothing about the indirect effect be able to explain variation in abundance well enough that it would be considered useful? Certainly, while this example is used to argue that knowledge of a fine-detailed mechanism is a pre-requisite for understanding population dynamics (Boggs & Inouye 2012), where fairly generic phenomenological models have been applied to other montane species of butterfly, these can, in some cases, explain variation in abundance quite well (Roland & Matter 2013).

The ability, or lack thereof, of phenomenological models to adequately resolve drivers of population growth thus remains unclear. Knape & de Valpine (2011) apply models with generic sets of weather variables to population time-series in the Global Population Dynamics Database, and find that the explanatory capacity is typically weak, suggesting that models of this form are strongly limited. Conversely, analyses of the population dynamics of European birds and butterflies generally report associations between inter-annual growth rates and variation in climatic conditions (Roy *et al.* 2001; Pearce-Higgins *et al.* 2015). Further, analyses that take a more macro-scale perspective, for example by modelling longer-term regional population trends of European birds find that these display broad congruence with climatic suitability models (Stephens *et al.* 2016). Similarly work that takes a more holistic approach, by focussing on the community as a whole, detect consistent shifts in composition through time that are consistent with the effects of climate change (Devictor *et al.* 2012). Finally, distribution models that link average site abundances of North American birds to temperature and precipitation averages can, for many species, predict temporal changes in abundance well, despite the fact they do not incorporate information on demography, indirect effects, or any other mechanistic detail (Illán *et al.* 2014).

Overall, while the distinction between phenomenological models and mechanistic models, and their ability to explain temporal dynamics, has been widely-discussed (Coulson *et al.* 2001; Knape & de Valpine 2011; Boggs & Inouye 2012), this remains an unresolved issue. As we travel from individual to population-level responses, we increasingly trade the ability to resolve fine-scale population processes for increasing data availability and generality. No specific one of these positions is obviously "best"- or at least, if there is, it is not yet clear which one it is. The physiologist has gained experimental control but lost generality. The demographer can resolve the birth and death processes that drive population growth directly, but in order to do so they have become tied to focal populations. The population dynamicist or species distribution modeller is able to make general statements about the effects of climate and weather across wide taxonomic and spatial extents, but has sacrificed predictive power and also has to grapple with difficult questions about causality and appropriate null models (Beale *et al.* 2008, 2014).

There is one final complication that merits brief discussion- when characterising the action of weather and climate on populations, it is not always clear what we need to be measuring (Grosbois *et al.* 2008). In particular, there is growing interest in the roles of climatic variation and ECEs in determining population growth, which I briefly discuss.

1.1.4 Climatic means, stochasticity, and Extreme Climatic Events

There is a growing awareness of the inadequacy of climatic means alone to capture the effects of climate on populations (Vasseur *et al.* 2014), but this awareness has largely developed in two separate literatures: one on variability and the role of environmental stochasticity (e.g. Boyce *et al.* 2006; Martin & Huey 2008; Lawson *et al.* 2015), and a literature on Extreme Climatic Events (ECEs; e.g. (Gutschick & BassiriRad 2003; Smith 2011a). While ECEs are often described in terms that seemingly set them apart from environmental stochasticity (e.g. Newton 1998; Leech & Crick 2007), with a distinction between 'normal' climatic variation and 'climatic events' (Jentsch *et al.* 2007; Smith 2011a), these can in fact be treated under a shared conceptual framework of environmental stochasticity (Boyce *et al.* 2006).

In order to understand drivers of long-term abundance (i.e. equilibrium abundance defined over some temporal period), it is only when population response to individual events is completely linear that this can be determined from climatic averages alone (Lawson *et al.* 2015). If there is any non-linearity in the climatic response function, average climatic conditions alone will not be sufficient to understand variation in abundance. To do so, the full distribution of events that a population is exposed to must be considered (Vasseur *et al.* 2014; Buckley *et al.* 2015).

Additionally, if a population can be sufficiently perturbed that it can be extirpated, then even in the event that the climatic response function is linear, it is still necessary to consider variation around the mean. A population can now either be present and thus responding to variation in conditions, or absent. In this scenario, it is possible that there is a location with no population present, despite the fact that in the vast majority of years conditions are perfectly suitable for presence (Denny *et al.* 2009). It is now necessary to know something about the probability of extirpation over a particular time-frame (Gaines & Denny 1993).

Importantly, the role of environmental stochasticity and extremes can also be considered at a different temporal scale, but in an equivalent fashion. If, for example, a particular species has a non-linear response to overwinter temperature, then there will be temperature-driven variation in response that is not identified by the mean temperature for winter alone (Ruel & Ayres 1999). Rather, the population response will hinge on the full set of exposure events, and additional information not captured in the mean is required to characterise these (e.g. maxima and minima, standard deviation, etc.). Though there is relatively little empirical work on effects of this form, there is some evidence that considering extreme percentiles of distributions of temperature and precipitation events can enhance our capacity to explain population growth in UK butterflies (McDermott Long *et al.* 2016).

Non-linearity in population response thus clearly motivates considering the full distribution of environmental events (Lawson *et al.* 2015). The upper and lower extremes of this distribution will frequently be important (as it is these that maximally peturb a population), but it is not the case that these events are conceptually distinct from environmental variation in general (Harris *et al.* 2018), and it may not be helpful to define them in such a way (though for an alternative take see Gutschick & BassiriRad 2003; Smith 2011b).

1.2 Thesis aims and objectives

In this thesis I use monitoring datasets from across Europe (described below) to investigate the role of weather in regulating populations of birds and butterflies. Specifically, I focus on the importance of weather for understanding temporal variation in abundance, and how we characterise these drivers of abundance in the context of large surveying datasets.

In Chapter II, I assess the sensitivity of 12 species of univoltine butterfly to variation in weather across their geographic range. Population dynamics are affected by a range of factors, which are likely to vary in their relative importance across a species' range (Beale *et al.* 2014). Climatic conditions are likely to be most important in regions where they represent a limiting factor, such as at range edges, but relatively less important away from these areas (Gaston, 2003). Where studies have investigated geographical variation in the importance of weather for determining population dynamics, patterns are variable, and suggest both positive, negative, and neutral associations with latitude Importantly however, these studies do not explicitly place observed variation in weather importance in the context of the species range, and it is therefore possible that these conflicting results arise as a consequence of this. Where gradients of sensitivity to weather have been explicitly studied in relation to a species range, studies report general increases in sensitivity towards latitudinal and altitudinal range edges (e.g. Ettinger, Ford, & HilleRisLambers, 2011; Myers-Smith et al., 2015). If it is the case that range-margin populations are relatively more sensitive to variation in climatic conditions, then it is likely that it is in these regions we will see the earliest, and the most substantial, changes in population dynamics due to climate change.

This chapter sets out to assess whether this there was evidence for systematic variation in the importance of weather for regulating butterfly populations across Europe. I chose to focus on univoltine species as these represent ideal cases with which to study this question, due to their very simple demography, marked by a single generation per annum. The finding that range-limits are more sensitive to variation in climatic conditions suggest that it is these ranges that are most sensitive to climate change.

Chapter III addresses the extent to which weather variables enhance our capacity to explain temporal variation in European bird abundance using large-scale survey datasets. There is increasingly interest in leveraging these datasets to make inferences about the role of weather in regulating populations (e.g. Jørgensen *et al.* 2015; Stephens *et al.* 2016; Bowler *et al.* 2018), and, indeed, this was the initial goal in working with these datasets. However, I found that even when including very large and complex sets of variables in models that allowed for considerable flexibility in the form of covariate associations across climatic and geographical gradients, models typically had low predictive capacity and weather terms made negligible contributions to this. These initial findings contrast significantly with previous work that often employs equivalent analytical approaches and conclude that weather is an important driver of population dynamics (e.g. Pearce-Higgins *et al.* 2014). There is a further conflict between studies such as these and those that suggest that there are general constraints on our capacity to understand weather drivers of population dynamics using in time-series that do not model demography directly (e.g. Coulson *et al.* 2003; Knape and de Valpine, 2009).

Developing a firmer understanding of the limitations of these models and datasets is crucial for informing future work that wishes to harness large-scale monitoring datasets to address drivers of population change and has further significant implications for our capacity to build predictive models of population dynamics more generally. In this chapter I therefore set out to systematically assess the extent to which weather drivers of population growth can be identified in these datasets, and how they contribute to our ability to understand and predict population growth.

In Chapter IV, I ask whether quantifying variation in thermal exposure improves predictions of population growth for 32 species of butterfly in the UK. There is growing interest in the respective roles of climatic means, variances, and extremes in determining population growth. While means capture the average conditions experienced at a particular location, they do not index the full set of climatic events that a population is exposed to (i.e. total climatic variation). Importantly however, it is the full climatic set of climatic events that a population experience, not simply what they are like on average, and it is therefore likely that this information should enhance our capacity to explain population dynamics.

While the theoretical expectation of how considering the full climatic regime that a population experiences should affect population dynamics is well developed (e.g. Kingsolver *et al.* 2013; Sunday *et al.* 2014; Lawson *et al.* 2015), there is currently limited empirical demonstration of these effects. Finding that considering the full thermal regime enhances our capacity to explain population dynamics would suggest that models of inter-annual population growth need to consider weather effects happening at fine temporal scales, and further suggest that future should consider how to better quantify the conditions that a population is directly exposed to. I therefore set out to address this question, focussing specifically on how quantifying variation in thermal exposure during these periods alters our ability to explain population growth, beyond models that simply consider the average temperature alone.

1.3 Datasets

I use two sets of monitoring data in the course of this thesis- Butterfly Monitoring datasets and Breeding Bird Survey datasets which I briefly outline below.

1.3.1 Butterfly Monitoring Datasets

The first Butterfly Monitoring Programme was initiated in the UK in 1974 (Pollard & Yates 1993), and since then a number of other European countries have adopted equivalent programmes. All follow a shared methodology in which, weather permitting, volunteers visit a site every week over between early spring and late summer, and count the number of individuals observed for each species. While an idealised abundance index for a particular {site, year, species} combination would be calculated as the sum of the weekly counts, this calculation is impractical due to the fact that counts may be missed due to poor weather or due to recorder unavailability. Dennis *et al.* (2013) therefore developed a method in which first a spatial unit is defined, and then an average flight-curve across this area is calculated using a General Additive Model (GAM) fitted to each sites' observations over the course of the season. The resulting abundance index is a site-specific measure of the area under the curve, with missing counts interpolated across by pooling information from nearby sites. While Dennis et al. (2013) applied this specifically in the context of UK monitoring (using the UK as the spatial unit), Schmucki *et al.* (2015) subsequently expanded on it using bioclimatic zone as the spatial unit, allowing for this methodology to be applied across Europe. In chapter II I use abundance indices calculated according to Schmucki et al. (2015), in order to model European butterflies for five countries/regions (UK, Catalonia, Germany, Netherlands, Finland) for the 1980-2014 period, while in chapter IV, I use abundance indices calculated for the UK alone for the 1974-2016 period.

1.3.2 Breeding Bird Survey Datasets

Many countries across Europe run Breeding Bird Monitoring Surveys (Gregory *et al.* 2005). These were largely motivated by a need to have systematic monitoring programmes to monitor change to our natural populations over the course of the 20th and 21st centuries, but there is increasingly interest in harnessing these to understand the drivers of population change (e.g. Jørgensen *et al.* 2015; Stephens *et al.* 2016; Bowler *et al.* 2018). Though there is some variation in the specific methodology employed by each scheme, they all follow a broadly consistent model in which skilled volunteers visit a site between one and four times over the course of the breeding season with an abundance index estimated by taking the maximum count for each species. In two cases- Spain and the Czech Republic- the mean rather than the maximum is taken. The Netherlands further differs by following a territory-counting method, in which sites are visited up to ten times and number of territories counted. The temporal period covered by each scheme is variable, but all broadly cover the 1990-2014 period, with a median length of 25 years. Datasets for individual schemes were accessed through a centralised monitoring programme, the Pan-European Common Bird Monitoring Scheme (PECBMS; http://www.ebcc.info/pecbm.html). I accessed datasets for eleven European countries: Spain, France, Belgium, UK, Netherlands, Germany, Czech Republic, Denmark, Sweden, Finland, and Estonia.

1.4 References

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Chapter 2:

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

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2.1 Abstract

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

Location Europe

Time period 1980-2014

Major taxa studied Butterflies

Methods We use long-term (35 years) butterfly monitoring data from over 900 sites, ranging from Finland to Spain, grouping sites into 2° latitudinal bands. For 12 univoltine butterfly species with sufficient data from at least 4 bands we construct population growth rate models that include density dependence, temperature, and precipitation during distinct life-cycle periods, which are defined taking regional variation in phenology into account. We use partial R^2 values as indicators of butterfly population dynamics' sensitivity to weather and density dependence, and assess how these vary with latitudinal position within a species' distribution.

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

Main conclusions Range-edge populations appear more sensitive to changes in weather than those nearer the centre of species' distributions but density dependence does not exhibit this pattern. Precipitation is as important as temperature in driving

butterfly population dynamics. Intra-specific variation in the form and strength of sensitivity to weather suggests that there may be important geographical variation in populations' responses to climate change.

2.2 Introduction

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

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

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

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

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

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

Our central hypothesis is that sensitivity to weather increases towards species' geographical latitudinal range edges, and we further ask whether there is evidence of asymmetry in sensitivity across this range.

2.3 Methods

2.3.1 Butterfly and climate datasets

We use annual site-level indices of abundance gathered from the butterfly monitoring schemes of five European Countries: Finland, Germany, UK, the Netherlands, and Spain. Length of coverage for each scheme varies: Finland (1999), Germany (2005), UK (1976), the Netherlands (1990), and Spain (1994). Annual site-level abundance indices are calculated from counts made at weekly intervals over the course of the season using a standardised Pollard-walk methodology. Due to the pronounced patterns of abundance seen in butterfly numbers over the course of a season, abundance indices are derived from these weekly counts by fitting a General Additive Model (GAM) and generating a measure of the area under the curve (Dennis *et al.* 2013). Where counts are missing, the GAM provides an interpolated estimate based on counts made at other sites in the same bioclimatic zone (Metzger *et al.* 2013; Schmucki *et al.* 2015). This method has been demonstrated to generate unbiased abundance estimates, and outperform a simple linear interpolation method, which would be the alternative to our chosen approach (Schmucki *et al.* 2015). To prevent spurious estimates, sites with more than 50% observations missing were removed prior to analysis (Schmucki *et al.* 2015). To model inter-annual changes in abundance, an index of population growth was calculated from the relative change in abundance between two consecutive years, $\ln(N_t+1) - \ln(N_{t-1}+1)$, which is hereafter referred to as relative growth rate. Sites with fewer than five years non-zero data were removed prior to further analysis.

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

The influence of climatic variables on population growth rates can vary between different life-stages (Radchuk *et al.* 2013), the timing of which can vary across the species' range (Schmucki *et al.* 2015). To accommodate this regional and temporal variation, we used information about the flight-period of each species, defined at the level of the bioclimatic zone (Metzger *et al.* 2013), to tailor climatic indices to specific periods of the butterfly's life-cycle. For each species in each latitudinal band (see below), we first obtained an average flight-curve from relative abundances over the course of the season, following the methodology of Schmucki et al. (2015). We then extracted daily temperature and precipitation variables for each 25km grid-cell, using four time periods that reflect different life-stages occurring in an annual cycle: the post flight, over-wintering, pre-flight and flight periods (Fig. 1), and standardised these to unit standard deviation. Flight-period temperature and precipitation were then defined as the mean of the daily temperature and precipitation indices falling between the 10th and 90th percentiles of this flight-period distribution. We used the same process to define the pre-flight and post-flight periods as the three months before and after the flight period. The over-winter period was defined as November-January for all species in all zones (Fig 1.). While over-winter periods could be defined over alternative time-periods, for example December-February, this results in substantial overlap between overwinter and adjacent time periods for some species in some regions. This particular definition was therefore chosen on the basis that it minimises such overlaps and these are marginal where they do occur. Analyses are restricted to univoltine species, for which our methods of defining life-cycle periods are most appropriate.

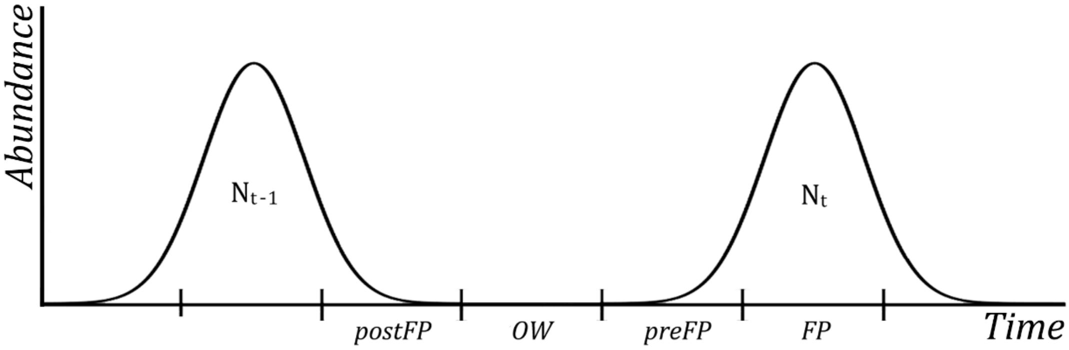

Figure 1 Schematic of life-cycle periods and their correspondence to two annual abundance indices, N_t and N_{t-1}. Life-cycle periods are post flight-period (postFP), over-wintering period (OW), pre-flight period (preFP) and flight period (FP).

2.3.2 Process model of population growth rates

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

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

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

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

Where x_{it} and x_{it-1} are the log abundances at site i and times t and time $t\text{-}1$ respectively, and y_{it} is thus the relative population growth rate at site i in year t. To confirm that the weather terms included in these models had significance for the population dynamics of the species modelled, we used F-tests to compare each model with a reduced model containing no weather terms. Collinearity of weather variables in each model was assessed using pairwise Pearson correlation coefficients. Just 2.4% (43 of 1792) of pairwise comparisons had absolute correlation coefficients exceeding 0.7 and therefore the vast majority of individual parameter estimates were considered robust to collinearity.

2.3.3 Butterfly species inclusion

12 univoltine species were sufficiently well represented across at least four latitudinal bands to be included in analyses (at least 150 data points in a latitudinal band; Fig. 2 and Fig. S1) with a total of 52 species/latitudinal band combinations. The 12 species were Orange Tip, *Anthocharis cardamines,* Ringlet, *Aphantopus hyperantus,* Dark-green Fritillary, *Argynnis aglaja,* Silver-washed Fritillary, *Argynnis paphia*, Pearl-bordered Fritillary, *Boloria euphrosyne,* Green Hairstreak, *Callophrys rubi,* Purple Hairstreak, *Favonius quercus,* Brimstone, *Gonepteryx rhamni*, Meadow Brown, *Maniola jurtina*, Gatekeeper, *Pyronia tithonus*, Essex Skipper, *Thymelicus lineola*, and Small Skipper, *Thymelicus sylvestris*. One species, Brimstone, overwinters as an adult, and we are consequently unable to distinguish between overwintering individuals and those which emerged that year. To check that this did not alter our conclusions, we therefore also ran the analyses excluding this species. These did not qualitatively affect our results and we therefore just report the full analysis with this species included. While the distributions of our focal species vary, they all have a pan-European distribution, with some extending slightly into north Africa (which was taken into account when defining range edges, see below).

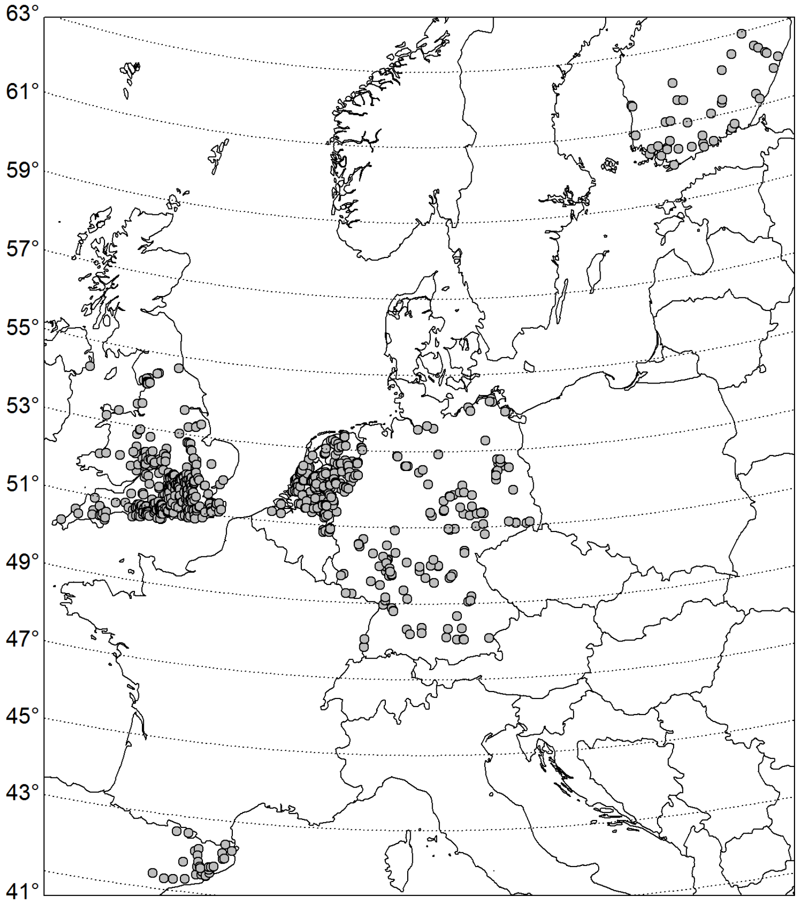

Figure 2 Sites retained following exclusion based on criteria outlined in text, with 2° latitudinal bands overlaid (dashed lines).

2.3.4 Assessing variation in sensitivity to weather

Measuring range position

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

$$\text{relative range position, RRP}=\frac{\mathrm{lat}_{\mathrm{average}}-\mathrm{lat}_{\mathrm{min}}}{\mathrm{lat}_{\mathrm{max}}-\mathrm{lat}_{\mathrm{min}}} \qquad [3]$$

Where lat_{max} and lat_{min} are the latitudes of the species' northern and southern range extents defined from the European butterfly atlas (Kudrna *et al.* 2011), and Tennent (1996) for species whose distributions extended into north Africa (i.e. the relative range position metric does not impose an artificial boundary at the southern European range edge). Thus our measure of relative range position scales between 0 (southern range edge) to 1 (northern range edge).

Due to the predominantly European global distribution of all species modelled here, absolute latitude and the derived relative range position are highly correlated (Pearson correlation coefficient of 0.80). Consequently, it is not possible to distinguish between the effects of absolute latitude and relative latitude. We continue to report results in terms of relative latitude, but this opens up the possibility that patterns of sensitivity may be driven by alternative factors associated with absolute latitude, rather than distance from range edge per se. We discuss alternative explanations in the Discussion section.

Assessing sensitivity to weather in relation to relative range position

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

Latitudinal variation in partial R^2 measures was analysed using mixed-effects models, with a random Gaussian intercept on species, using the *lme4* package in R (Bates *et al.* 2015). Three models of increasing complexity were fitted (equations 4, 5, and 6). Model improvement through adding latitudinal predictors was tested with an F-test with the Kenward-Rogers correction for estimating degrees of freedom in a mixed-modelling framework (Bolker *et al.* 2009) using the *pbkrtest* package in R (Halekoh & Højsgaard 2014). We calculated mixed-effect R^2s for these models based on the framework outlined in Nakagawa and Schielzeth (2013).

$$\text{sensitivity} = s_j + \varepsilon \quad [4]$$

$$\text{sensitivity} = s_j + RRP + \varepsilon \quad [5]$$

$$\text{sensitivity} = s_j + RRP + RRP^2 + \varepsilon \quad [6]$$

Where s_j is a random species-intercept, RRP is the relative range position for each model, and ε is a normally-distributed error term. To check whether phylogenetic relationships between the modelled species could influence our conclusions, we constructed a second model that incorporated the phylogeny of Brooks *et al.* (2016) into the random effects structure using the MCMCglmm package (Hadfield 2010). We found that the phylogenetic variance terms approached zero and the model fit was almost identical (Appendix S1 and Fig. S2). We therefore report models that do not incorporate phylogeny in the main manuscript.

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

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

We further set out to assess whether there was any evidence of asymmetry in the latitudinal relationship by assessing whether the rate of change in climatic sensitivity with latitude varied between the northern and southern halves of the range. To do this, we defined the relative range position in terms of distance from the range centre (i.e. difference between the relative range position and the range centre, 0.5) and allowed the slope to vary depending on whether the relative position was in the northern or southern half of the range:

$$\text{sensitivity} = s_j + \text{distance} + I(\text{RRP}<0.5) + \text{distance} \times I(\text{RRP}<0.5) + \varepsilon \qquad [7]$$

Where s_j is a random species-intercept, *distance* is the distance from the range centre (scaling between 0 at the range centre and 0.5 at a range edge) and I is an indicator function for range position (i.e. 1 in the southern half of the range and 0 in the northern half). If there is no asymmetry in latitudinal pattern, both halves of the range should display similar slopes, with no interaction term between slope and range portion. Degrees of freedom were estimated using the Satterthwaite approximation (Bates *et al.* 2015).

2.4 Results

Population dynamics were frequently associated with weather, with F-tests demonstrating that the inclusion of weather terms significantly improved 75% of models (39 out of 52, Table S1), and for each species this was the case in at least two regions (Fig. 3). Individual parameter estimates for weather terms vary in magnitude and direction, with 31% being significant across the 52 models ($P \leq 0.05$; Table S2). The precise form of the relationships between butterfly population growth rate and weather is highly variable across life-stages, both within and across species, but significant parameter estimates are fairly evenly distributed across life-stages and weather variables (Table S2). Models typically explained around 40% of variation in population dynamics (mean $R^2 = 0.39$; Table S3), with variable contributions from weather terms in these (partial R^2s range from 1% to 22%, with a mean value of 5%). Negative density dependence was ubiquitous, with all models containing significant negative parameter estimates for log-density ($P < 0.05$; Table S2). Partial R^2 values for density dependence terms were uniformly larger than those for weather terms, with a mean partial R^2 of 29% (range: 1-52%; Table S3). While the inclusion of weather terms significantly improved model performance, the ability of the final models to predict relative growth rate remained highly variable, and a large amount of residual variation remained unexplained (mean residual root mean squared error = 0.69; Table S3).

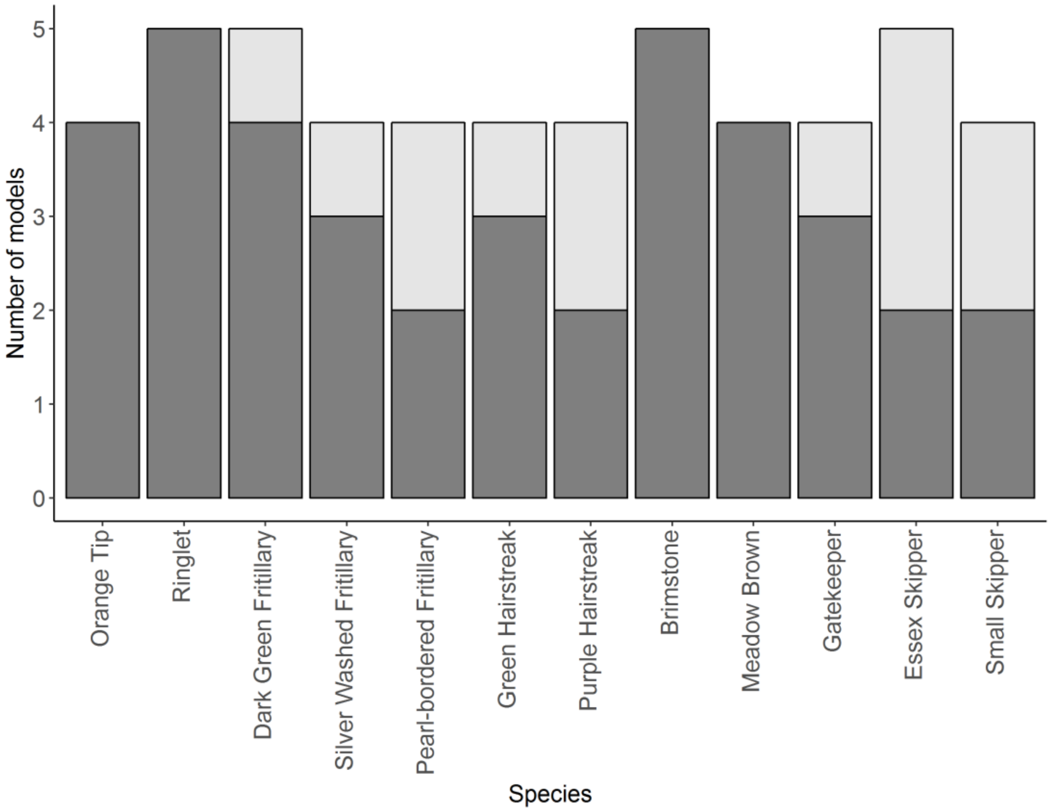

Figure 3 Number of models by species, where each model for each species is for a different latitudinal band. Darker shading indicates that inclusion of climate terms resulted in significant model improvement (F-test; $P \leq 0.05$).

There was support for latitudinal variation in sensitivity to weather, with the partial R^2 values for weather terms in butterfly population dynamic models displaying curvature across the gradient of relative range position, with lowest sensitivity to weather in populations closer to the centre of the species' European distribution (Fig.

4). The explanatory capacity of weather variables, as measured by partial R^2, display a distinct latitudinal pattern, with the model containing quadratic terms performing better than both intercept-only (F test for difference between these two models: $F_{2, 44.4} = 8.46$, $P < 0.001$) and linear-slope models ($F_{1, 42.62} = 16.08$, $P < 0.001$). For the quadratic model, the curve inflection point (minima) is at a relative range position of 0.52 (i.e. close to the centre of species' latitudinal range). Latitudinal terms explained a reasonable proportion of the variation in partial R^2 values, with a marginal R^2 of 24%. Conversely, there were no statistically significant patterns of latitudinal variation in density dependence when measured by partial R^2 values (linear model: $F_{1, 46.13} = 0.28$, $P = 0.602$; quadratic model: $F_{2, 42.94} = 0.19$, $P = 0.830$; Fig. 5).

Measures of climatic sensitivity were tested for asymmetry in the change in sensitivity across the latitudinal gradient using a break-point at the range-centre (RPP = 0.5). These indicate an average increase of 0.20 units partial R^2 per 0.1 increase in distance from the range centre ($t = 3.87$, $df = 46.9$, $P > 0.001$), but no significant difference in slope between the upper and lower range halves ($t = 0.57$, $df = 44.0$, $P = 0.570$; Fig. 6).

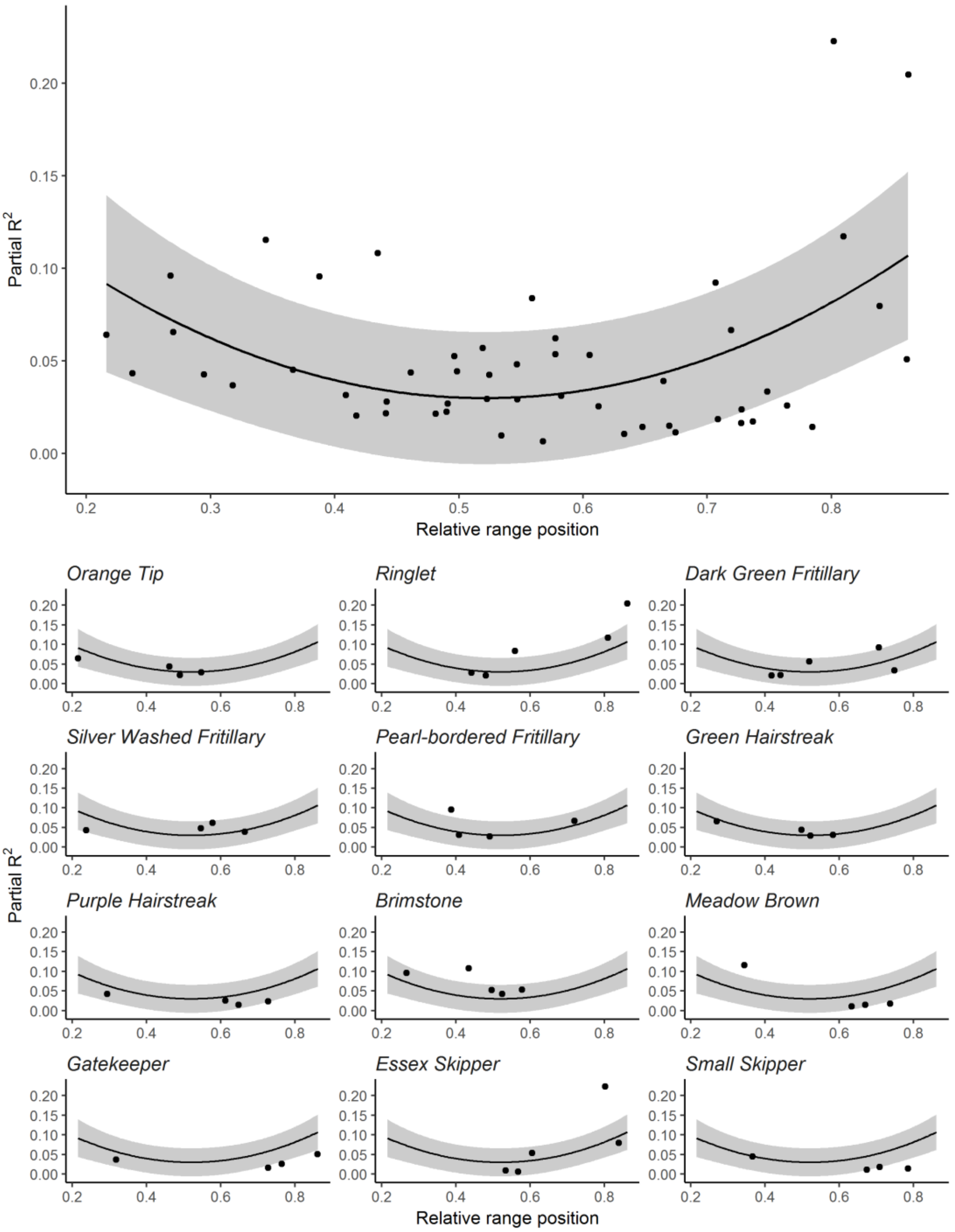

Figure 4 Partial R^2s for the weather terms in each model by their relative position within the geographic range (i.e. each point is a species/latitudinal band combination). The upper panel displays partial R^2s for all species; the lower panel displays same results, split by species. Fitted curve displays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

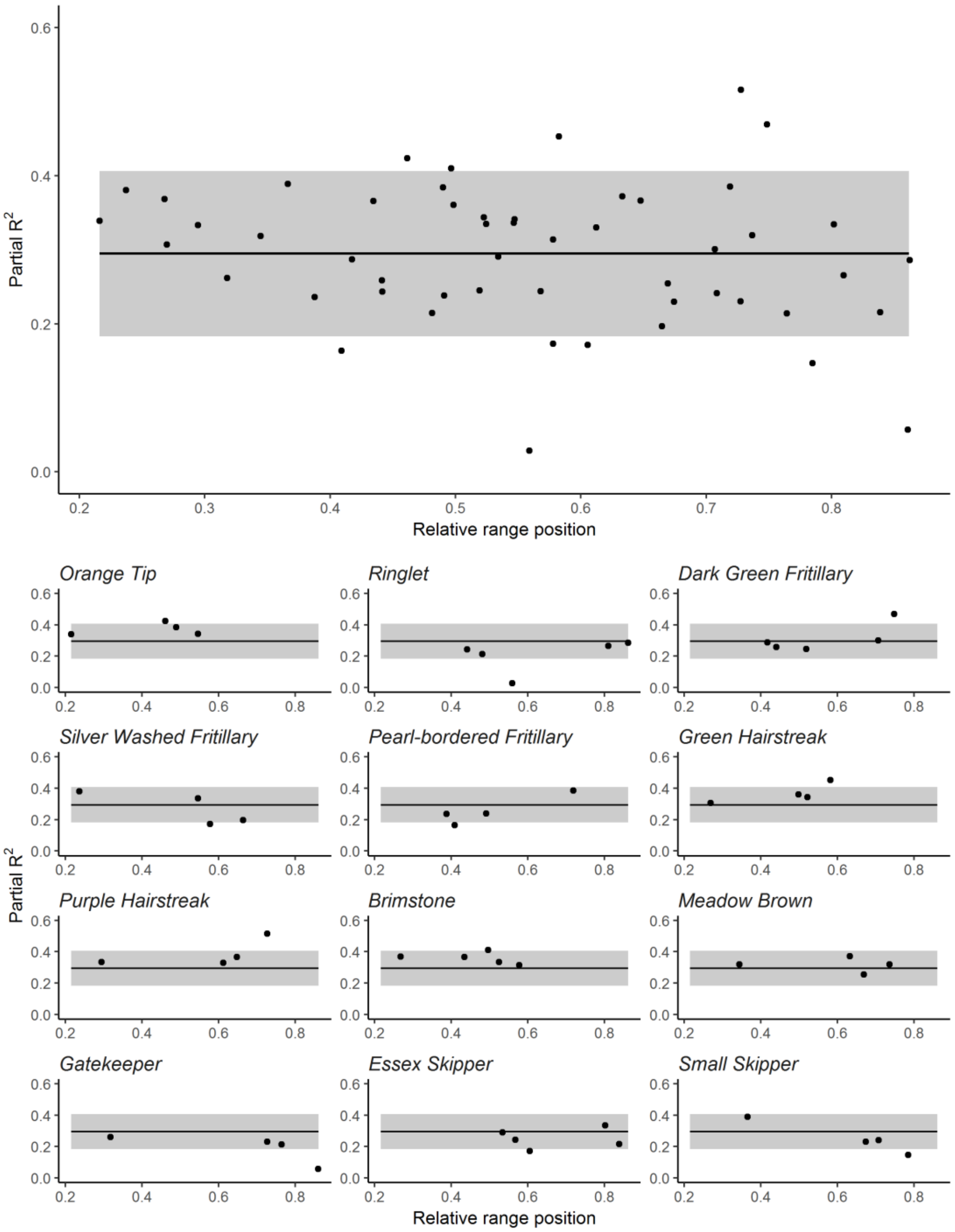

Figure 5 Partial R²s for the density-dependence terms in each model by their relative position within the geographic range (i.e. each point is a species/latitudinal band combination). The upper panel displays partial R²s for all species; the lower panel displays the same results, split by species. The fitted line displays the intercept only model (best supported of the three alternative models), with the 95% confidence band overlaid.

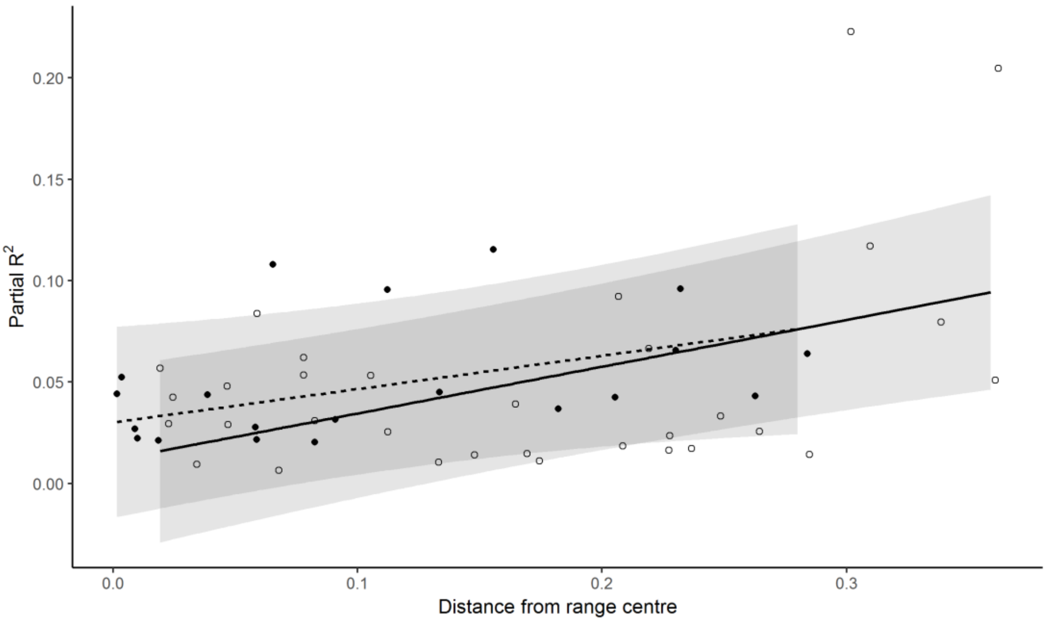

Figure 6 Model fits for asymmetry analysis. Plotted is each model's partial R^2 (upper panel) for the suite of weather terms against the distance from range centre. Closed circles indicate points that lie in the southern range half (i.e. RRP < 0.5) while open circles indicate points that lie in the northern range half (i.e. RRP > 0.5). The modelled latitudinal relationship (outlined in methods) is illustrated with a dashed line for the southern range half, and a solid line for the northern part of the range (grey shading indicates the 95% confidence bands).

2.5 Discussion

Modelling population dynamics of regional populations of 12 univoltine butterfly species suggests that populations towards species' range edges are relatively more sensitive to weather than those in the range centre. This pattern contrasts with the uniform strength of density dependence across species' latitudinal distributions. There was limited evidence of asymmetry in sensitivity, with the amount of variation in population dynamics driven by weather variables being similar at northern and southern range boundaries. The size of the datasets used here necessitated the pooling of observations both within latitudinal bands as well as across species (in the mixed-effects framework). While the overall pattern is one of increased sensitivity towards range margins, this result is tempered by the typically weaker within species pattern as well as the limited number of observations for any single species. Future work to investigate range-wide patterns of sensitivity to various environmental drivers at a finer spatial grain for individual species would thus be of considerable interest.

Our analyses focus on populations' relative position within a species range, because ecological theory predicts that range edge populations will be more sensitive to weather conditions due to inhospitable conditions at the edge of species' fundamental niche space (Oliver *et al.* 2012). Our results appear to be robust to a range of potential alternative explanations including the effects of phylogeny, latitudinal extent of species' distributions and variation in inter-annual variation in weather conditions across the range. Given that we focus on widely distributed species whose ranges are centred on a single region there is, however, an inevitable strong correlation between a population's relative range position and absolute latitude. Consequently, it is difficult to tease apart the effects of relative and absolute range position, with most of our range edge populations being located in Spain and Finland. It is thus possible that butterfly populations in these two countries display heightened sensitivity to weather for reasons that are unrelated to range position. This seems unlikely, however, given that there are no systematic differences in site selection across schemes, nor did we find any influence of topographic heterogeneity on butterfly populations' sensitivity to weather. In principle, higher habitat quality or connectivity could also partly buffer butterfly populations from adverse conditions thus reducing their apparent sensitivity to weather (e.g. Oliver et al., 2012); however, our focal countries in central Europe typically have greater agricultural intensification and habitat fragmentation and lower quality habitats than in Spain and Finland (EEA 2016), which would act in opposition to the observed pattern.

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

Importantly, if species displayed a strong degree of adaptation to local climate, we would not observe range-wide patterns in weather sensitivity, as species would be uniformly sensitive to local climatic conditions (Bennett *et al.* 2015; Myers-Smith *et al.* 2015). Adaptation could arise as a result of intra-specific variation in tolerance (Fischer & Karl 2010), or through behavioural plasticity, for example, behavioural thermoregulation (Buckley *et al.* 2015). Our finding that increased sensitivity is observed towards the range edges thus suggests general limitations to these mechanisms of climatic adaptation and supports the hypothesis that latitudinal range limits are at least partially explained by climate. This complements previous results that document elevational range contraction for several European butterfly species in Spain (Wilson *et al.* 2005) and recent northern range edge expansions as a result of climate change (Mair *et al.* 2012).

An alternative mechanism that could drive the observed increased sensitivity towards range edges is a reverse density dependence effect. If factors such as density-dependence are relatively more important in the species' range core than at the edges (i.e. show a reverse pattern to climatic sensitivity), these could mask climatic influences towards the range centre (Sæther *et al.* 2008). This could potentially arise as a result of lower population densities towards the range edge, or through variation in the importance of intra- or inter-specific competition across the range (e.g. Leisnham *et al.*, 2009). However, the lack of relationship in our results between latitudinal position within a species' range and density dependence effects suggests that the observed latitudinal gradient in climatic sensitivity exists independently of variation in the strength of density dependence.

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

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

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

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

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2.7 Supplementary material

Appendix S1

Phylogenetic effects

The MCMCglmm package (Hadfield, 2010) was used to construct a model containing both species and phylogenetic random effects within the model, using a phylogeny obtained from Brooks et al. (2016). As with the main set of analyses, sensitivity was allowed to vary as a quadratic function of relative range position, RRP, with a species-specific random intercept term, s_j. Using the MCMCglmm package we could additionally incorporate phylogenetic information as p_j. to render the model,

$$\text{sensitivity} = s_j + p_j + RRP + RRP^2 + \varepsilon$$

Where both s_j and p_j are assumed to be normally distributed random effects, with the variance term estimated from the data. As the model requires priors for each parameter, we used the default non-informative prior for the fixed effects and for the variance terms in the random effects used a weakly informative inverse Gamma, with shape and scale parameters set to 0.01. Models were run for 500000 iterations, with a burn-in of 1000 and a thin of 500.

The variance terms for the phylogenetic random effect was negligible, with a mean of 0.004, and a 95% confidence interval of 0.001 to 0.009. The difference in shape of the latitudinal relationship was correspondingly minor (Fig. S2), deviating only slightly from the pattern seen in the main set of models in which phylogeny was not incorporated.

Additional robustness checks

To assess the influence of other potential drivers of sensitivity, we fitted three models of increasing complexity but with the addition of terms for latitudinal range size, weather variability and topographic heterogeneity (A1, A2, A3). Methodology follows that in the main text.

$$\text{sensitivity} = s_j + \text{latRange} + SD_w + SD_{topo} + \varepsilon \qquad [A1]$$

$$\text{sensitivity} = s_j + RRP + \text{latRange} + SD_w + SD_{topo} + \varepsilon \qquad [A2]$$

$$\text{sensitivity} = s_j + RRP + RRP^2 + \text{latRange} + SD_w + SD_{topo} + \varepsilon \qquad [A3]$$

The effect of adding latitudinal terms mirrored that of the models without the additional predictors, with the model containing quadratic terms (A3) performing better than both intercept-only (A1; F test for difference between these two models: $F_{2, 44.1} = 7.99$, $P = 0.001$) and linear-slope models ($F_{1, 44.4} = 11.57$, $P = 0.001$).

The associated coefficient estimates for these three controlling variables (in the full model, A3) were: (1) *latRange*, t=1.79 (df=9.9, P=0.105), (2) SD_w, t=0.34 (df=45.9, P=0.736), and (3) SD_{topo}, (df=36.9, P=0.643).

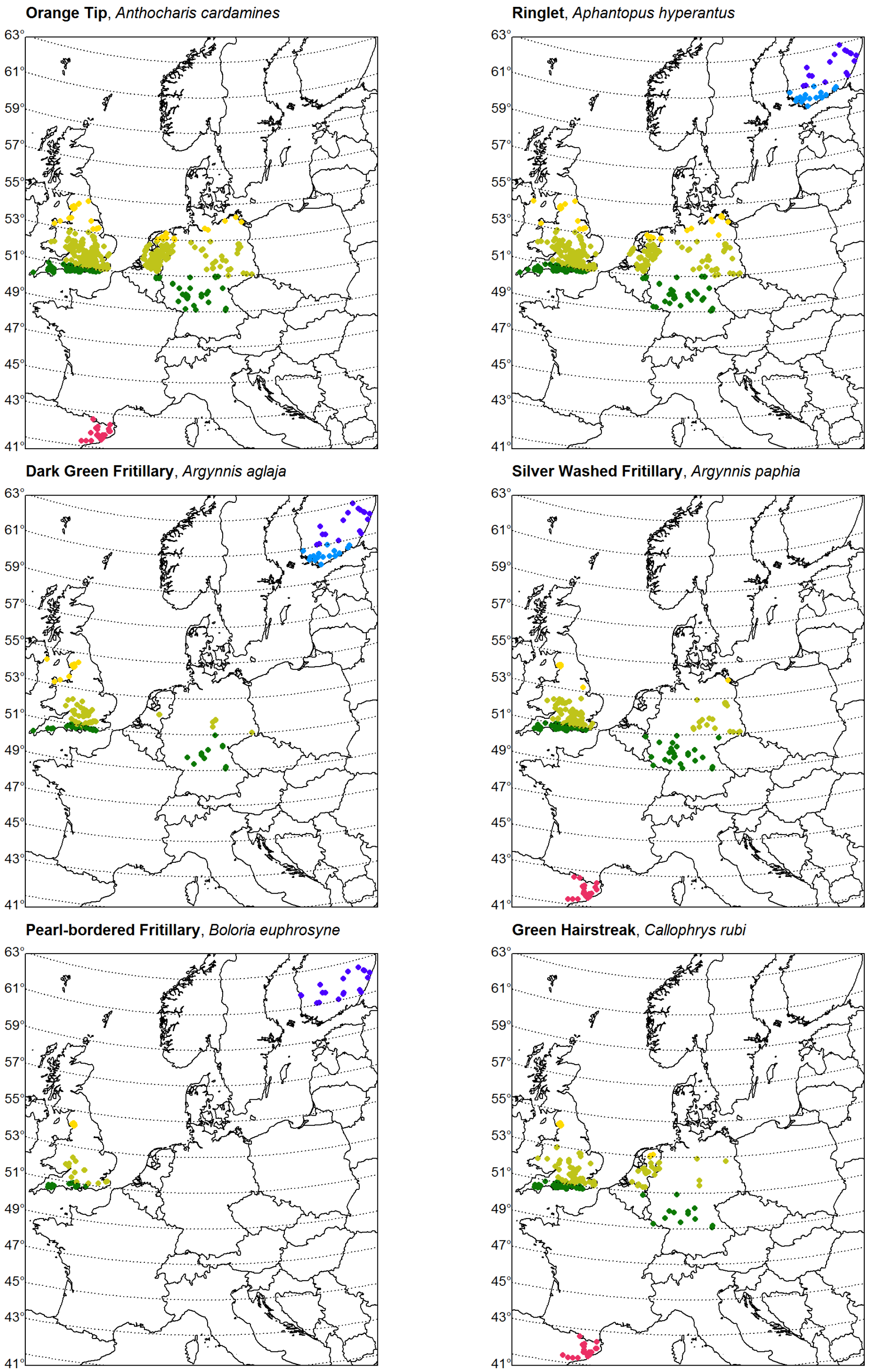
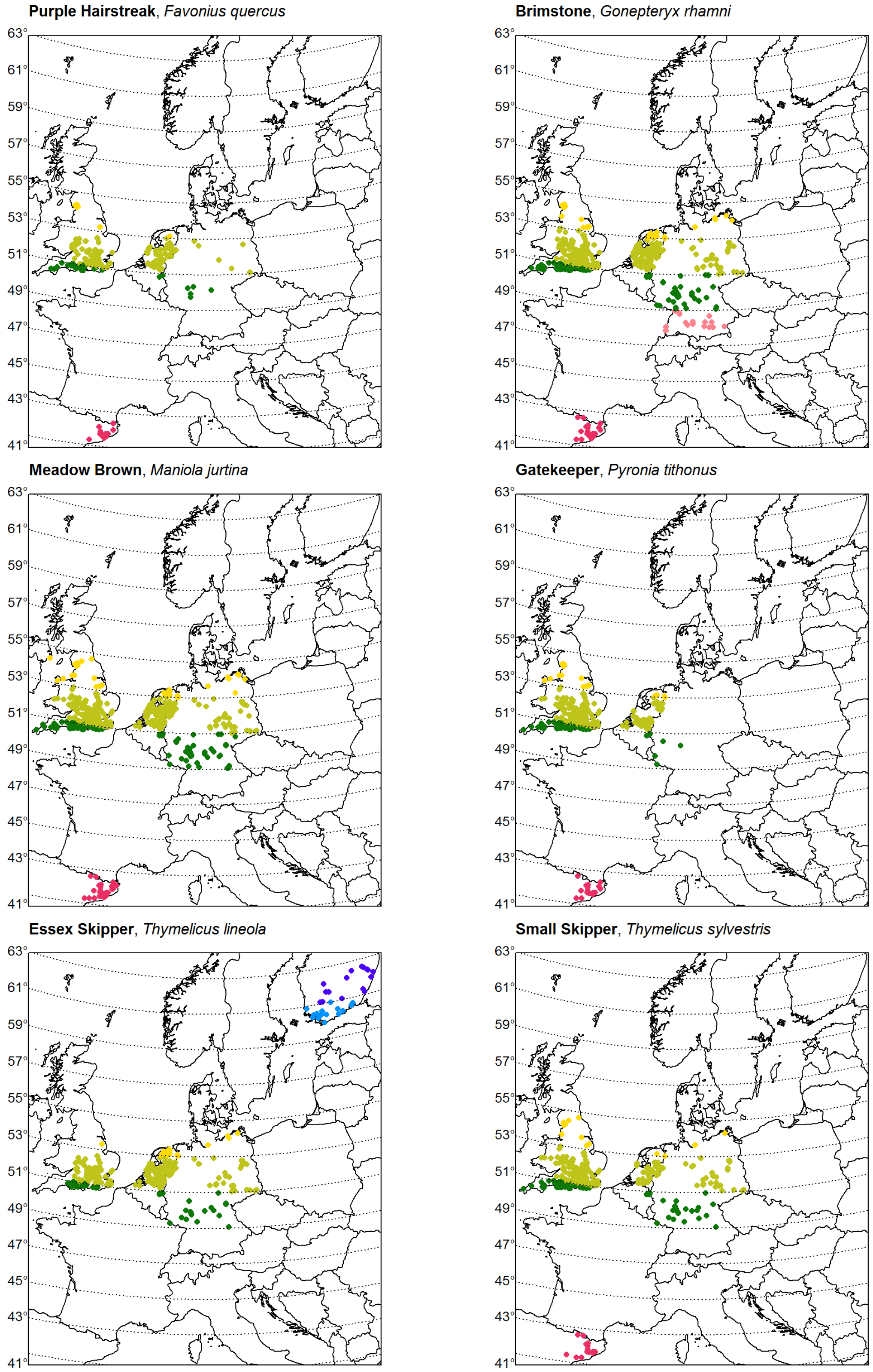


Figure S1 Spatial distribution of sites retained following exclusion based on criteria outlined in text, with 2° latitudinal bands overlaid (dashed lines). Colours distinguish between each latitudinal band.



Purple Hairstreak, *Favonius quercus*

Brimstone, *Gonepteryx rhamni*

Meadow Brown, *Maniola jurtina*

Gatekeeper, *Pyronia tithonus*

Essex Skipper, *Thymelicus lineola*

Small Skipper, *Thymelicus sylvestris*

Figure S1 continued Spatial distribution of sites retained following exclusion based on criteria outlined in text, with 2° latitudinal bands overlaid (dashed lines). Colours distinguish between each latitudinal band.

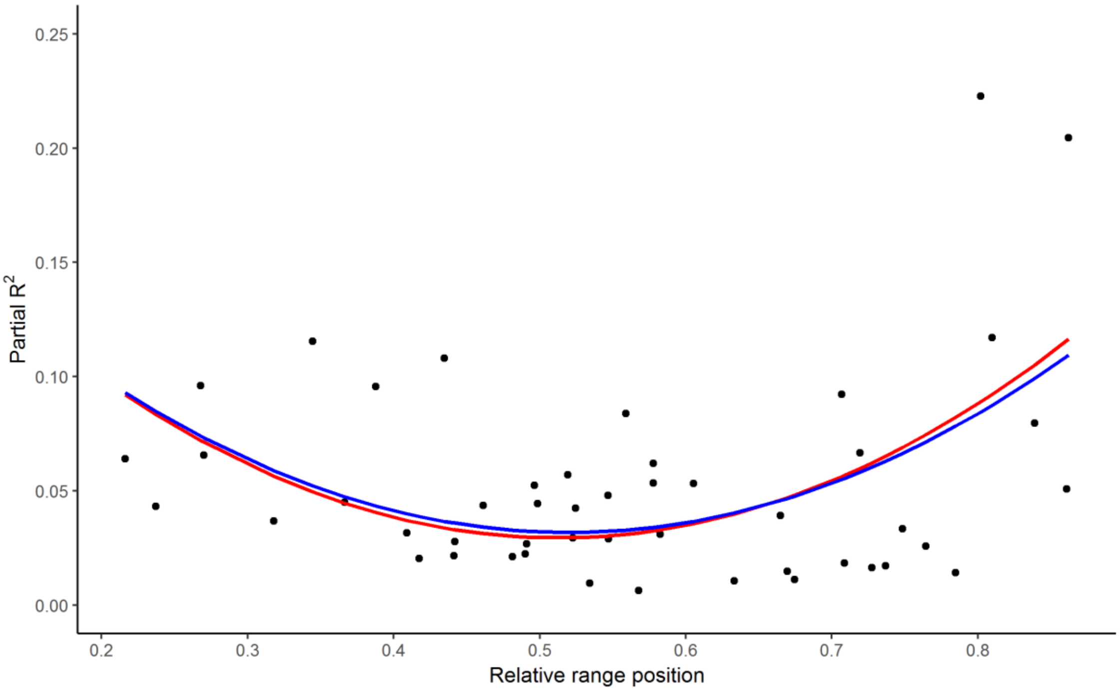


Figure S2 Partial R^2s for the weather terms in each model by their relative position within the geographic range (i.e. each point is a species/latitudinal band combination), with two models overlaid. The model that incorporates phylogenetic information (described in Appendix S1) is displayed by the red line, while the model without (as described in the main text) is in blue.

Table S1 Model comparison results. Full models containing all climate terms compared with reduced models containing just density dependence and site effects.

Species	Lat. band	F value	P value
Orange Tip	41° - 43°	3.1	0.002
Orange Tip	49° - 51°	13.09	<.001
Orange Tip	51° - 53°	19	<.001
Orange Tip	53° - 55°	3	0.003
Ringlet	49° - 51°	5.76	<.001
Ringlet	51° - 53°	14.69	<.001
Ringlet	53° - 55°	4.11	<.001
Ringlet	59° - 61°	3.84	<.001
Ringlet	61° - 63°	7.39	<.001
Dark Green Fritillary	49° - 51°	1.98	0.047
Dark Green Fritillary	51° - 53°	3.58	<.001
Dark Green Fritillary	53° - 55°	3.57	<.001
Dark Green Fritillary	59° - 61°	3.01	0.004
Dark Green Fritillary	61° - 63°	1.23	0.285
Silver Washed Fritillary	41° - 43°	2.27	0.024
Silver Washed Fritillary	49° - 51°	9.68	<.001
Silver Washed Fritillary	51° - 53°	16.42	<.001
Silver Washed Fritillary	53° - 55°	0.79	0.615
Pearl-bordered Fritillary	49° - 51°	3.09	0.003
Pearl-bordered Fritillary	51° - 53°	1.26	0.263
Pearl-bordered Fritillary	53° - 55°	1.02	0.422
Pearl-bordered Fritillary	61° - 63°	2.14	0.036
Green Hairstreak	41° - 43°	2.97	0.004
Green Hairstreak	49° - 51°	7.36	<.001
Green Hairstreak	51° - 53°	8.64	<.001
Green Hairstreak	53° - 55°	1.46	0.177
Purple Hairstreak	41° - 43°	1.34	0.226
Purple Hairstreak	49° - 51°	2.22	0.025
Purple Hairstreak	51° - 53°	7.19	<.001
Purple Hairstreak	53° - 55°	0.84	0.570
Brimstone	41° - 43°	5.2	<.001
Brimstone	47° - 49°	3.94	<.001
Brimstone	49° - 51°	18.5	<.001
Brimstone	51° - 53°	43.84	<.001
Brimstone	53° - 55°	5.34	<.001
Meadow Brown	41° - 43°	8.55	<.001

Meadow Brown	49° - 51°	3.48	<.001
Meadow Brown	51° - 53°	15.38	<.001
Meadow Brown	53° - 55°	2.07	0.037
Gatekeeper	41° - 43°	1.2	0.303
Gatekeeper	49° - 51°	3.49	<.001
Gatekeeper	51° - 53°	16.57	<.001
Gatekeeper	53° - 55°	2.05	0.041
Essex Skipper	49° - 51°	1.15	0.325
Essex Skipper	51° - 53°	3.98	<.001
Essex Skipper	53° - 55°	1.26	0.268
Essex Skipper	59° - 61°	8.72	<.001
Essex Skipper	61° - 63°	1.92	0.062
Small Skipper	41° - 43°	1.21	0.299
Small Skipper	49° - 51°	2.34	0.017
Small Skipper	51° - 53°	9.51	<.001
Small Skipper	53° - 55°	0.55	0.819

Table S2 Parameter estimates for the relationship between relative population growth rate and weather variables for all latitudinal bands. Estimates that differ significantly from 0 at the P ≤ .05 level are in bold-font, and at the P ≤ .01 level are underlined and in bold-font. All climate variables are standardised to have unit standard deviation and standard errors of each estimate are provided in parentheses. See Figure 1 for abbreviations for the time periods over which temperature and precipitation variables were measured; log-density refers to density dependent effects, log(N_{t-1}).

			Temperature				**Precipitation**			
# significant parameter estimates		52	19	15	16	13	15	20	16	14
Species	**Latitudinal band**	**Log-density**	**postFP**	**OW**	**preFP**	**FP**	**postFP**	**OW**	**preFP**	**FP**
Orange Tip	41° - 43°	**-0.77 (±0.07)**	0.18 (±0.13)	-0.16 (±0.17)	**0.54 (±0.17)**	-0.08 (±0.1)	0.05 (±0.07)	-0.04 (±0.06)	-0.01 (±0.07)	0.04 (±0.06)
Orange Tip	49° - 51°	**-0.89 (±0.03)**	0.04 (±0.03)	**-0.22 (±0.04)**	**0.18 (±0.03)**	**-0.14 (±0.03)**	-0.04 (±0.03)	0.01 (±0.03)	-0.03 (±0.02)	0.05 (±0.03)
Orange Tip	51° - 53°	**-0.8 (±0.02)**	0.03 (±0.02)	0 (±0.02)	**0.05 (±0.01)**	**-0.09 (±0.01)**	**-0.07 (±0.02)**	0.01 (±0.01)	**-0.03 (±0.01)**	-0.02 (±0.01)
Orange Tip	53° - 55°	**-0.79 (±0.05)**	0.11 (±0.06)	**-0.12 (±0.04)**	-0.03 (±0.04)	-0.03 (±0.04)	0.07 (±0.05)	-0.12 (±0.07)	-0.04 (±0.06)	-0.03 (±0.04)
Ringlet	49° - 51°	**-0.51 (±0.03)**	**-0.07 (±0.03)**	**0.22 (±0.05)**	0 (±0.03)	0.07 (±0.03)	-0.03 (±0.03)	0.03 (±0.03)	**0.09 (±0.03)**	**0.06 (±0.03)**
Ringlet	51° - 53°	**-0.44 (±0.01)**	**-0.05 (±0.01)**	**0.09 (±0.02)**	0.01 (±0.01)	**0.04 (±0.01)**	0.02 (±0.01)	**0.03 (±0.01)**	**0.04 (±0.01)**	**0.03 (±0.01)**
Ringlet	53° - 55°	**-0.13 (±0.04)**	**-0.17 (±0.06)**	0.03 (±0.06)	**0.17 (±0.06)**	-0.11 (±0.07)	-0.08 (±0.07)	0.11 (±0.1)	**0.2 (±0.06)**	-0.04 (±0.05)
Ringlet	59° - 61°	**-0.78 (±0.09)**	-0.08 (±0.07)	0 (±0.07)	0.12 (±0.06)	**-0.19 (±0.06)**	**0.17 (±0.06)**	**0.16 (±0.07)**	-0.01 (±0.05)	**-0.22 (±0.06)**
Ringlet	61° - 63°	**-0.69 (±0.08)**	0.01 (±0.05)	**0.16 (±0.05)**	**-0.19 (±0.06)**	**-0.11 (±0.04)**	**0.14 (±0.04)**	**0.12 (±0.04)**	-0.06 (±0.05)	-0.05 (±0.04)
Dark Green Frit.	49° - 51°	**-0.61 (±0.04)**	-0.03 (±0.05)	0.02 (±0.09)	0.06 (±0.04)	0.08 (±0.05)	0.02 (±0.04)	**0.15 (±0.05)**	-0.01 (±0.04)	0.06 (±0.04)
Dark Green Frit.	51° - 53°	**-0.55 (±0.03)**	-0.06 (±0.03)	0.02 (±0.04)	**0.06 (±0.03)**	0 (±0.03)	0.03 (±0.03)	**0.09 (±0.03)**	0.04 (±0.03)	0 (±0.03)
Dark Green Frit.	53° - 55°	**-0.41 (±0.04)**	**0.19 (±0.05)**	0.05 (±0.05)	-0.01 (±0.05)	**0.15 (±0.05)**	0 (±0.04)	**0.14 (±0.06)**	0.07 (±0.05)	**0.12 (±0.05)**
Dark Green Frit.	59° - 61°	**-0.74 (±0.08)**	-0.01 (±0.08)	0.1 (±0.09)	**-0.3 (±0.09)**	-0.14 (±0.08)	**-0.18 (±0.07)**	-0.02 (±0.07)	-0.09 (±0.07)	0.05 (±0.07)
Dark Green Frit.	61° - 63°	**-0.97 (±0.08)**	-0.01 (±0.07)	-0.04 (±0.08)	-0.11 (±0.09)	0.01 (±0.06)	-0.03 (±0.07)	**0.17 (±0.06)**	-0.04 (±0.07)	0.05 (±0.07)
S-w. Fritillary	41° - 43°	**-0.83 (±0.07)**	0.2 (±0.14)	0.32 (±0.2)	-0.3 (±0.17)	-0.18 (±0.16)	-0.09 (±0.07)	-0.07 (±0.08)	-0.07 (±0.07)	-0.1 (±0.07)
S-w. Fritillary	49° - 51°	**-0.71 (±0.03)**	**-0.06 (±0.03)**	**0.21 (±0.05)**	**-0.09 (±0.03)**	-0.07 (±0.03)	**-0.06 (±0.02)**	**0.09 (±0.03)**	-0.03 (±0.03)	**-0.1 (±0.03)**
S-w. Fritillary	51° - 53°	**-0.39 (±0.02)**	**-0.06 (±0.02)**	**0.1 (±0.03)**	0.02 (±0.02)	-0.02 (±0.02)	**-0.05 (±0.02)**	**0.11 (±0.02)**	**-0.07 (±0.02)**	**-0.12 (±0.02)**

S-w. Fritillary	53° - 55°	**-0.45 (±0.08)**	-0.06 (±0.11)	-0.02 (±0.1)	-0.12 (±0.1)	-0.12 (±0.14)	0.15 (±0.14)	0.11 (±0.17)	0.01 (±0.12)	-0.16 (±0.11)
P.-b. Fritillary	49° - 51°	**-0.48 (±0.06)**	**0.23 (±0.08)**	-0.08 (±0.08)	0.01 (±0.08)	-0.06 (±0.07)	**0.17 (±0.08)**	0.06 (±0.06)	0 (±0.06)	**-0.2 (±0.06)**
P.-b. Fritillary	51° - 53°	**-0.35 (±0.05)**	**0.19 (±0.07)**	-0.08 (±0.07)	0 (±0.07)	-0.03 (±0.07)	0.06 (±0.07)	-0.06 (±0.06)	0.1 (±0.06)	-0.04 (±0.05)
P.-b. Fritillary	53° - 55°	**-0.52 (±0.06)**	0.13 (±0.09)	-0.05 (±0.08)	0.03 (±0.08)	-0.03 (±0.08)	0.04 (±0.09)	0 (±0.07)	-0.08 (±0.08)	-0.04 (±0.06)
P.-b. Fritillary	61° - 63°	**-0.83 (±0.08)**	**0.25 (±0.1)**	-0.12 (±0.09)	0.02 (±0.1)	0.12 (±0.09)	0.01 (±0.08)	0.02 (±0.08)	-0.13 (±0.08)	0.07 (±0.09)
Green Hairstreak	41° - 43°	**-0.69 (±0.07)**	-0.21 (±0.12)	-0.12 (±0.17)	0.2 (±0.16)	-0.14 (±0.09)	**0.16 (±0.08)**	**0.15 (±0.07)**	**-0.21 (±0.07)**	**-0.32 (±0.08)**
Green Hairstreak	49° - 51°	**-0.76 (±0.03)**	-0.03 (±0.04)	-0.03 (±0.06)	0.04 (±0.04)	**-0.15 (±0.03)**	**-0.11 (±0.04)**	**0.09 (±0.03)**	0.01 (±0.03)	0 (±0.03)
Green Hairstreak	51° - 53°	**-0.7 (±0.02)**	0.04 (±0.03)	0.02 (±0.03)	0.04 (±0.03)	**-0.11 (±0.02)**	**-0.09 (±0.03)**	0.01 (±0.02)	0.03 (±0.02)	0.02 (±0.02)
Green Hairstreak	53° - 55°	**-0.89 (±0.07)**	0.16 (±0.1)	-0.15 (±0.08)	0.12 (±0.09)	-0.08 (±0.08)	0.09 (±0.09)	0.1 (±0.1)	-0.18 (±0.1)	-0.09 (±0.07)
Purple Hairstreak	41° - 43°	**-0.75 (±0.08)**	0.21 (±0.15)	-0.27 (±0.26)	0.26 (±0.24)	0.27 (±0.22)	0.04 (±0.12)	0.02 (±0.14)	0.06 (±0.13)	0.16 (±0.13)
Purple Hairstreak	49° - 51°	**-0.69 (±0.05)**	-0.05 (±0.04)	0.08 (±0.07)	-0.02 (±0.04)	-0.08 (±0.06)	**-0.11 (±0.04)**	0.08 (±0.05)	**-0.11 (±0.05)**	-0.04 (±0.04)
Purple Hairstreak	51° - 53°	**-0.76 (±0.02)**	-0.03 (±0.02)	0.04 (±0.02)	0 (±0.02)	-0.01 (±0.02)	0 (±0.02)	-0.03 (±0.02)	**-0.11 (±0.02)**	0.03 (±0.02)
Purple Hairstreak	53° - 55°	**-1.05 (±0.09)**	0.08 (±0.07)	-0.04 (±0.06)	-0.02 (±0.07)	0.01 (±0.09)	-0.1 (±0.07)	-0.1 (±0.08)	0.05 (±0.07)	0.05 (±0.07)
Brimstone	41° - 43°	**-0.79 (±0.06)**	**-0.72 (±0.17)**	0.24 (±0.18)	0.29 (±0.18)	**-0.24 (±0.12)**	0.05 (±0.06)	0.02 (±0.07)	0.09 (±0.06)	0.04 (±0.06)
Brimstone	47° - 49°	**-1.01 (±0.1)**	**-0.41 (±0.1)**	**0.31 (±0.12)**	**-0.3 (±0.1)**	-0.09 (±0.12)	-0.11 (±0.1)	0.02 (±0.12)	0.15 (±0.09)	-0.21 (±0.11)
Brimstone	49° - 51°	**-0.9 (±0.03)**	**-0.09 (±0.02)**	-0.05 (±0.03)	**-0.05 (±0.02)**	-0.03 (±0.03)	-0.02 (±0.02)	**0.11 (±0.02)**	**-0.1 (±0.02)**	**-0.12 (±0.02)**
Brimstone	51° - 53°	**-0.72 (±0.01)**	**-0.12 (±0.01)**	**0.03 (±0.01)**	**-0.05 (±0.01)**	**0.03 (±0.01)**	0.02 (±0.01)	**0.08 (±0.01)**	**-0.09 (±0.01)**	**-0.04 (±0.01)**
Brimstone	53° - 55°	**-0.63 (±0.04)**	-0.01 (±0.03)	-0.05 (±0.04)	0.03 (±0.05)	**-0.16 (±0.06)**	**-0.16 (±0.06)**	**0.18 (±0.06)**	-0.1 (±0.06)	-0.08 (±0.04)
Meadow Brown	41° - 43°	**-0.75 (±0.05)**	0.09 (±0.09)	**0.79 (±0.12)**	**-0.29 (±0.1)**	0.07 (±0.13)	0 (±0.05)	**-0.13 (±0.05)**	**0.15 (±0.05)**	0.09 (±0.05)
Meadow Brown	49° - 51°	**-0.76 (±0.02)**	0.03 (±0.02)	**0.08 (±0.03)**	**-0.04 (±0.02)**	-0.01 (±0.02)	0.01 (±0.02)	0 (±0.02)	**0.07 (±0.02)**	0.01 (±0.02)
Meadow Brown	51° - 53°	**-0.54 (±0.01)**	**-0.05 (±0.01)**	**0.03 (±0.01)**	**0.02 (±0.01)**	0 (±0.01)	0.02 (±0.01)	**0.04 (±0.01)**	**0.06 (±0.01)**	0 (±0.01)
Meadow Brown	53° - 55°	**-0.72 (±0.04)**	-0.01 (±0.04)	0.03 (±0.03)	-0.03 (±0.03)	-0.03 (±0.05)	0.02 (±0.05)	-0.06 (±0.05)	**0.12 (±0.04)**	-0.04 (±0.04)
Gatekeeper	41° - 43°	**-0.49 (±0.06)**	-0.02 (±0.16)	0.34 (±0.21)	-0.28 (±0.22)	-0.11 (±0.19)	-0.01 (±0.08)	-0.07 (±0.09)	0.06 (±0.08)	0.11 (±0.09)
Gatekeeper	49° - 51°	**-0.49 (±0.02)**	**0.06 (±0.02)**	-0.02 (±0.03)	-0.03 (±0.02)	0.02 (±0.02)	0.01 (±0.02)	**0.04 (±0.02)**	0.01 (±0.02)	**-0.06 (±0.02)**
Gatekeeper	51° - 53°	**-0.44 (±0.01)**	**0.07 (±0.01)**	**0.06 (±0.01)**	**0.03 (±0.01)**	**0.03 (±0.01)**	0.02 (±0.01)	**0.04 (±0.01)**	0 (±0.01)	**-0.04 (±0.01)**
Gatekeeper	53° - 55°	**-0.18 (±0.04)**	-0.05 (±0.06)	0.09 (±0.06)	0.1 (±0.06)	0.09 (±0.08)	-0.16 (±0.09)	0.08 (±0.1)	0.1 (±0.07)	**0.19 (±0.07)**

Essex Skipper	49° - 51°	**-0.63 (±0.04)**	-0.05 (±0.05)	0.06 (±0.07)	-0.04 (±0.04)	-0.01 (±0.05)	-0.04 (±0.04)	-0.02 (±0.04)	0.07 (±0.04)	-0.01 (±0.04)
Essex Skipper	51° - 53°	**-0.51 (±0.01)**	-0.02 (±0.02)	**-0.06 (±0.02)**	-0.01 (±0.02)	-0.04 (±0.02)	**0.07 (±0.02)**	0 (±0.02)	0.03 (±0.02)	**-0.04 (±0.02)**
Essex Skipper	53° - 55°	**-0.46 (±0.08)**	-0.02 (±0.1)	0.05 (±0.09)	0.12 (±0.08)	-0.03 (±0.11)	-0.05 (±0.1)	0.08 (±0.11)	**0.21 (±0.09)**	-0.11 (±0.09)
Essex Skipper	59° - 61°	**-0.75 (±0.07)**	**-0.24 (±0.05)**	**-0.12 (±0.06)**	0.05 (±0.06)	**-0.12 (±0.05)**	**-0.23 (±0.05)**	-0.08 (±0.05)	**-0.16 (±0.05)**	-0.02 (±0.06)
Essex Skipper	61° - 63°	**-0.51 (±0.08)**	0.02 (±0.08)	0 (±0.08)	0.08 (±0.07)	-0.06 (±0.07)	-0.1 (±0.08)	**-0.18 (±0.08)**	-0.08 (±0.08)	0.04 (±0.07)
Small Skipper	41° - 43°	**-0.82 (±0.09)**	0.42 (±0.31)	-0.07 (±0.31)	-0.07 (±0.25)	0.18 (±0.17)	-0.13 (±0.1)	0.08 (±0.13)	-0.01 (±0.12)	0.03 (±0.1)
Small Skipper	49° - 51°	**-0.48 (±0.02)**	**-0.1 (±0.04)**	0.07 (±0.06)	0.04 (±0.03)	-0.02 (±0.05)	-0.03 (±0.04)	0.06 (±0.04)	-0.03 (±0.04)	-0.05 (±0.04)
Small Skipper	51° - 53°	**-0.5 (±0.02)**	**-0.17 (±0.03)**	-0.03 (±0.03)	**0.09 (±0.02)**	0 (±0.03)	**-0.06 (±0.02)**	**0.05 (±0.02)**	-0.01 (±0.02)	-0.03 (±0.02)
Small Skipper	53° - 55°	**-0.39 (±0.06)**	-0.07 (±0.1)	0 (±0.09)	0.06 (±0.09)	0.12 (±0.11)	-0.06 (±0.1)	0.04 (±0.15)	0.07 (±0.1)	0.05 (±0.09)

Table S3 R^2, partial R^2s and root mean square error (RMSE) by species and latitudinal band.

Species	**Lat. band**	**R^2**	**RMSE**	**Dens. partial R^2**	**Clim. partial R^2**
Orange Tip	41° - 43°	0.47	0.65	0.34	0.06
Orange Tip	49° - 51°	0.49	0.64	0.42	0.04
Orange Tip	51° - 53°	0.44	0.64	0.38	0.02
Orange Tip	53° - 55°	0.45	0.64	0.34	0.03
Ringlet	49° - 51°	0.3	0.74	0.24	0.03
Ringlet	51° - 53°	0.28	0.66	0.21	0.02
Ringlet	53° - 55°	0.18	0.73	0.03	0.08
Ringlet	59° - 61°	0.53	0.45	0.27	0.12
Ringlet	61° - 63°	0.55	0.38	0.29	0.2
Dark Green Frit.	49° - 51°	0.33	0.81	0.29	0.02
Dark Green Frit.	51° - 53°	0.31	0.74	0.26	0.02
Dark Green Frit.	53° - 55°	0.31	0.69	0.24	0.06
Dark Green Frit.	59° - 61°	0.51	0.6	0.3	0.09
Dark Green Frit.	61° - 63°	0.56	0.54	0.47	0.03
S-w. Fritillary	41° - 43°	0.48	0.69	0.38	0.04
S-w. Fritillary	49° - 51°	0.42	0.63	0.34	0.05
S-w. Fritillary	51° - 53°	0.26	0.69	0.17	0.06
S-w. Fritillary	53° - 55°	0.28	0.8	0.2	0.04
P.-b. Fritillary	49° - 51°	0.37	0.58	0.24	0.1
P.-b. Fritillary	51° - 53°	0.23	0.77	0.16	0.03
P.-b. Fritillary	53° - 55°	0.31	0.8	0.24	0.03
P.-b. Fritillary	61° - 63°	0.48	0.75	0.39	0.07
Green Hairstreak	41° - 43°	0.44	0.76	0.31	0.07
Green Hairstreak	49° - 51°	0.43	0.69	0.36	0.04
Green Hairstreak	51° - 53°	0.4	0.73	0.34	0.03
Green Hairstreak	53° - 55°	0.55	0.73	0.45	0.03
Purple Hairstreak	41° - 43°	0.44	0.97	0.33	0.04
Purple Hairstreak	49° - 51°	0.39	0.74	0.33	0.03
Purple Hairstreak	51° - 53°	0.41	0.74	0.37	0.01
Purple Hairstreak	53° - 55°	0.58	0.53	0.52	0.02
Brimstone	41° - 43°	0.49	0.64	0.37	0.1
Brimstone	47° - 49°	0.63	0.62	0.37	0.11
Brimstone	49° - 51°	0.51	0.52	0.41	0.05
Brimstone	51° - 53°	0.41	0.61	0.34	0.04
Brimstone	53° - 55°	0.41	0.61	0.31	0.05
Meadow Brown	41° - 43°	0.56	0.53	0.32	0.12
Meadow Brown	49° - 51°	0.42	0.52	0.37	0.01

Meadow Brown	51° - 53°	0.32	0.61	0.25	0.01
Meadow Brown	53° - 55°	0.39	0.58	0.32	0.02
Gatekeeper	41° - 43°	0.33	0.73	0.26	0.04
Gatekeeper	49° - 51°	0.3	0.58	0.23	0.02
Gatekeeper	51° - 53°	0.29	0.61	0.21	0.03
Gatekeeper	53° - 55°	0.17	0.74	0.06	0.05
Essex Skipper	49° - 51°	0.33	0.78	0.29	0.01
Essex Skipper	51° - 53°	0.29	0.93	0.24	0.01
Essex Skipper	53° - 55°	0.3	0.77	0.17	0.05
Essex Skipper	59° - 61°	0.62	0.46	0.33	0.22
Essex Skipper	61° - 63°	0.38	0.63	0.22	0.08
Small Skipper	41° - 43°	0.46	0.66	0.39	0.05
Small Skipper	49° - 51°	0.27	1.02	0.23	0.01
Small Skipper	51° - 53°	0.28	1.03	0.24	0.02
Small Skipper	53° - 55°	0.18	1.03	0.15	0.01

2.8 Addendum (response to examiner's comment)

Note: not peer reviewed or in published version of article

There was interest in whether or not northern or southern range margins exhibited more positive or negative effects of temperature and precipitation. I have plotted the coefficient estimates for northern (>59° latitude) and southern (<43° latitude) range-margins (numerical estimates given in Table S2) below. There is no clear tendency for estimates to be systematically above or below 0, and in all cases 95% confidence intervals for coefficient estimates substantially overlap 0.

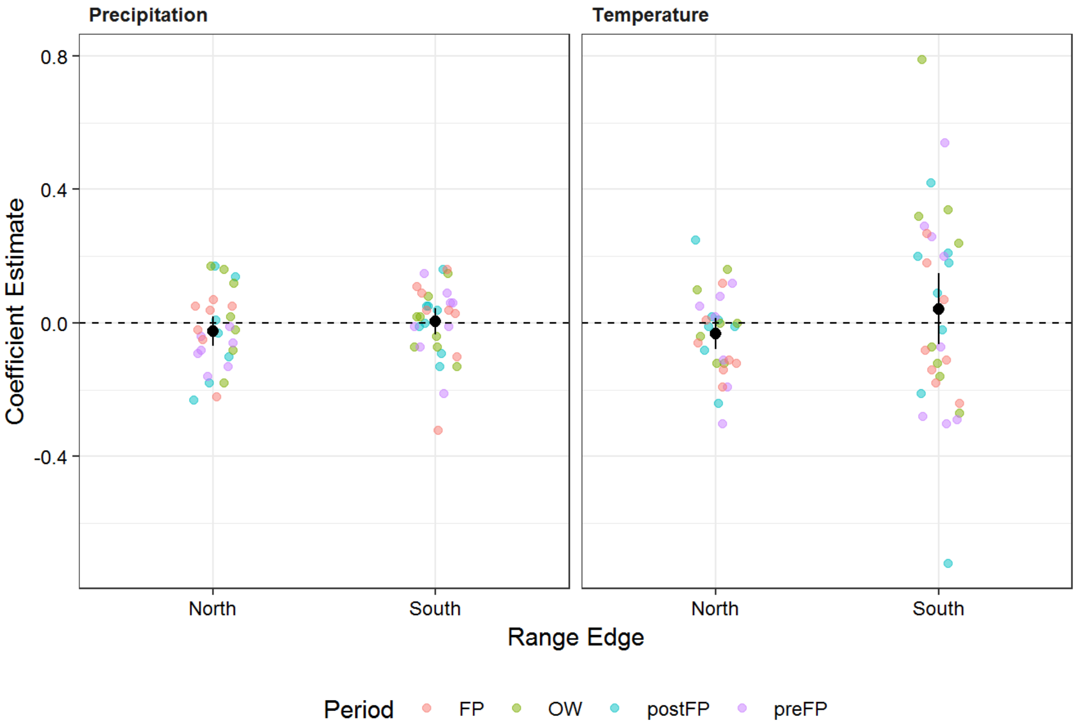


Figure A1 Coefficient estimates for weather associations at range margins, by variable type (precipitation or temperature) and life-cycle period (preFP, FP, postFP, and OW). Means and 95% confidence intervals are overlaid (black points and bars)

Chapter 3:

Weather variables make minor contributions to explanatory capacity of population dynamic models of European bird populations in an era of climate change

3.1 Abstract

Aim Though weather is widely regarded as playing an important role in determining population dynamics, the extent to which generally formulated phenomenological models can capture population response to variation in climatic conditions remains unclear. We assess the ability of weather to explain variation in inter-annual population growth rates at continental scales.

Location Europe

Time Period 1990-2014

Major Taxa Studied Birds

Methods We model temporal variation in site-level abundance using long-term monitoring datasets from 11 countries across Europe (c. 8500 sites). We quantify i) the statistical signal of weather in site-level inter-annual population growth rates, ii) the extent to which these weather effects improve models' explanatory capacities and reduce residual uncertainty, and iii) assess if these explanatory capacities vary systematically in space and with species' ecological and life history traits.

Results For the majority of species, we observe a statistical signal of weather in inter-annual growth rates, with more small P-values than would arise by chance. However, the explanatory capacity of these variables is typically limited, and models retain substantial residual uncertainty. Consequently, models containing no weather terms at all often have similar capacities to explain population growth as models containing large and flexible sets of weather variables. The contribution of weather terms is not significantly associated with species' ecological or life history traits.

Main Conclusions Our results raise important questions about the ability to understand drivers of population growth through application of general phenomenological models to large-scale survey datasets. In particular, they suggest a greater need to focus on the contributions of census error to observed population growth as well as to better appraise how model data requirements and model performance trade off against each other. If we are to adequately capture how

populations respond to inter-annual variation in climatic conditions then approaches that acknowledge and account for these issues are required.

3.2 Introduction

Understanding the relative importance of environmental variation in driving population dynamics is a central question in population ecology (Turchin 1999). While complex population dynamics can arise in the absence of any external forcing (Turchin 2003), weather and climate are thought to play an important role in a range of population processes, from driving variation in vital rates (Dybala *et al.* 2013) and inter-annual population growth (Mills *et al.* 2017) through to determining long-term trends and population persistence (Beale *et al.* 2014; Stephens *et al.* 2016). Given the apparent importance of weather and climate across a range of scales, there is substantial concern about how populations will respond to climate change and much interest in quantifying these responses (Bellard *et al.* 2012). Statistical models that elucidate precisely how weather drives population dynamics are central to this task and can be used to forecast ecological responses to climate change, and to assess and inform strategies for conservation and climate change adaptation (Oliver & Roy 2015).

Approaches to understanding population responses to weather can be broadly categorised according to the level of detail included in the model structure and their corresponding data requirements. These range from detailed population growth models that model demographic responses directly (e.g. Dybala et al. 2013) or invoke precise mechanisms through which weather affects population growth (e.g. Boggs and Inouye 2012), through to more general phenomenological models that model variation in temporal abundance in the absence of demographic detail and often apply similar model forms containing general suites of weather variables across wide taxonomic and geographic extents (e.g. Knape & de Valpine 2011; Pearce-Higgins *et al.* 2015).

Demographic models of population growth have shown both that weather can play an important role in driving demography and temporal variation in abundance, and also that the linkages between weather and population dynamics can be complex, requiring substantial population detail in order to explain how weather drives population growth (Coulson *et al.* 2001; Robinson *et al.* 2007; Dybala *et al.* 2013; Cleasby *et al.* 2017). For example, when effects of weather vary with population structure, such as when response varies with age or gender, variation in the demographic composition of a population drives heterogeneity in how the population as a whole responds to a given weather event (Dybala *et al.* 2013; Cleasby *et al.* 2017). Population models that do not incorporate demographic detail cannot resolve these separate processes and, consequently, can be limited in their ability to explain temporal variation in abundance (Coulson *et al.* 2001).

While intensive population-specific studies can resolve weather impacts well, these approaches come with the cost of high data requirements that tend to limit their applicability to individual populations (though see Coulson *et al.* 2005; Nicolè *et al.* 2011). As a consequence, it is often difficult to make general inferences that extend beyond the focal population from these studies alone. There is therefore considerable interest in less data-intensive modelling approaches that are not tailored to specific populations or landscapes (e.g. Boggs & Inouye 2012), but that can be applied more generally, in order to understand population responses across wider geographic and taxonomic extents. For example, long-term population monitoring schemes that use standardised methodologies may provide essential data to fit more generally-formulated phenomenological models to predict population responses to climate change across large (e.g. continental) scales. Though these modelling approaches will necessarily incur some cost to their explanatory capacity (Knape & de Valpine 2011), the question is whether, despite this, they can still be used to shed light on how populations respond to variation in environmental conditions.

There is increasingly interest in harnessing datasets from long-term population monitoring schemes to make inferences about the role of weather in regulating populations (e.g. Pearce-Higgins *et al.* 2014; Jørgensen *et al.* 2015; Stephens *et al.* 2016; Bowler *et al.* 2018), and addressing how well we are able to do so with standard approaches is thus timely. In particular, there is a need to resolve the apparent conflict between studies that conclude that weather plays an important role in regulating the populations recorded in long-term monitoring schemes (e.g. Pearce-Higgins *et al.* 2014) and those that suggest that there are general constraints on our capacity to understand weather drivers of population dynamics using in time-series that do not model demography directly (e.g. Coulson *et al.* 2003; Knape and de Valpine, 2009).

To this end, we carry out the first continental-scale assessment of the capacity of monthly and seasonal weather variables to explain site-level inter-annual variation in population growth rate. We do so using long-term data on population growth rates of 153 bird species at c. 8,500 sites spread across 11 European countries that span a latitudinal and longitudinal gradient from Spain to Finland. Data are derived from long-term Breeding Bird Surveys (BBS) that have been widely used to model population responses to a range of environmental drivers (Jiguet *et al.* 2006; Both *et al.* 2010; Jørgensen *et al.* 2015; Pearce-Higgins *et al.* 2015; Stephens *et al.* 2016) and are typical of the types of datasets employed to understand population responses to environmental variation. Specifically, we quantify i) the statistical signal of weather in site-level inter-annual population growth rates, ii) the extent to which these weather effects improve models' explanatory capacities and reduce residual uncertainty, and iii) assess if these explanatory capacities vary systematically in space and with species' ecological and life history traits.

3.3 Materials and methods

3.3.1 Datasets

We obtained BBS datasets for 11 countries in the Pan-European Common Bird Monitoring Scheme (PECBMS): Finland, Sweden, UK, Estonia, Denmark, Germany, Netherlands, Belgium, France, Czechia, and Spain. While there is some variation in the specific methodology followed by each country, each scheme follows a broadly consistent standardised model in which skilled volunteers visit a site between one and four times over the course of the breeding season and a single breeding season abundance estimate index is calculated by taking the maximum count for each species, or, in two cases (Spain and Czechia), taking the mean (http://www.ebcc.info/pecbm.html: Gregory et al. 2005). In the Netherlands, sites are visited up to ten times and territories counted. By their nature, these surveys cover the commoner and more abundant bird species in each country. Temporal coverage of each scheme varied but following data cleaning steps (see below), they typically cover the 1990-2014 period, with a median length of 25 years (Table S1). Site-species combinations with five or fewer population growth rate data points (i.e. a count at time *t* and time *t+1,* at least one of which is non-zero) were removed prior to analysis.

Climate data were obtained from the European Climate and Assessment Dataset (ECAD; Haylock et al. 2008). This is a 25 km-resolution gridded dataset (.22° rotated grid; version 12.0), comprised of daily estimates of temperature (average temperature; °C) and precipitation (total rainfall; mm) for grid-cells across Europe. Sites that were not covered by the climate surface were removed prior to further analysis.

3.3.2 Weather variables

Due to geographical variation in the number of data points at each site, there is a trade-off between the number of weather terms that can be included in the model (i.e. model complexity) and the number of sites and regions that can be included, especially for rarer species. While larger sets of variables allow for more robust conclusions regarding the influence of weather on population growth rate, the cost is that any conclusions risk loss of generality as an increasingly small set of regions and species are investigated. To manage this trade-off, we formulated two sets of models. The first contains 12 monthly average temperature and 12 monthly summed precipitation variables, counting from May in year *t* to April in year *t+1* (Figure S1), to cover the period between the counts that make up each inter-annual population growth rate datum (i.e. 24 weather variables; *full variable set models*). The second set used the maximum and minimum mean monthly temperature during the winter (December-February) and breeding (April-June) seasons, and the maximum and minimum summed precipitation during these seasons (i.e. eight weather variables; *reduced variable set models*).

Weather effects are further allowed to vary regionally (across 200 km x 200 km grid cells, see below) such that, for example, January temperature might be the main driver of population growth rate in one part of the range, while in another it might be July precipitation. Similarly, in the reduced variable set of models a species may respond to minimum winter temperature and maximum breeding season temperature in part of its range, but respond to breeding season precipitation in another region. While these sets of weather variables are by no means comprehensive, temperature and precipitation are considered important drivers of temporal variation in bird abundance across a range of spatial and temporal scales, particularly during the breeding season and over winter, which represent critical periods for recruitment and survival processes (Dybala *et al.* 2013; Illán *et al.* 2014; Pearce-Higgins *et al.* 2015).

3.3.3 Population growth rate model

We use a stochastic Gompertz, or first-order autoregressive, model (Dennis *et al.* 2006), which is used widely in population ecology (e.g. Roy et al. 2001, Knape et al. 2013, Pearce-Higgins et al. 2015). The fundamental logic of the model is that the abundance in a given year, N_{t+1}, is the abundance in the year before, N_t, multiplied by a growth-rate term. Environmental drivers act directly upon the growth rate, along with a first-order density dependence term. For a single site and species, the model can be written as:

$$N_{t+1} = N_t exp(\alpha + \beta_0 ln N_t + \textstyle\sum_{k=1}^{n} \beta_k W_{k,t} + \varepsilon_t) \qquad (1)$$

Where α is the site-level intercept, β_0 is the lag-1 density-dependence coefficient, and β_k $(k = 1, \dots, n)$ are the coefficients estimated for each weather term, $W_{k,t}$, in the model. Residual error, ε_t (process error) is normally-distributed with mean 0 and variance σ^2. This equation log-linearises and rearranges to form:

$$r_t = X_{t+1} - X_t = \alpha + \beta_0 X_t + \textstyle\sum_{k=1}^{n} \beta_k W_{k,t} + \varepsilon_t \qquad (2)$$

Where r_t is the inter-annual population growth rate at time *t*, and X_t is the log-abundance at time *t*. In order to extend this site-level model to accommodate data from multiple sites taken from across the range of each species, a number of additional covariates are needed. Firstly, to accommodate the fact that weather covariates may systematically deviate from site-level conditions (due to variation in elevation, for example), a site-level intercept term is required. Effects of weather are also likely to vary across species' ranges as they represent different regions of a species' climatic niche space (Mills *et al.* 2017). To accommodate this, we split Europe into 200 x 200 km grid-cells, allowing weather effects to vary at this spatial-grain – although note that the estimate of local weather conditions remains at the resolution of the 25 km gridded climate data. To allow weather covariate effects to vary spatially, we estimate weather covariates in each 200 km grid-cell independently of the others (i.e. there is no sharing of information, or "pooling of variance", across grid-cells). The full model is thus written as:

$$r_{i,j,t} = \alpha_i + \gamma_j + \beta_{0,j} X_{i,j,t} + \sum_{k=1}^{n} \beta_{k,j} W_{i,j,k,t} + \varepsilon_{i,j,t} \qquad (3)$$

where growth rate at site *i*, in grid-cell *j*, at time *t*, is a function of a normally-distributed, random-site intercept, α_i, and a grid-cell intercept (treated as a fixed effect), γ_j. As specified above, the density-dependence term, $\beta_{0,j}$ and weather terms, $\beta_{k,j}$, are now estimated for each 200km grid-cell individually.

While site-intercepts are estimated by pooling variation across all grid-cells, weather-effects and grid-cell intercepts are estimated locally. To ensure that there were enough data to estimate grid-cell specific weather effects, we only included grid-cells with ≥500 data points in the *full variable set*, and ≥300 in the *reduced variable set*. After applying these criteria, models could be run for 130 species using the full-variable set, and 153 using the reduced variable set, with a spatial coverage of much of the latitudinal gradient of Europe (Figure 1). For the small number of species that had models with just a single grid-cell (full variable set, n = 16; reduced variable set, n = 19), the respective grid-cell terms were dropped from the model.

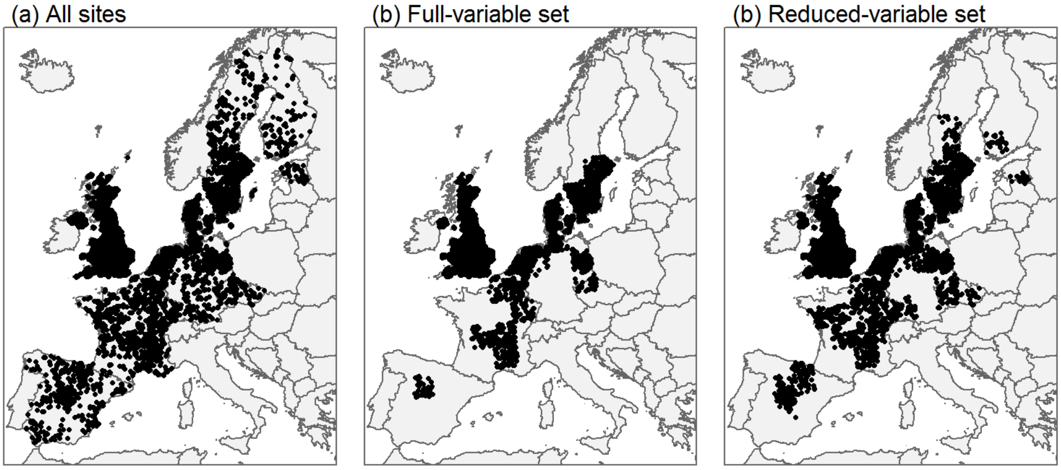


Figure 1 Spatial distribution of sites (a) with at least 5 years of data, (b) used in full variable set models, and (c) reduced variable models.

3.3.4 Evaluation of weather importance

The effects of weather on population growth rate are appraised in three ways. First, we summarise the distributions of coefficient *P*-values (calculated under the Satterthwaite approximation), which under the null hypothesis of weather terms having no effect on population growth rate should be uniformly distributed between 0 and 1. Departures from this, with more small *P*-values than expected to occur by chance, are thus indicative of underlying weather effects. We summarise these patterns across all species and by species and weather variable.

Second, we summarise the improvement in model explanatory capacity that is achieved through addition of weather variables (hereafter contribution of weather). We measure contribution of weather as $1 - \sigma_w^2/\sigma_{null}^2$, where σ_w^2 is the residual variance of the model containing weather terms (defined above) and σ_{null}^2 is the residual variance in a null model that just contains the random site-intercept, fixed grid-cell intercepts and density-dependence terms:

$$r_{i,j,t} = \alpha_i + \gamma_j + \beta_{0,j} X_{i,j,t} + \varepsilon_{i,j,t} \qquad (4)$$

This measure thus captures the proportional improvement in explanatory capacity of models through addition of weather terms, where a value of 0 indicates no improvement, and values above 0 indicate improvement in model explanatory power. As with the full weather model, species represented by just a single grid-cell had grid-cell terms removed. Lastly, we examine the residual variation that exists in the full weather model, which determines the accuracy of population growth rate predictions.

3.3.5 Robustness check using finer resolution climate datasets

One concern with using a 25 km resolution climate dataset is that weather variables might represent imprecise estimates of the local weather experienced by a population. Substantial error in predictors can generate regression dilution (McInerny & Purves 2011) and weak weather effects could therefore arise trivially if the 25 km dataset is a highly noisy estimate of site-level weather. For the UK, a finer resolution climate dataset is available (5 km resolution, UKCP09; Perry and Hollis 2005). To confirm that our results do not simply arise as a result of imprecise local weather estimates, we repeated the full-variable set analyses using just the UK dataset (83 species at 2979 sites across 20 years) and 5 km UKCP09 climate data.

3.3.6 Variation in contribution of weather with species traits

Species' sensitivity to weather may be influenced by a wide range of ecological and life history traits (Leech & Crick 2007) and we therefore assess whether population growth rates of species with particular characteristics exhibit greater sensitivity to weather. We use Phylogenetic Generalised Least Squares (PGLS) regression to model the relationship between the importance of weather and the following species' traits (all of which have received some empirical support): a) Log body mass (natural log), on the basis that this can modify physiological responses to temperature (Sinclair *et al.* 2016), b) migratory status (long distance migrants versus other species), with migration potentially increasing vulnerability to climate change due to trophic mismatch (Both *et al.* 2010), c) diet (vertebrate, invertebrate, plant; coded as a binary trait for each dietary component) and d) habitat type (forest, aquatic and open habitats) as both feeding guild and habitat have previously been implicated as correlates of population change (Van Turnhout *et al.* 2010), e) single versus multi-brooded species, which may give some buffering against adverse weather conditions during any single breeding attempt (Jiguet *et al.* 2007), and f) adult life-span, as population growth rates of longer lived species may be relatively buffered against short-term weather effects. The phylogeny was obtained from Roquet et al. (2014), and two recently-split species that are not included in this phylogeny, *Corvus cornix* and *Acanthis cabaret*, were excluded. Trait data were obtained from Storchová and Hořák (2018), and a further four species (*Cuculus canorus*, *Regulus ignicapilla*, *Cisticola juncidis*, and *Tetrax tetrax*) were excluded due to incomplete trait data.

3.3.7 Variation in contribution of weather with geographical position

To check that an overall species-level contribution of weather score did not conceal systematic spatial trends in the contribution of weather (Mills *et al.* 2017), we model spatial variation in grid-cell level estimates of the importance of weather in driving population dynamics. For each species and grid-cell, we calculated the Mean Square Error (MSE) for the full model containing weather terms and the null model that contained no weather terms, and for each species calculated a contribution of weather score for each individual grid cell as $1 - MSE_w/MSE_{null}$, calculated for each individual species and grid-cell combination. We then assessed whether there are systematic latitudinal or longitudinal patterns in regional contribution of weather scores while controlling for between species variation in sensitivity and accounting for statistical non-independence of observations within a grid-cell (Table S2). While these analyses do not directly control for phylogenetic relatedness, the results of the PGLS trait-based analysis suggest that phylogenetic signal is negligible in these data (Table 1).

All analyses were all carried out in the R programming environment (version 13.0) and code is available at github.com/SimonCMills/PopnResponseToWeather.

3.4 Results

There was a readily discernible statistical signal of weather in site level inter-annual population growth rates of European breeding bird populations, with weather coefficients displaying substantially more small *P*-values than expected by chance (Figure 2). This held when considering species individually, with the vast majority exhibiting a larger number of statistically significant weather coefficients than would be expected by chance (full variable set: 117 of 130 species, 90%; reduced variable set: 123 of 153 species, 80%; Figure 3). There was no clear tendency for particular periods of the year or specific weather variables to exhibit stronger or weaker statistical signals of weather effects, with all weather variables showing very similar skewed distributions towards smaller *P*-values than expected by chance (Figures S2, S3).

Incorporating weather terms typically generated marginal improvements in explanatory capacity, with a mean contribution of weather (i.e. proportional reduction in residual uncertainty) of approximately 3% in the full-variable set, and approximately 2% in the reduced-variable set (Figure 4). For species that were included in both full and reduced variable set models, there was broad consistency in the contribution of weather to population models (Pearson correlation coefficient = 0.80, n = 130). Species displayed some variation in the magnitude of the contribution of weather, but across all species values are typically low, with a minority of species having values above 5% (full variable set: 17 of 130 species, 13%; reduced variable set: 4 of 153 species, 3%; Figure 3).

Levels of residual uncertainty were typically high, indicating a low predictive capacity of the models (Figure 5). The mean residual uncertainty term is 0.52 in both model sets, which corresponds to a 95% predictive interval of 0.36μ- 2.77μ, where μ is the model predicted inter-annual growth rate (i.e. if the model predicted a stable population growth rate of 1, this interval includes populations that crashed to 36% or increased to 277% of their abundance in the year prior). Thus, for population growth rate models that contain 24 monthly weather variables and abundance in the previous year, along with site and grid-cell intercepts, substantial uncertainty remains in the predicted growth rates. The lowest predictive uncertainties observed correspond to a 95% predictive interval of 0.57μ- 1.75μ.

Qualitatively identical results (Figure S4) were obtained when modelling the UK subset of data using a finer resolution climate dataset, suggesting that our results are not due to using a coarse climate surface.

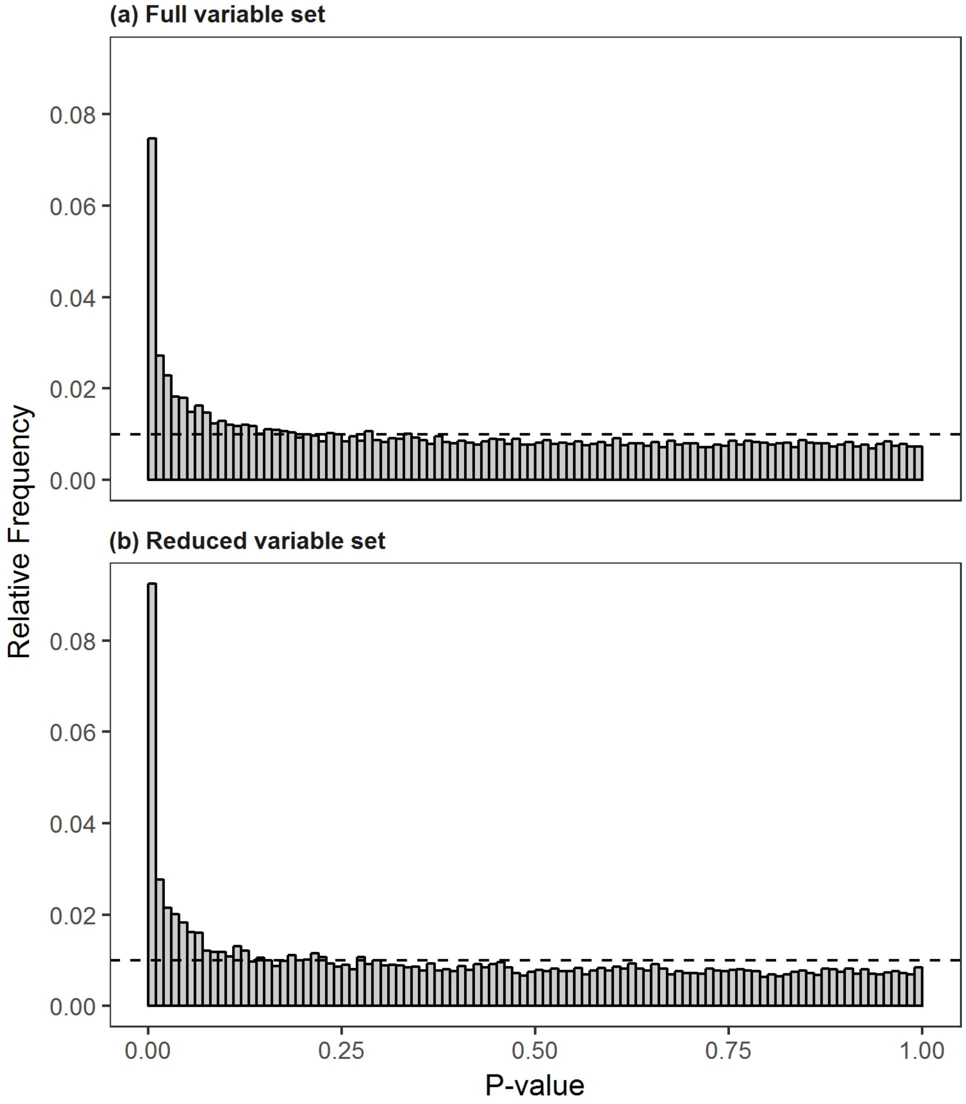
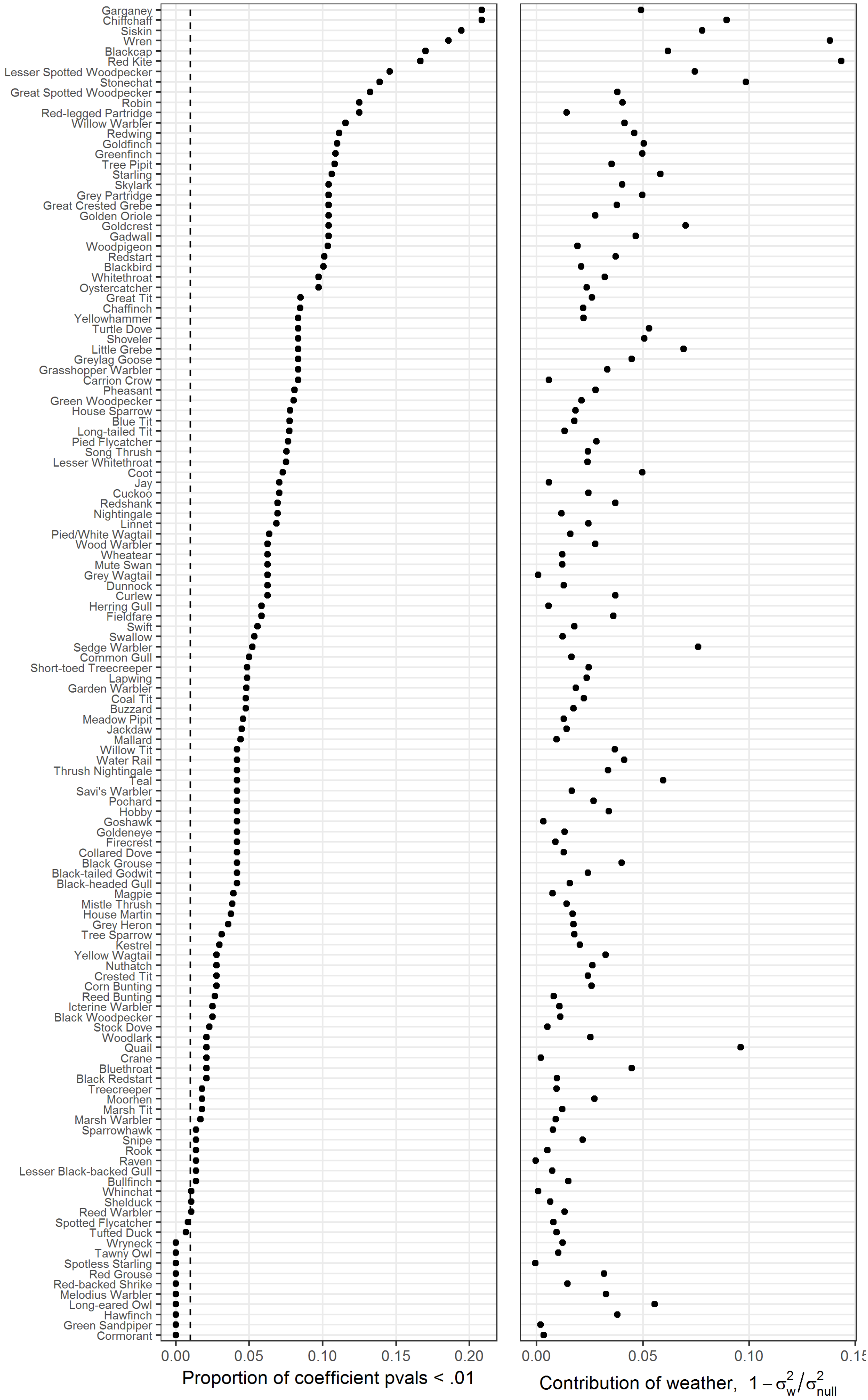


Figure 2 Histogram of P-values for all weather coefficients across all models, for both the full variable set and reduced variable set. Column widths are 0.01 and the dashed line indicates the corresponding uniform null expectation. Equivalent plots, but broken down by weather variable are given in Figures S2 and S3.

(a)


Garganey
Chiffchaff
Siskin
Wren
Blackcap
Red Kite
Lesser Spotted Woodpecker
Stonechat
Great Spotted Woodpecker
Robin
Red-legged Partridge
Willow Warbler
Redwing
Goldfinch
Greenfinch
Tree Pipit
Starling
Skylark
Grey Partridge
Great Crested Grebe
Golden Oriole
Goldcrest
Gadwall
Woodpigeon
Redstart
Blackbird
Whitethroat
Oystercatcher
Great Tit
Chaffinch
Yellowhammer
Turtle Dove
Shoveler
Little Grebe
Greylag Goose
Grasshopper Warbler
Carrion Crow
Pheasant
Green Woodpecker
House Sparrow
Blue Tit
Long-tailed Tit
Pied Flycatcher
Song Thrush
Lesser Whitethroat
Coot
Jay
Cuckoo
Redshank
Nightingale
Linnet
Pied/White Wagtail
Wood Warbler
Wheatear
Mute Swan
Grey Wagtail
Dunnock
Curlew
Herring Gull
Fieldfare
Swift
Swallow
Sedge Warbler
Common Gull
Short-toed Treecreeper
Lapwing
Garden Warbler
Coal Tit
Buzzard
Meadow Pipit
Jackdaw
Mallard
Willow Tit
Water Rail
Thrush Nightingale
Teal
Savi's Warbler
Pochard
Hobby
Goshawk
Goldeneye
Firecrest
Collared Dove
Black Grouse
Black-tailed Godwit
Black-headed Gull
Magpie
Mistle Thrush
House Martin
Grey Heron
Tree Sparrow
Kestrel
Yellow Wagtail
Nuthatch
Crested Tit
Corn Bunting
Reed Bunting
Icterine Warbler
Black Woodpecker
Stock Dove
Woodlark
Quail
Crane
Bluethroat
Black Redstart
Treecreeper
Moorhen
Marsh Tit
Marsh Warbler
Sparrowhawk
Snipe
Rook
Raven
Lesser Black-backed Gull
Bullfinch
Whinchat
Shelduck
Reed Warbler
Spotted Flycatcher
Tufted Duck
Wryneck
Tawny Owl
Spotless Starling
Red Grouse
Red-backed Shrike
Melodius Warbler
Long-eared Owl
Hawfinch
Green Sandpiper
Cormorant
0.00
0.05
0.10
0.15
0.20
Proportion of coefficient pvals < .01
0.00
0.05
0.10
0.15
Contribution of weather, $1 - \sigma_w^2/\sigma_{null}^2$

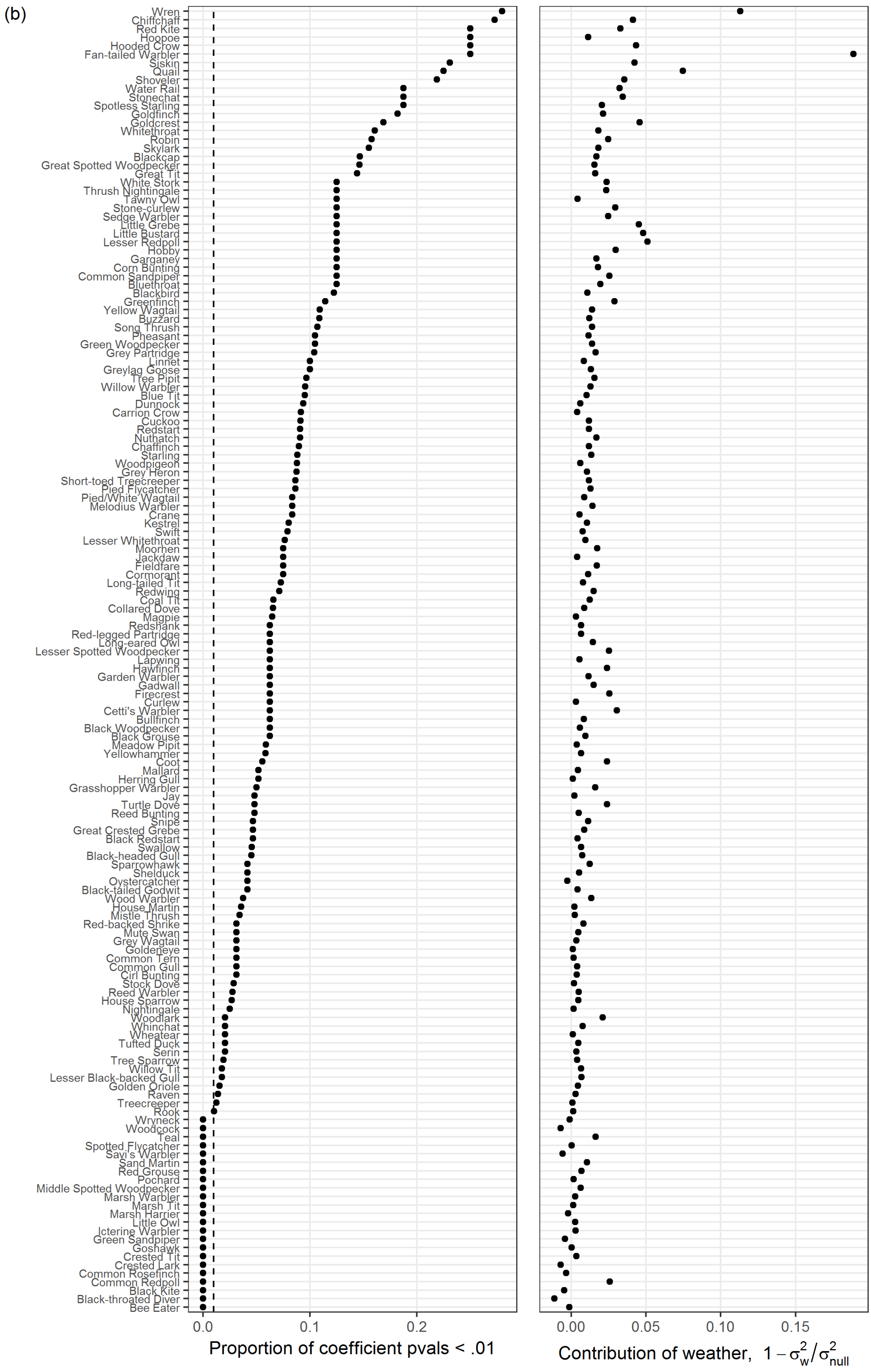

(b)
Wren
Chiffchaff
Red Kite
Hoopoe
Hooded Crow
Fan-tailed Warbler
Siskin
Quail
Shoveler
Water Rail
Stonechat
Spotless Starling
Goldfinch
Goldcrest
Whitethroat
Robin
Skylark
Blackcap
Great Spotted Woodpecker
Great Tit
White Stork
Thrush Nightingale
Tawny Owl
Stone-curlew
Sedge Warbler
Little Grebe
Little Bustard
Lesser Redpoll
Hobby
Garganey
Corn Bunting
Common Sandpiper
Bluethroat
Blackbird
Greenfinch
Yellow Wagtail
Buzzard
Song Thrush
Pheasant
Green Woodpecker
Grey Partridge
Linnet
Greylag Goose
Tree Pipit
Willow Warbler
Blue Tit
Dunnock
Carrion Crow
Cuckoo
Redstart
Nuthatch
Chaffinch
Starling
Woodpigeon
Grey Heron
Short-toed Treecreeper
Pied Flycatcher
Pied/White Wagtail
Melodious Warbler
Crane
Kestrel
Swift
Lesser Whitethroat
Moorhen
Jackdaw
Fieldfare
Cormorant
Long-tailed Tit
Redwing
Coal Tit
Collared Dove
Magpie
Redshank
Red-legged Partridge
Long-eared Owl
Lesser Spotted Woodpecker
Lapwing
Hawfinch
Garden Warbler
Gadwall
Firecrest
Curlew
Cetti's Warbler
Bullfinch
Black Woodpecker
Black Grouse
Meadow Pipit
Yellowhammer
Coot
Mallard
Herring Gull
Grasshopper Warbler
Jay
Turtle Dove
Reed Bunting
Snipe
Great Crested Grebe
Black Redstart
Swallow
Black-headed Gull
Sparrowhawk
Shelduck
Oystercatcher
Black-tailed Godwit
Wood Warbler
House Martin
Mistle Thrush
Red-backed Shrike
Mute Swan
Grey Wagtail
Goldeneye
Common Tern
Common Gull
Cirl Bunting
Stock Dove
Reed Warbler
House Sparrow
Nightingale
Woodlark
Whinchat
Wheatear
Tufted Duck
Serin
Tree Sparrow
Willow Tit
Lesser Black-backed Gull
Golden Oriole
Raven
Treecreeper
Rook
Wryneck
Woodcock
Teal
Spotted Flycatcher
Savi's Warbler
Sand Martin
Red Grouse
Pochard
Middle Spotted Woodpecker
Marsh Warbler
Marsh Tit
Marsh Harrier
Little Owl
Icterine Warbler
Green Sandpiper
Goshawk
Crested Tit
Crested Lark
Common Rosefinch
Common Redpoll
Black Kite
Black-throated Diver
Bee Eater
0.0
0.1
0.2
Proportion of coefficient pvals < .01
0.00
0.05
0.10
0.15
Contribution of weather, $1 - \sigma_w^2/\sigma_{null}^2$

Figure 3 (overleaf) Breakdown of *P*-values and explanatory capacities by species, for (a) full variable set models and (b) reduced variable set models. In the left-hand panel, the x-axis is the proportion of coefficient *P*-values that are 0.01. The dashed line at 0.01 signifies the baseline proportions that we would expect to observe if observed effects were entirely driven by chance. The right-hand panel gives the corresponding contribution of weather terms to each model. Scientific names are given in Table S3.

3.3.1 Effects of species' traits and geographical position

Using data on the contribution of weather terms to model performance from both the full and reduced variable model sets revealed similar associations with species' ecological and life history traits (Table 1). These models contained negligible phylogenetic signal ($\lambda<0.2$, both sets) and had R^2 values of 0.06 and 0.13 respectively in the full and reduced variable set models. Traits had negligible effect sizes and 95% confidence intervals that overlapped zero in all cases.

There was some variation across grid-cells in the contribution of weather to population growth rate models (Figures S5 and S6). The strength of weather effects still tend to be limited, however; in the full variable set, just 19 of 130 species (14%) and in the reduced variable set just 4 of 153 species (3%) had a maximum grid-cell contribution of weather to model explanatory power that exceeded 5%. Overall, 120 of 1102 grid-cells in the full variable set (10%), and 55 out of 1911 grid-cells in the reduced variable set (3%) had contribution of weather scores that exceeded 5%. Thus, even in models that consider spatial heterogeneity in contribution of weather to population growth rate, contributions of weather are still typically low.

There were weak but statistically significant linear associations between contribution of weather and longitude for both model sets (full variable set- $F_{1,\ 33.90} = 9.92$, $P=0.003$; reduced variable set- $F_{1,\ 50.24} = 4.61$, $P = 0.037$; Table S2). This amounts to a difference of 2.6% across the modelled longitudinal range in the full model set and 1.0% in the reduced model set, such that variation in population growth was marginally better explained by weather variables in Eastern Europe (Figure S6; Table S2). By comparison, there were no statistically significant associations with latitude (Figure S6; Table S2).

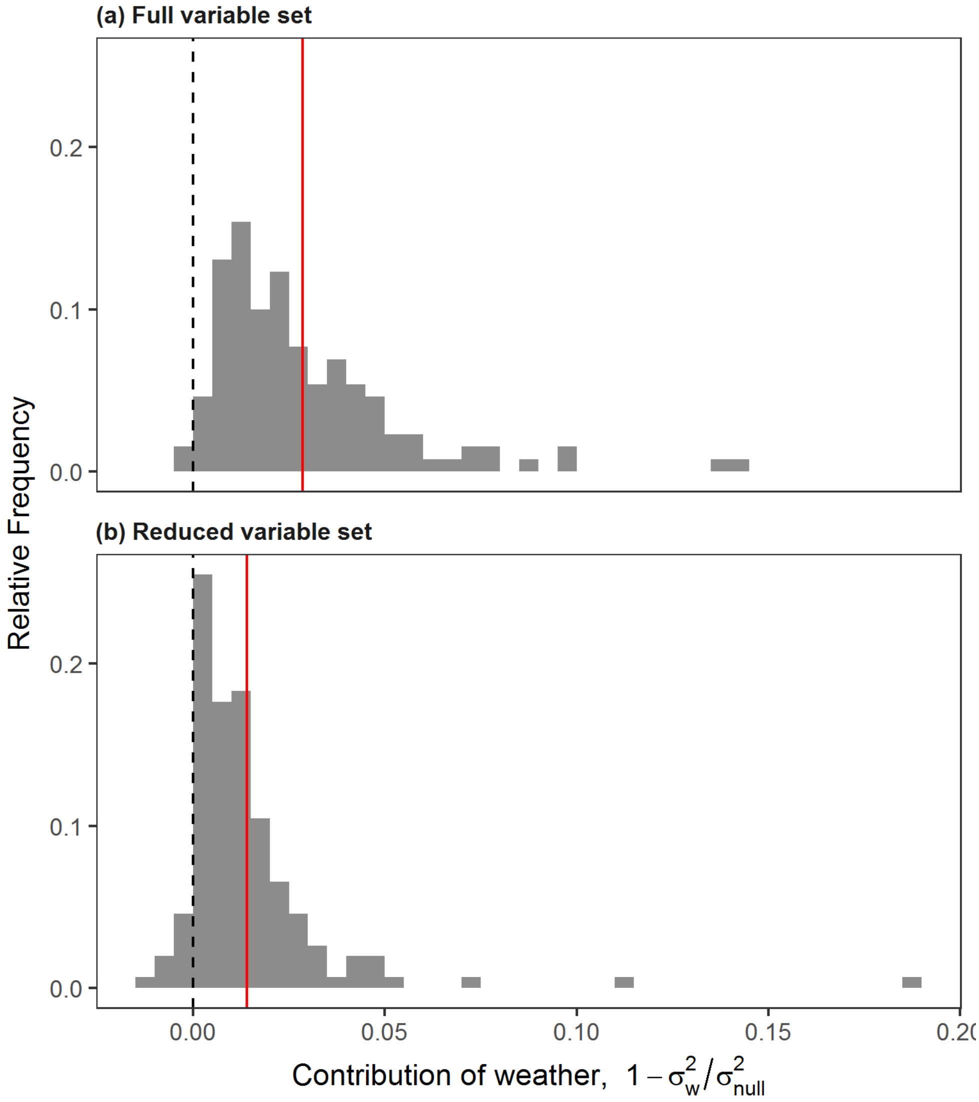


Figure 4 Histograms of contribution of weather terms to models across all species. The upper panel displays the frequency distributions for the full variable set, while the lower panel is for the reduced variable set. The dashed line at 0 indicates the level at which addition of weather terms did not improve the explanatory capacity of the model (i.e. residual variance was identical in the null and the model containing weather terms). The red line indicates the mean contribution of weather across all species, for each model set.

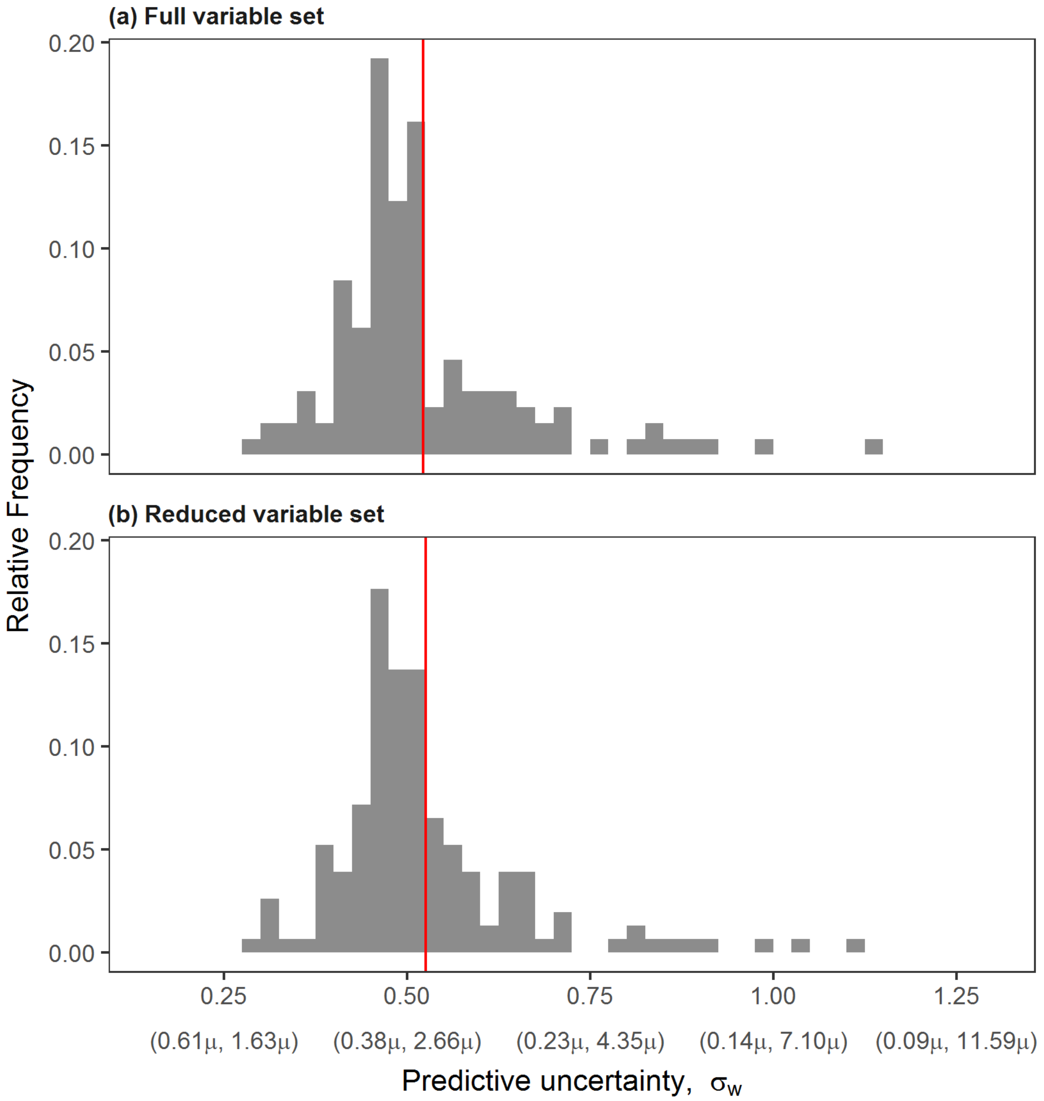


Figure 5 Histograms of the predictive capacity of models, across all species. The upper number on the x-axis gives the standard deviation (σ_w), while the intervals below these represent the corresponding 95% predictive interval, based on this value. The red line corresponds to the average predictive uncertainty in each set.

Table 1 Coefficient estimates and model R^2 for analyses of associations between contribution of weather scores and species' traits.

	(a) full-variable set			(b) reduced-variable set		
Coefficient	**Estimate**	**95% C.I.**	***P*-value**	**Estimate**	**95% C.I.**	***P*-value**
Intercept	0.037	(0.009, 0.066)	0.011	0.026	(0.008, 0.045)	0.006
Log(body mass)	-0.001	(-0.006, 0.003)	0.600	-0.002	(-0.005, 0.001)	0.114
Multibrooded	0.002	(-0.009, 0.014)	0.698	0.006	(0.000, 0.013)	0.068
LD migrant	-0.004	(-0.016, 0.008)	0.518	-0.001	(-0.008, 0.005)	0.686
Life span	0.000	(-0.001, 0.001)	0.478	0.000	(-0.001, 0.000)	0.459
Diet: vertebrate	0.004	(-0.010, 0.019)	0.546	0.006	(-0.002, 0.015)	0.161
Diet: invertebrate	-0.003	(-0.016, 0.011)	0.698	0.006	(-0.002, 0.014)	0.119
Diet: plant	-0.005	(-0.015, 0.006)	0.395	-0.001	(-0.008, 0.005)	0.697
Habitat: forest	0.003	(-0.009, 0.016)	0.583	-0.001	(-0.007, 0.006)	0.859
Habitat: open	0.009	(-0.001, 0.019)	0.084	0.002	(-0.004, 0.007)	0.590
Habitat: aquatic	0.002	(-0.011, 0.016)	0.743	-0.003	(-0.011, 0.004)	0.396
λ	0.000	(0.000, 0.537)		0.295	(0.000, 0.811)	
R^2		0.06			0.13	

3.5 Discussion

We present the first continental-scale analysis of the effects of weather on site-level population dynamics, using breeding bird population data for 153 widespread European bird species. For the majority of species, we found statistically significant effects of weather on population growth rates, with approximately equal contributions across all seasons and for both temperature- and precipitation-based variables. However, the explanatory contribution of weather terms was typically marginal, with an average associated improvement in variance explained of less than 3%, even when using a large suite of weather variables, and allowing effects to vary both regionally and between species. Variation in the ability of weather to explain site-level population growth rate was not associated with phylogeny or species' ecological or life history traits.

We do however find a weak association between the importance of weather and longitude across both sets of models. Effect sizes are however small, and overall explanatory contributions remain low even when within-species spatial variation is considered. It is possible that the limited geographical association we observe owes in part to the fact that these coordinates are not standardised relative to the range limits of each species (i.e. as they were in Chapter II). By failing to do this, a given latitude or longitude could lie close to the range limits for one species but far from the range limits of another, and we would therefore not expect to see a shared response across these. It is important to note however that this fact is very unlikely to affect our conclusions about limited geographical pattern, due to the fact that almost all cases (species:200km grid cell combinations) continue to have very limited explanatory contributions of weather (<5% model improvement), even after allowing these to vary spatially. Consequently, even if it was the case that the most sensitive regions were consistently towards range edges, the conclusion would still be that weather appears to play a weak role in driving variation in abundance, relative to other processes.

There are three broad sets of explanations for these results. First, impacts of weather on population growth rates may only be weakly captured by generic phenomenological models that use 'off-the-shelf' covariates (Knape & de Valpine 2011) and do not incorporate population detail such as age-structure or timing of life-history events. Second, unquantified census error may contribute substantially to observed population growth rates, limiting the explanatory capacity of weather. Third, inter-annual site-level population growth rates may be driven in large part by non-climatic factors, such that weather plays a relatively weak regulatory role at present. We discuss each of these in turn, and their implications for future work on the population impacts of weather and climate.

3.5.1 Phenomenological models and complex weather drivers

There has been extensive debate over the extent to which drivers of population dynamics can be captured in the absence of demographic or other population detail (Knape & de Valpine 2011; Boggs & Inouye 2012). In particular, this has focussed on the role of complex demographic responses, which are well documented (Benton *et al.* 2006; Cleasby *et al.* 2017), but population detail can prove critical in a number of other ways. For example, detailed knowledge of how the timing of weather events coincides with the life-history events such as breeding or fledging (Hallett *et al.* 2004; Benton *et al.* 2006) and interactions with habitat (Nicolè *et al.* 2011; Oliver & Morecroft 2014) can also be crucial in order for a statistical model to adequately resolve weather drivers. Similarly, where weather drivers act via indirect pathways, information on the mediating variable can be essential to understanding weather impacts (Boggs & Inouye 2012; Ogilvie *et al.* 2017).

Collecting this level of population detail across any wide spatial extent would require a substantial, if not insurmountable, increase in surveying effort. If it is the case that models that contain high levels of demographic detail or otherwise invoke intricate mechanistic detail are required to adequately capture weather impacts on population growth, then large survey datasets may be ill-suited to the task due to their inability to resolve critical population processes.

Despite the apparent importance of including mechanistic detail in statistical models of weather impacts on population dynamics (Knape & de Valpine 2011), there is relatively little research that directly addresses how the costs to explanatory capacity accumulate as lower levels of population detail are included (though see Coulson et al. 2001 as an example of this). Developing a stronger understanding of these trade-offs seems a particularly important avenue of exploration if we are to understand the inherent limitations of population growth models that do not incorporate context-specific (e.g. demographic age-structure or local habitat) detail. In particular, identifying critical features that explanatory capacity hinges upon would be useful for (i) determining whether, given the constraints of a particular dataset, there is the potential for informative models of inter-annual growth, and (ii) directing efforts for obtaining additional information to incorporate into statistical models.

3.5.2 Unquantified census error

The growing availability of population time-series increasingly allows for ecologists to investigate drivers of population change. However, a recurring difficulty comes in the form of census error (i.e. inaccurate estimates of population size), the magnitude of which is often unknown (Freckleton *et al.* 2006; Lindén & Knape 2009). While census error should not in principle bias estimates of environmental effects (though see Lindén and Knape 2009), if the proportion of variance in growth rate arising through census error is high, then weather terms will have only a weak capacity to explain growth rate, irrespective of their underlying importance. It is difficult to directly assess the extent to which this contributes to the results observed here, but census error can be large in breeding bird surveys, e.g. 70% of the variation in American Redstart (*Setophaga ruticilla*) abundance in the North American BBS is attributable to census error (Dennis *et al.* 2006).

While methods exist that attempt to partition observed variation into observation and process error, these are typically difficult to fit and estimates of the respective variance terms can perform poorly (Dennis et al. 2006, Knape and de Valpine, 2012; Auger-Méthé et al. 2016). Estimating census error from time-series directly is thus considerably problematic; the median time-series length at any individual site in the datasets used here is nine years, and thus estimates of census error would have to be estimated across multiple sites, schemes, habitat-types, etc. It is not clear that census error should be consistent across these various groupings, and choosing an adequate observation model can be critical to obtaining sensible estimates of uncertainty (Knape *et al.* 2011). A more robust approach would be to directly assess the magnitude of census error through replicated sampling of populations, and to explore the implications of the various sampling methods employed by a particular scheme (Brian *et al.* 2010). This would allow for the contribution of census error to be partitioned out, which would enable much stronger conclusions to be made about the relative support that different models of population growth receive.

Importantly, while an alternative response to the issue of substantial and unquantified census error might be to average away census error to coarser-scale regional or national units and model these annual averages instead (e.g. Pearce-Higgins *et al.* 2015), these approaches do not appear to resolve the issues that we describe here, and, where reported, explanatory capacities also appear generally low (Jørgensen *et al.* 2015; Martay *et al.* 2017; Bowler *et al.* 2018). This likely arises in part due to the loss of information incurred as explanatory variables are aggregated to a more coarse-scale regional index. While the result is a less variable abundance measure, the corresponding costs seem to negate the improvement in explanatory capacity that might otherwise be achieved.

3.5.3 Non-climatic drivers of population growth

Non-climatic drivers are also likely to be involved in population regulation. Over the last 30 years, numerous non-climatic changes have also occurred within Europe, many of which have been implicated in population change. These include factors such as the increased application of pesticides and other factors linked to agricultural intensification (Hallmann *et al.* 2014), change in landscape management (Jørgensen *et al.* 2015), and release from historical persecution (Lorrilliere *et al.* 2010). Non-climatic factors such as these are not captured by our population growth models, and, indeed, they are difficult to capture at the annual resolution required for such a model. However, factors such as these are likely to be involved in population regulation and could outweigh the effect of weather on populations (Maxwell *et al.* 2016), and are therefore likely to contribute, at least in part, to the results we observe.

3.5.4 Conclusion

Understanding and predicting population responses to changes in weather conditions is critical for assessing and responding to the impacts of climate change on biodiversity. Survey datasets that cover wide spatial and taxonomic extents offer much opportunity to address these questions, and indeed may be necessary if we are to make general inferences about how populations will respond to changing climatic conditions. To date, these schemes have demonstrated great utility in understanding climate change impacts on species (e.g. Oliver *et al.* 2015; Stephens *et al.* 2016; Urban *et al.* 2016), and documenting contemporary population trends of European birds (Inger *et al.* 2015). However, our work here on birds, along with that on a diversity of other taxa (Coulson *et al.* 2001; Knape & de Valpine 2011; Boggs & Inouye 2012), indicates that not only are there important challenges that need resolution before datasets of this form can be usefully employed to predict how population growth rates respond to varying weather conditions and climate change, but also that there may be general constraints on the capacity of these models to achieve this goal. While the statistical signal that we detect indicates that climate is influencing European bird populations, it is important to recognise that at present, for many species, models that include no weather effects at all have a similar capacity to explain population growth as models that contain large sets of weather variables. Our results highlight the importance of considering explanatory capacity of weather terms rather than focussing solely on their statistical significance and also suggest a need to develop a greater understanding of the contribution of census error in order to understand the relative importance of various drivers of population growth.

3.6 References

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3.7 Supplementary material

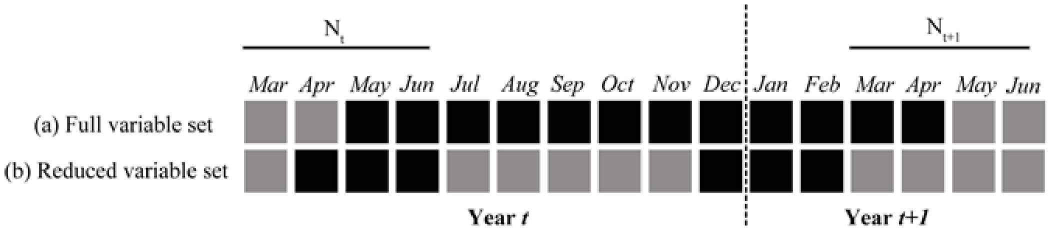

Figure S1 Schematic of periods used in models (black squares), with approximate breeding season sampling periods indicated above. Note that in the case of the reduced variable set, the black squares indicate the breeding season and overwinter periods, which the maximum and minimum monthly temperature averages and precipitation sums were taken from.

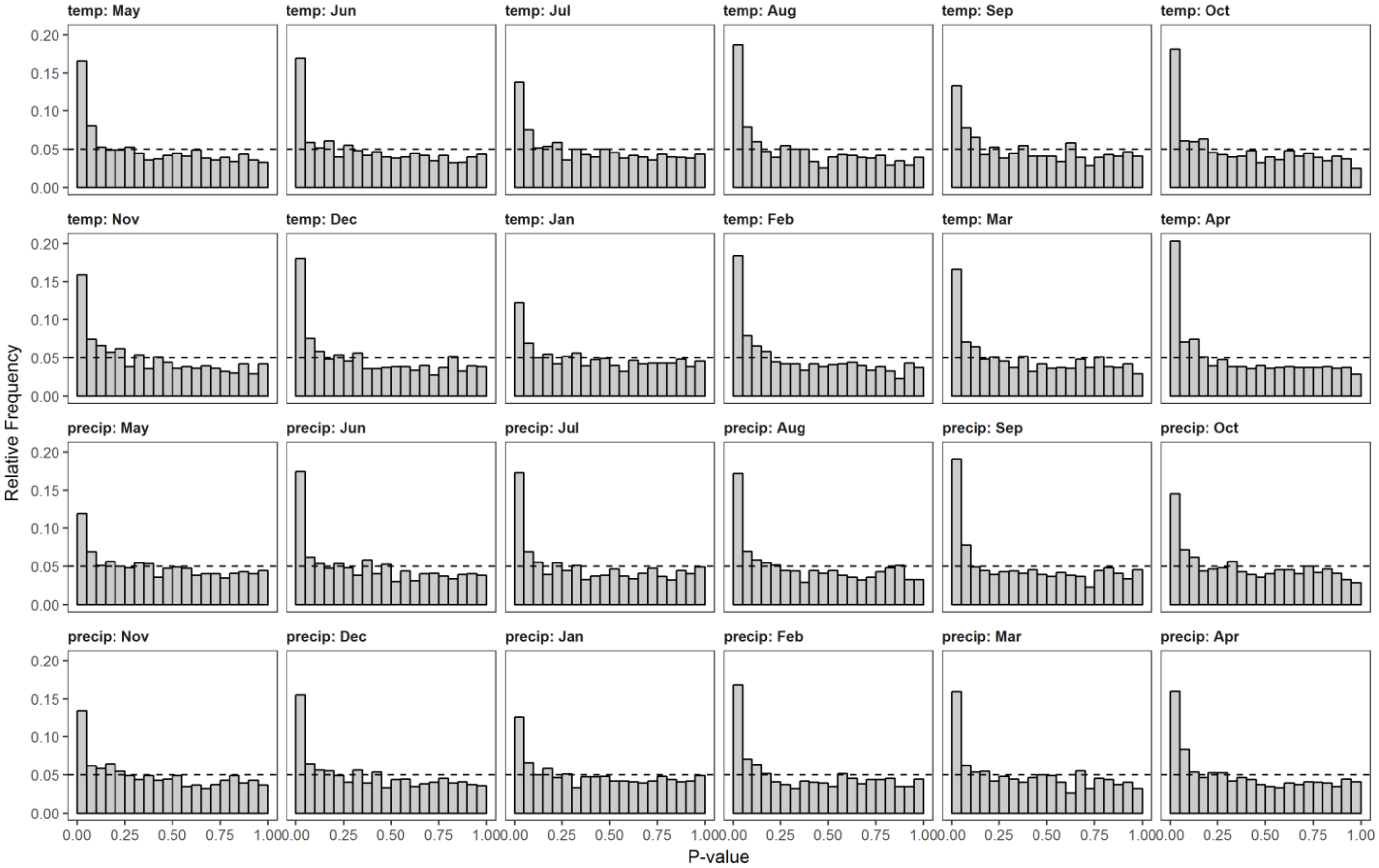

Figure S2 Histogram of *P*-values for all weather coefficients across all models, for each variable in the full variable set. Column widths are 0.05 and dashed line indicates the corresponding uniform null expectation.

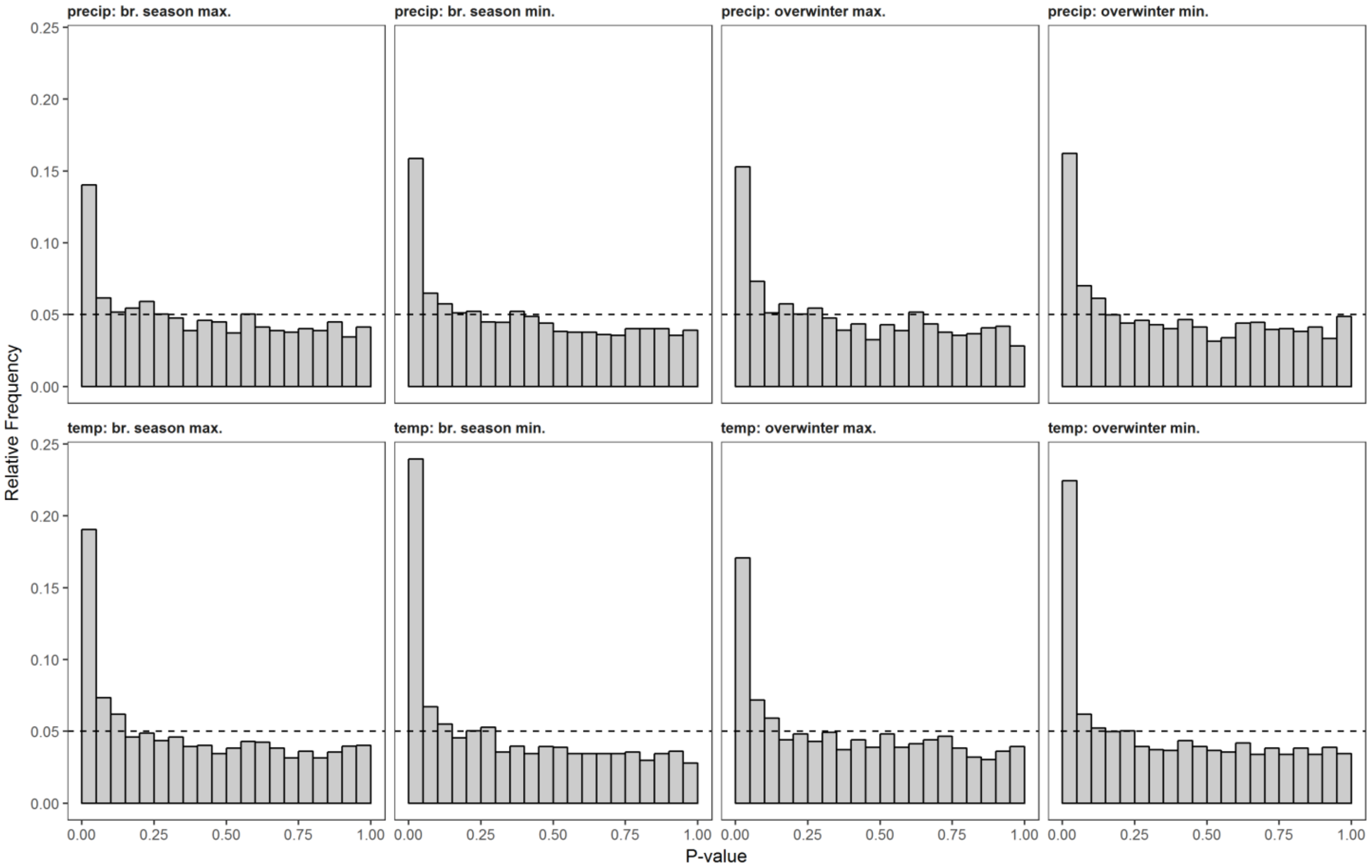

Figure S3 Histogram of *P*-values for all weather coefficients across all models, for each variable in the reduced variable set. Column widths are 0.05 and dashed line indicates the corresponding uniform null expectation.

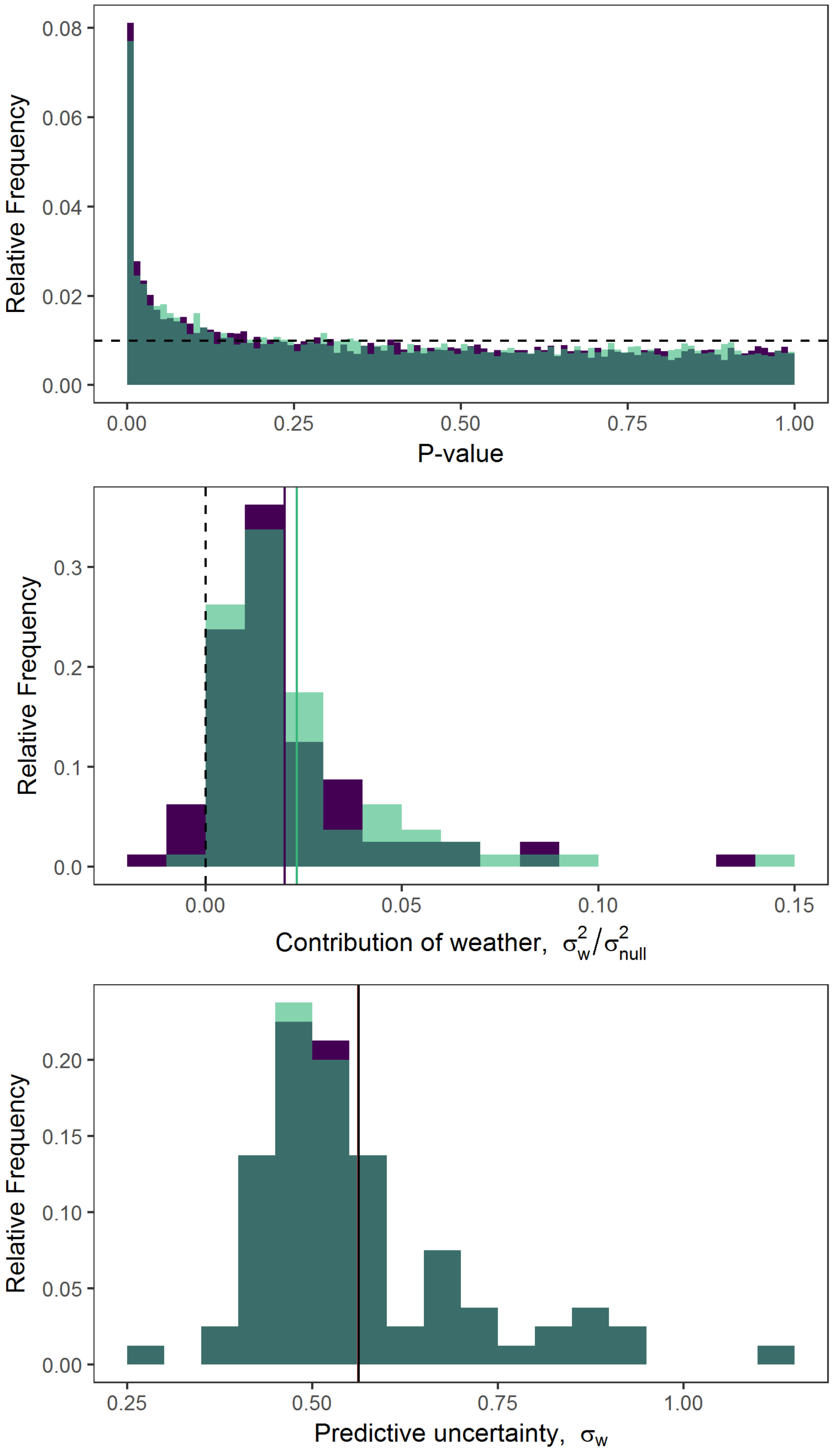

Figure S4 *P*-value distribution (upper panel), predictive uncertainty (middle panel), and contribution of weather terms (lower panel) for models fitted to UK datasets only, using 5km resolution climate dataset (UKCP09; light green, translucent), and 25km resolution climate dataset (ECAD; dark blue, solid). In the centre panel, the dashed line at 0 indicates the level at which addition of weather terms did not improve the explanatory capacity of the model (i.e. residual variance was identical in the null and the model containing weather terms). In the lower two panels, lines indicate the mean contribution of weather and the mean predictive uncertainty respectively, when using the UKCP09 dataset (light green) and the ECAD dataset (dark blue); note that in the bottom panel, the lines overlap with the green line sitting behind the blue.

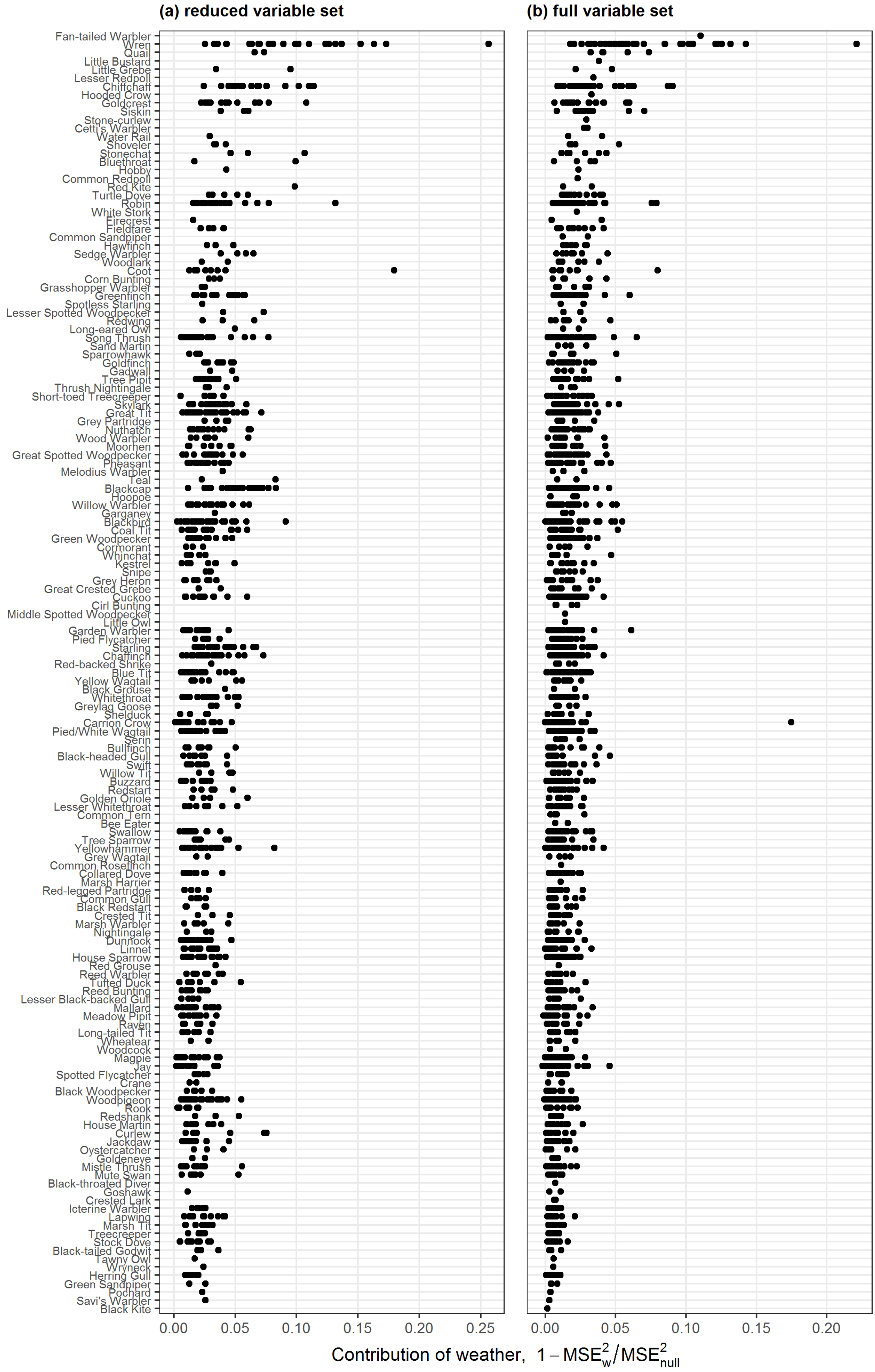
(a) reduced variable set
(b) full variable set
Fan-tailed Warbler
Wren
Quail
Little Bustard
Little Grebe
Lesser Redpoll
Chiffchaff
Hooded Crow
Goldcrest
Siskin
Stone-curlew
Cetti's Warbler
Water Rail
Shoveler
Stonechat
Bluethroat
Hobby
Common Redpoll
Red Kite
Turtle Dove
Robin
White Stork
Firecrest
Fieldfare
Common Sandpiper
Hawfinch
Sedge Warbler
Woodlark
Coot
Corn Bunting
Grasshopper Warbler
Greenfinch
Spotless Starling
Lesser Spotted Woodpecker
Redwing
Long-eared Owl
Song Thrush
Sand Martin
Sparrowhawk
Goldfinch
Gadwall
Tree Pipit
Thrush Nightingale
Short-toed Treecreeper
Skylark
Great Tit
Grey Partridge
Nuthatch
Wood Warbler
Moorhen
Great Spotted Woodpecker
Pheasant
Melodius Warbler
Teal
Blackcap
Hoopoe
Willow Warbler
Garganey
Blackbird
Coal Tit
Green Woodpecker
Cormorant
Whinchat
Kestrel
Snipe
Grey Heron
Great Crested Grebe
Cuckoo
Cirl Bunting
Middle Spotted Woodpecker
Little Owl
Garden Warbler
Pied Flycatcher
Starling
Chaffinch
Red-backed Shrike
Blue Tit
Yellow Wagtail
Black Grouse
Whitethroat
Greylag Goose
Shelduck
Carrion Crow
Pied/White Wagtail
Serin
Bullfinch
Black-headed Gull
Swift
Willow Tit
Buzzard
Redstart
Golden Oriole
Lesser Whitethroat
Common Tern
Bee Eater
Swallow
Tree Sparrow
Yellowhammer
Grey Wagtail
Common Rosefinch
Collared Dove
Marsh Harrier
Red-legged Partridge
Common Gull
Black Redstart
Crested Tit
Marsh Warbler
Nightingale
Dunnock
Linnet
House Sparrow
Red Grouse
Reed Warbler
Tufted Duck
Reed Bunting
Lesser Black-backed Gull
Mallard
Meadow Pipit
Raven
Long-tailed Tit
Wheatear
Woodcock
Magpie
Jay
Spotted Flycatcher
Crane
Black Woodpecker
Woodpigeon
Rook
Redshank
House Martin
Curlew
Jackdaw
Oystercatcher
Goldeneye
Mistle Thrush
Mute Swan
Black-throated Diver
Goshawk
Crested Lark
Icterine Warbler
Lapwing
Marsh Tit
Treecreeper
Stock Dove
Black-tailed Godwit
Tawny Owl
Wryneck
Herring Gull
Green Sandpiper
Pochard
Savi's Warbler
Black Kite
0.00
0.05
0.10
0.15
0.20
0.25
0.00
0.05
0.10
0.15
0.20
Contribution of weather, $1 - \mathrm{MSE}_w^2 / \mathrm{MSE}_{null}^2$

Figure S5 (overleaf) Break down of spatial contribution of weather terms by species, for (a) reduced variable set models and (b) full variable set models. Scientific names are given in Table S3.

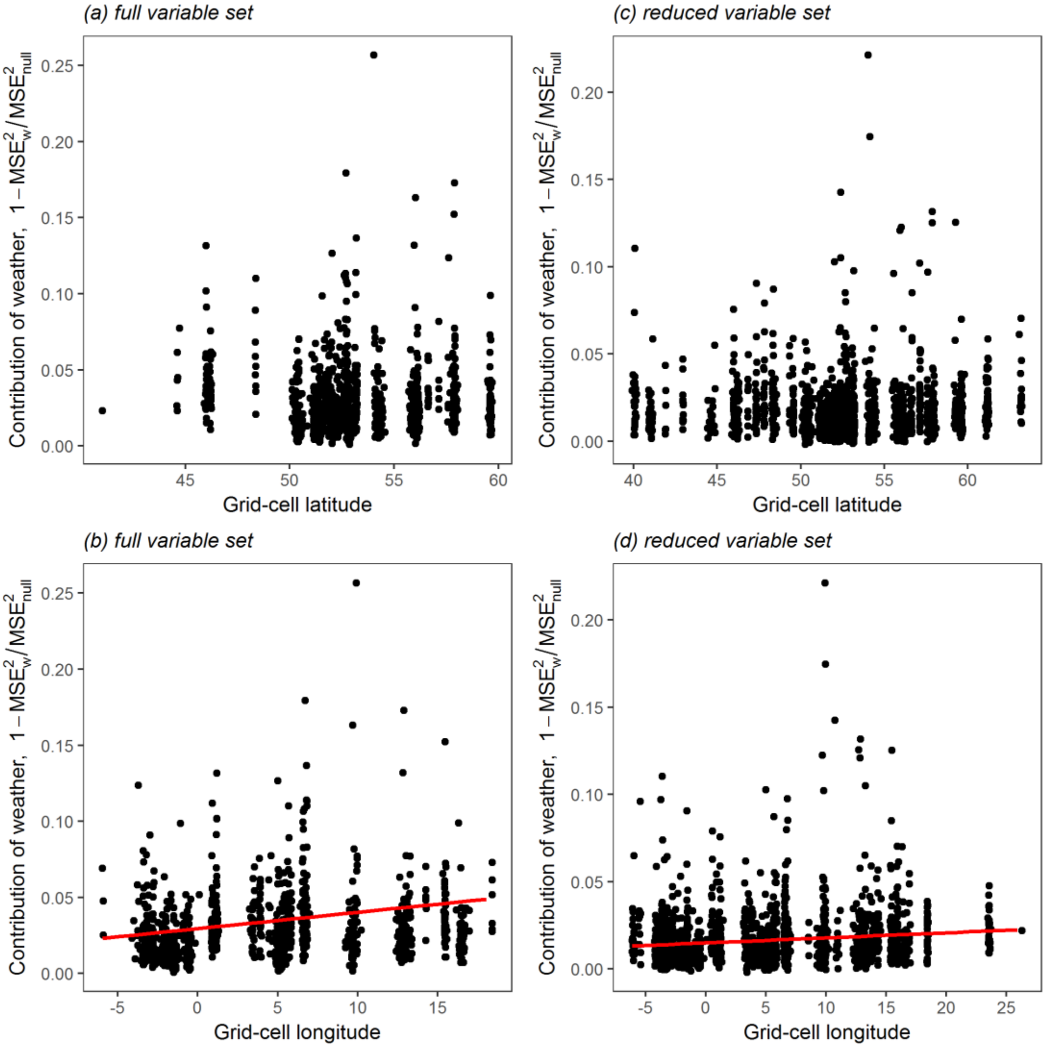

Figure S6 Latitudinal and longitudinal associations with contribution of weather scores, for full variable set models (a, b) and reduced variable set models (c, d). Where statistically significant associations exist (see Table S2), these are represented by the red lines.

Table S1 Breakdown of temporal coverage of data for each scheme.

Country	First year	Last year	Year range
Belgium	1990	2014	24
Czechia	1982	2013	31
Denmark	1976	2013	37
Estonia	1983	2013	30
Finland	1975	2013	38
France	1989	2014	25
Germany	2005	2014	9
Netherlands	1990	2014	24
Spain	1998	2014	16
Sweden	1975	2014	39
UK	1994	2014	20

Table S2 Results for model comparisons between spatial contribution of weather terms and models with varying latitudinal and longitudinal associations (no association, 1&3; linear association, 2&4; quadratic association, 3&6). F-statistics and associated degrees of freedom (df) and *P*-values (calculated with Kenward-Roger correction) are calculated for each successive addition of terms. Potential longitudinal associations are controlled for while making latitudinal comparisons and vice-versa (as higher latitudes are typically only observed at higher longitudes also), and statistical non-independence of species and grid-cell contribution of weather scores is controlled for with random effects placed on these factors (1|species) + (1|grid-cell). Statistically significant associations at the 5% level are highlighted in bold.

			(a) full variable set			(b) reduced variable set		
Model			**F-statistic**	**df**	**p**	**F-statistic**	**df**	**p**
(1)		lon + lon^2 + (1|species) + (1|grid-cell)	-			-		
(2)	lat +	lon + lon^2 + (1|species) + (1|grid-cell)	2.62	40.90	0.113	3.13	51.31	0.083
(3) lat^2 +	lat +	lon + lon^2 + (1|species) + (1|grid-cell)	0.00	42.38	0.959	2.45	52.53	0.123
(4)		lat + lat^2 + (1|species) + (1|grid-cell)	-			-		
(5)	lon +	lat + lat^2 + (1|species) + (1|grid-cell)	**9.92**	**33.90**	**0.003**	**4.61**	**50.24**	**0.037**
(6) lon^2 +	lon +	lat + lat^2 + (1|species) + (1|grid-cell)	2.45	52.53	0.123	0.20	64.43	0.656

Table S3 Scientific names of all breeding bird species incorporated in analyses.

Species	Latin binomial
Bee Eater	*Merops apiaster*
Black-headed Gull	*Chroicocephalus ridibundus*
Black-tailed Godwit	*Limosa limosa*
Black-throated Diver	*Gavia arctica*
Black Grouse	*Tetrao tetrix*
Black Kite	*Milvus migrans*
Black Redstart	*Phoenicurus ochruros*
Black Woodpecker	*Dryocopus martius*
Blackbird	*Turdus merula*
Blackcap	*Sylvia atricapilla*
Blue Tit	*Cyanistes caeruleus*
Bluethroat	*Luscinia svecica*
Bullfinch	*Pyrrhula pyrrhula*
Buzzard	*Buteo buteo*
Carrion Crow	*Corvus corone*
Cetti's Warbler	*Cettia cetti*
Chaffinch	*Fringilla coelebs*
Chiffchaff	*Phylloscopus collybita*
Cirl Bunting	*Emberiza cirlus*
Coal Tit	*Periparus ater*
Collared Dove	*Streptopelia decaocto*
Common Gull	*Larus canus*
Common Redpoll	*Carduelis flammea*
Common Rosefinch	*Carpodacus erythrinus*
Common Sandpiper	*Actitis hypoleucos*
Common Tern	*Sterna hirundo*
Coot	*Fulica atra*
Cormorant	*Phalacrocorax carbo*
Corn Bunting	*Emberiza calandra*
Crane	*Grus grus*
Crested Lark	*Galerida cristata*
Crested Tit	*Lophophanes cristatus*
Cuckoo	*Cuculus canorus*
Curlew	*Numenius arquata*
Dunnock	*Prunella modularis*
Fan-tailed Warbler	*Cisticola juncidis*
Fieldfare	*Turdus pilaris*
Firecrest	*Regulus ignicapilla*

Gadwall	*Anas strepera*
Garden Warbler	*Sylvia borin*
Garganey	*Anas querquedula*
Goldcrest	*Regulus regulus*
Golden Oriole	*Oriolus oriolus*
Goldeneye	*Bucephala clangula*
Goldfinch	*Carduelis carduelis*
Goshawk	*Accipiter gentilis*
Grasshopper Warbler	*Locustella naevia*
Great Crested Grebe	*Podiceps cristatus*
Great Spotted Woodpecker	*Dendrocopos major*
Great Tit	*Parus major*
Green Sandpiper	*Tringa ochropus*
Green Woodpecker	*Picus viridis*
Greenfinch	*Chloris chloris*
Grey Heron	*Ardea cinerea*
Grey Partridge	*Perdix perdix*
Grey Wagtail	*Motacilla cinerea*
Greylag Goose	*Anser anser*
Hawfinch	*Coccothraustes coccothraustes*
Herring Gull	*Larus argentatus*
Hobby	*Falco subbuteo*
Hooded Crow	*Corvus cornix*
Hoopoe	*Upupa epops*
House Martin	*Delichon urbicum*
House Sparrow	*Passer domesticus*
Icterine Warbler	*Hippolais icterina*
Jackdaw	*Corvus monedula*
Jay	*Garrulus glandarius*
Kestrel	*Falco tinnunculus*
Lapwing	*Vanellus vanellus*
Lesser Black-backed Gull	*Larus fuscus*
Lesser Redpoll	*Carduelis cabaret*
Lesser Spotted Woodpecker	*Dendrocopos minor*
Lesser Whitethroat	*Sylvia curruca*
Linnet	*Carduelis cannabina*
Little Bustard	*Tetrax tetrax*
Little Grebe	*Tachybaptus ruficollis*
Little Owl	*Athene noctua*
Long-eared Owl	*Asio otus*

Long-tailed Tit	*Aegithalos caudatus*
Magpie	*Pica pica*
Mallard	*Anas platyrhynchos*
Marsh Harrier	*Circus aeruginosus*
Marsh Tit	*Poecile palustris*
Marsh Warbler	*Acrocephalus palustris*
Meadow Pipit	*Anthus pratensis*
Melodius Warbler	*Hippolais polyglotta*
Middle Spotted Woodpecker	*Dendrocopos medius*
Mistle Thrush	*Turdus viscivorus*
Moorhen	*Gallinula chloropus*
Mute Swan	*Cygnus olor*
Nightingale	*Luscinia megarhynchos*
Nuthatch	*Sitta europaea*
Oystercatcher	*Haematopus ostralegus*
Pheasant	*Phasianus colchicus*
Pied Flycatcher	*Ficedula hypoleuca*
Pied/White Wagtail	*Motacilla alba*
Pochard	*Aythya ferina*
Quail	*Coturnix coturnix*
Raven	*Corvus corax*
Red-backed Shrike	*Lanius collurio*
Red-legged Partridge	*Alectoris rufa*
Red Grouse	*Lagopus lagopus*
Red Kite	*Milvus milvus*
Redshank	*Tringa totanus*
Redstart	*Phoenicurus phoenicurus*
Redwing	*Turdus iliacus*
Reed Bunting	*Emberiza schoeniclus*
Reed Warbler	*Acrocephalus scirpaceus*
Robin	*Erithacus rubecula*
Rook	*Corvus frugilegus*
Sand Martin	*Riparia riparia*
Savi's Warbler	*Locustella luscinioides*
Sedge Warbler	*Acrocephalus schoenobaenus*
Serin	*Serinus serinus*
Shelduck	*Tadorna tadorna*
Short-toed Treecreeper	*Certhia brachydactyla*
Shoveler	*Anas clypeata*
Siskin	*Carduelis spinus*

Skylark	*Alauda arvensis*
Snipe	*Gallinago gallinago*
Song Thrush	*Turdus philomelos*
Sparrowhawk	*Accipiter nisus*
Spotless Starling	*Sturnus unicolor*
Spotted Flycatcher	*Muscicapa striata*
Starling	*Sturnus vulgaris*
Stock Dove	*Columba oenas*
Stone-curlew	*Burhinus oedicnemus*
Stonechat	*Saxicola rubicola*
Swallow	*Hirundo rustica*
Swift	*Apus apus*
Tawny Owl	*Strix aluco*
Teal	*Anas crecca*
Thrush Nightingale	*Luscinia luscinia*
Tree Pipit	*Anthus trivialis*
Tree Sparrow	*Passer montanus*
Treecreeper	*Certhia familiaris*
Tufted Duck	*Aythya fuligula*
Turtle Dove	*Streptopelia turtur*
Water Rail	*Rallus aquaticus*
Wheatear	*Oenanthe oenanthe*
Whinchat	*Saxicola rubetra*
White Stork	*Ciconia ciconia*
Whitethroat	*Sylvia communis*
Willow Tit	*Poecile montana*
Willow Warbler	*Phylloscopus trochilus*
Wood Warbler	*Phylloscopus sibilatrix*
Woodcock	*Scolopax rusticola*
Woodlark	*Lullula arborea*
Woodpigeon	*Columba palumbus*
Wren	*Troglodytes troglodytes*
Wryneck	*Jynx torquilla*
Yellow Wagtail	*Motacilla flava*
Yellowhammer	*Emberiza citrinella*

Chapter 4:

Quantifying variation in thermal exposure during focal periods improves predictions of population growth in UK butterflies

4.1 Abstract

Aim Developing a robust understanding of the respective roles of climatic means, variances, and extremes in driving population growth is central to predicting how populations respond to variation in environmental conditions. Here we address the relative importance of considering thermal variation acting at fine-temporal scales in explaining variation in inter-annual population growth.

Location UK

Time period 1974-2016

Major taxa studied Butterflies

Methods We model inter-annual population growth rates of 32 species of UK butterfly at 460 sites across the UK. We first identify focal periods in which mean monthly temperature is most strongly associated with population growth, and then ask how the inclusion of information on the variation in within-month temperatures alters our ability to predict population growth, while controlling for a number of other potentially confounding covariates. We further assess whether a simple empirical model of population growth in which population growth is simply the average of responses to daily temperature exposures can explain differences in model predictive capacity.

Results For the majority of species, we find that inclusion of information on standard deviation of weather variables substantially enhances our ability to explain inter-annual population growth, and the biological significance of these terms can be substantial. We further find that the predictive capacities of the simple empirical models are limited, and typically do not outperform models that contain mean monthly temperatures alone.

Main conclusions The key implication of our results is that thermal variation at fine temporal scales appears to be involved in population regulation, and failure to incorporate this biologically relevant variation in temperature limits the capacity of models to explain variation in abundance. The finding that these model improvements

cannot be understood as arising through a simple accumulation of daily exposures indicates that the drivers of population growth may be difficult to characterise and suggests a role for more complex non-linear responses to thermal extremes.

4.2 Introduction

There is much interest in the respective roles of climatic means, variances, and extremes in determining population performance, not least to understand how climate change impacts populations (Thompson *et al.* 2013; Harris *et al.* 2018). While means capture the average conditions experienced at a particular location, they are limited in their capacity to index the full set of climatic events that a population is exposed to, as they contain no information about the width of the climatic distribution, or where the upper and lower extremes of the distribution lie. Considering climatic means alone when assessing population responses to climatic conditions is problematic, as even short-lived and infrequent events can have substantial impacts on population performance, and it is the full set of climatic events that a particular population experiences that is likely to determine population performance (Scheffers *et al.* 2014; Sunday *et al.* 2014). Furthermore, as climate change can involve many distributional changes beyond simple shifts in mean climatic conditions (Huntingford *et al.* 2013), it is important to develop a holistic understanding of how populations respond to changes in climate regimes that act at fine temporal scales, in order to forecast adequately how populations will respond to changes occurring across the full climatic distribution and into the future.

Considering the full climatic regime that a population experiences is particularly important when there are non-linearities in how populations respond to climatic variation (Vasseur *et al.* 2014; Lawson *et al.* 2015). When there are non-linear responses, how an organism or population responds cannot be understood in terms of the mean alone, as response depends upon the full set of exposure events (Martin & Huey 2008). Considering the climatic regime as a whole, rather than just what conditions are like on average, can considerably alter the predicted behaviour of biological systems, and can change long-term predicted population growth rate (Lawson *et al.* 2015), optimal thermal environment and organism behaviour (Martin & Huey 2008), species performance and distribution limits (Kingsolver *et al.* 2013; Sunday *et al.* 2014), predicted responses to climate change (Deutsch *et al.* 2008; Vasseur *et al.* 2014) and rate of disease transmission (Paaijmans *et al.* 2010).

Importantly, the effect of changing climatic regimes can be complex and is likely to be difficult to characterise (Sinclair *et al.* 2016). If we consider temperature specifically, a common approach is to construct a thermal performance curve (TPC) from in vivo experiments (e.g. Vasseur *et al.* 2014), and, from this, forecast how changing thermal regimes will alter the functional response of an organism, population, or species (e.g. Lawson *et al.* 2015). These forecasts are based on the assumption that the overall response is the average (or weighted sum; Martin & Huey 2008) across the response to finer scale exposure events (Ruel & Ayres 1999), and that the TPC is fixed (i.e. does not vary across different thermal regimes). According to this, when the response function is convex, increasing fine scale variation in temperature (e.g. in daily measurements that contribute to the mean measure, such as monthly or seasonal mean) enhances performance, while the opposite is true when the response is concave (following Jensen's inequality; see Figure 1a). Crucially however, the assumption that response curves are static across thermal regimes (i.e. there is no intra-specific variation) is, in many situations, unlikely to hold. There are numerous biological mechanisms that can cause the TPC to vary, including local adaptation (Williams *et al.* 2015), physiological acclimation (Dowd *et al.* 2015), behavioural plasticity (Buckley *et al.* 2015), and the occurrence of lethal exposures (Martin & Huey 2008; for review, see Sinclair et al. 2016). To illustrate the effect of just one of these, we pick an example in which there is a threshold that results in population extirpation when exceeded (Figure 1b). Thus, while we expect that considering the full thermal regime to which a population is exposed will improve our ability to explain observed variation in abundance, it is difficult to articulate a precise expectation about how thermal variation will modify the response to temperature in natural populations.

Here, we assess whether the inclusion of terms that capture the full range of thermal conditions that a population experiences improves the capacity of inter-annual population growth models to explain variation in abundance. We further assess whether these responses can be understood as a simple accumulation of daily exposures, as would occur if there is a fixed, shared TPC and the overall response is just the average across these, or whether associations with temperature are indicative of more complex responses to variation in temperature.

Using abundance datasets for 32 species of UK butterfly, spanning four decades and over 450 sites, we first identify focal periods in which temperature is most strongly associated with population growth. This first step of identifying monthly periods to focus on was carried out on the basis that we are interested in how inclusion of information on the thermal variation can affect the predicted population response. Across the life-cycle of a butterfly there are many periods in which population growth is relatively unaffected by variation in thermal conditions. We would *a priori* expect that including information on thermal variation would not affect population growth during such periods. By instead focussing on months in which thermal conditions appear involved in population growth we are better able to address whether or not fine-scale thermal variation is able to- at least in some cases- improve the predictive capacity of population growth models. Following this selection step, we assess whether including terms that measure the width of the thermal distribution (standard deviation) for these periods enhances our ability to predict population growth, beyond considering the average alone. Finally, we ask whether a model in which population growth is just the average of population responses to daily temperatures, assuming a fixed TPC, can explain population growth rate as well as the previously applied models containing monthly means and standard deviations, or whether the SD associations that we observe are indicative of more complex forms of response to thermal variation.

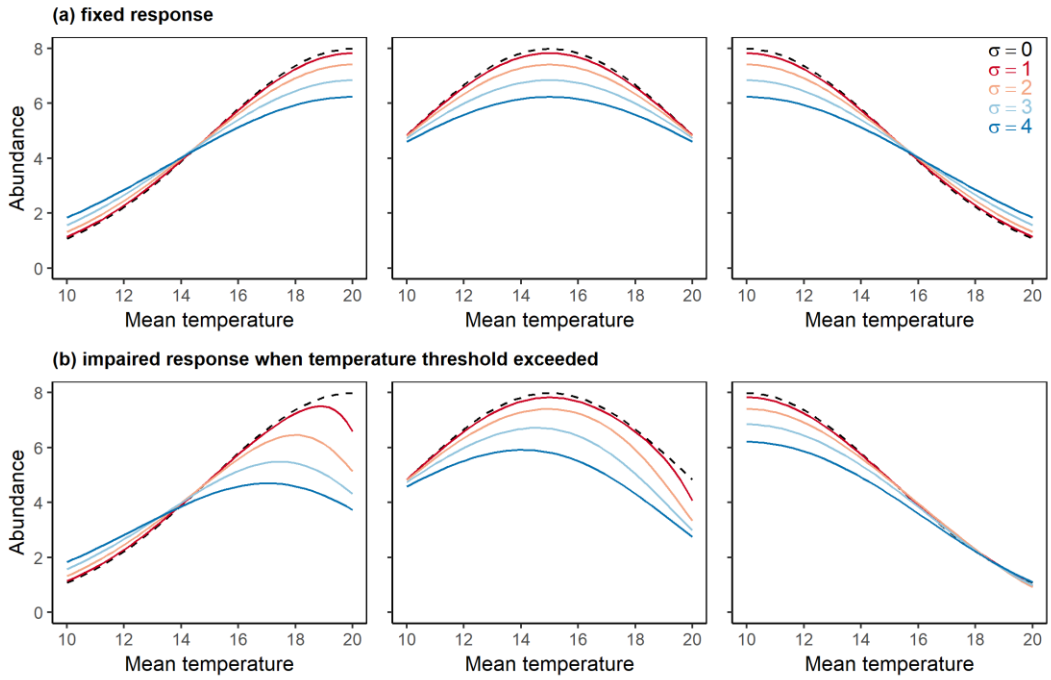

Figure 1 Two hypothetical examples of how varying thermal regime (normally distributed, with changing mean and SD, σ) alters population response when (a) there is a shared thermal performance curve (TPC) that is not modified by factors discussed in text, and (b) when there is a threshold-temperature (at 21 °C), which, if exceeded, results in population extirpation. In this latter model, the population response now partially depends on whether an event that exceeds this temperature threshold occurs, and the population response is therefore not captured by simply averaging over the response curve observed when σ=0. This varying response drives the discrepancy between upper and lower panels (see Appendix for full details). The black dashed lines indicate population response when SD is 0.

4.3 Methods

4.3.1 Datasets

Daily temperature data were extracted from the UKCP09 dataset, a 5-km resolution gridded dataset of interpolated daily temperatures since 1950 (Perry & Hollis 2005). Daily temperature data for butterfly monitoring sites were extracted and, for each year, monthly temperature means (Mean ˚C) and standard deviations of each month (SD ˚C) were calculated. Site elevations were calculated from the Shuttle Radar Topography Mission dataset (SRTM; 1-Arc second, ~30m resolution; Farr *et al.* 2007) by averaging across cells falling within a 50 metre buffer of site coordinates.

Butterfly population data were obtained from the UK Butterfly Monitoring Scheme (UKBMS; Pollard & Yates 1993), and, for each species, annual site-level abundance indices were generated using the methods outlined in Dennis *et al.* (2013). Briefly, throughout spring and summer, each site is visited weekly and butterflies are counted using a standardised Pollard-walk methodology. Butterfly abundance varies markedly over the course of the season, characterised by a flight-curve; for species with just a single generation per year (univoltine) there is a single flight curve, while for species with multiple generations per year (multivoltine) there are multiple flight curves. The index of abundance is a measure of the area under the flight curve(s), and therefore corresponds to a single generation in the case of univoltine species, or is the abundance aggregated across multiple generations in multivoltine species. In principle the status of a species (univoltine or multivoltine) should not matter for the question we address here. However, we do later plot coefficient estimates for univoltine and multivoltine species to assess whether there are systematic differences between the two.

For each species, sites with fewer than 10 data points (i.e. a count in year t and year t+1, at least one of which is non-0) were removed prior to analysis, and, following this, species with fewer than 50 sites (and therefore at least 500 datapoints) were removed, as were 3 species that are long-distance immigrants to the UK (Red Admiral, *Vanessa atalanta*, Clouded Yellow, *Colias croceus*, and Painted Lady, *Vanessa cardui*), to leave 32 species. Retained sites have a spatial distribution given in Figure 2 (for individual species plots see Figure S1), and a temporal coverage from 1974-2016 (the number of data points, number of sites, year range of modelled data and species' scientific names are given in Table S1).

Figure 2 Distribution of sites contributing to analyses (for site distributions of individual species see Figure S2).

4.3.2 Identifying focal time periods for temperature effects

For each individual species, we first identified periods for which temperature was most strongly associated with population growth. Temperature can be involved in regulating population growth across multiple stages of the life-cycle (Roy *et al.* 2001; Mills *et al.* 2017). Here, rather than attempting to characterise the full set of temperature drivers of population growth, to address our key questions we identified a single period for each species in which temperature is most strongly associated with population growth. We opted to focus on monthly temperature variables which is a frequently-used temporal resolution within which to assess weather impacts on population change (e.g. Roy *et al.* 2001; Pearce-Higgins *et al.* 2015; Fenberg *et al.* 2016; Dennis *et al.* 2017), often under the implicit-assumption that population responses will be similar at finer temporal resolutions. To identify focal weather variables for each individual species, we constructed a series of models that each contain just a single monthly temperature variable (formula 1);

$$rgr \sim \log(N[t-1]) + Mean[i] + (1|siteID) + error \qquad (1)$$

Where *rgr* is the relative growth rate, *log(N[t]) – log(N[t-1]),* Mean[i] is the ith monthly mean temperature variable, drawn from months between January in year t and August in year t+1. The model also contains a randomly varying site intercept, (1|siteID), as well as a lag-1 density term to control for non-independence of counts in consecutive years (i.e. arising through a density-dependent response).

For each species, the models for different temperature periods were then ranked according to their Watanabe-Akaike Information Criterion score (WAIC; Gelman *et al.* 2014). WAIC acts similarly to AIC (and any other information criterion), by indirectly trying to measure the out-of-sample predictive accuracy of a model, by measuring the improvement in predictive accuracy while penalising for the effective number of parameters in a model. It is however fully Bayesian, because it is estimated with a posterior density in addition to the point-estimate, which is useful for model comparison as it captures posterior uncertainty (unlike AIC or DIC). WAIC is implemented in R, using the *loo* package (Vehtari *et al.* 2016); for further details see (Gelman *et al.* 2014a; Vehtari *et al.* 2016). For each species, the month whose statistical model had the lowest WAIC score was selected and this was then used in subsequent modelling. Each species' selected coefficient is displayed alongside species names in all figures and also given in Table 1.

4.3.3 Assessing contribution of standard deviation terms to model performance

The additional contribution of standard deviation terms was assessed through the change in WAIC (ΔWAIC) resulting from the addition of standard deviation as both a main effect (i.e. intercept) and an interaction with mean monthly temperature (formulas 2 and 3 respectively). We consider both interactions and main effects of SD, as the effects of variation could plausibly be represented in either of these terms (see Figure 1). Negative ΔWAIC values indicate that the inclusion of SD terms increase the predictive capacity of the model, and, as a Bayesian statistic, we can calculate the proportion of the ΔWAIC posterior that is >0. This proportion is the probability that the inclusion of SD-terms only spuriously improve model predictive capacity. To give an example, a value of 0.1 would indicate that 10% of the posterior was positive, or the model assigns a 10% probability to the inclusion of standard deviation terms worsening model performance (McElreath 2016).

rgr ~ log(N[t-1]) + Mean[s] + (1|siteID) + error (2)

rgr ~ log(N[t-1]) + Mean[s] + SD[s] + Mean[s]* SD[s] + (1|siteID) + error (3)

Where Mean[s] and SD[s] are the model-selected monthly temperature variables from the previous step. We also fitted an additional set of models that included Northing and Easting (British National Grid datum; BNG), site elevation, and interactions between these and mean temperature effects, (i.e. ... + Easting +Northing + site elevation + Easting:mean + Northing:mean + elevation:mean), to ward against potential confounding associations with any of these 'nuisance' variables. We present these results alongside the models that do not contain these terms.

Across all models, coefficients were supplied with either flat or diffuse priors that provide negligible prior information to the model. Specifically, fixed effect coefficients have uniform priors across all real numbers, while site random intercepts have students t-distribution centred at 0 with 3 degrees of freedom and a standard deviation of 10. As models are expressed as log-growth rate, and a site has at least 10 years of data, site-level intercepts can in reality only take substantially smaller values than implied by this prior, so this prior is non-informative in the context of these models. All models were run across 4 chains for 10000 iterations, with the first 5000 discarded as the burn-in period, and convergence was checked using R-hat diagnostics.

4.3.4 Assessing performance of a daily-temperature model

Following the above procedure, we assessed whether any improvements in model explanatory capacity, generated by the addition of SD terms, could be explained by a model in which the realised population response arises through the simple accumulation of effects of shorter-term exposure events, i.e. as would occur under Jensen's inequality.

A model using monthly temperature is given in formula 2. To model daily temperatures, rather than the monthly average, we use the daily temperatures extracted from the UKCP09 dataset directly, incorporating them as:

$$\mathrm{rgr} \sim \log(\mathrm{N}[\mathrm{t}-1]) + \frac{1}{\mathrm{N}}\sum_{i=1}^{N} f(T_i) + (1|\mathrm{siteID}) + \mathrm{error} \qquad (4)$$

Where $f(T_i)$ describes the response to the i-th daily temperature, and it is the average of these daily responses that describes the overall population response. This is thus equivalent to the formulations described in Vasseur *et al.* (2014), but is summing across empirical exposures rather than integrating across a continuous density function. We opted to treat the functional form as $f(T_i) = b_1 * T_i + b_2 * T_i^2$, i.e. quadratic. Using this, formula 4 can be simplified to:

$$\mathrm{rgr} \sim \log(\mathrm{N}[\mathrm{t}-1]) + \mathrm{b}_1\overline{T} + b_2\overline{T^2} + (1|\mathrm{siteID}) + \mathrm{error}\ (5)$$

Where $\overline{T}$ is the mean of daily temperatures and $\overline{T^2}$ is the mean of squared daily temperatures (note the distinction between this and the square of mean daily temperature).

When b_2 is < 0, on the un-logged scale (i.e. N_t) this temperature response function corresponds to a symmetrical bell-shaped curve. As values of $b_2 > 0$ can readily generate biologically implausible shapes (it is difficult to find a theoretical justification for climatic associations that are not either monotonic or unimodal; Austin 2002), we constrain these values to be negative by placing an upper bound of 0 on the prior distribution of this variable (thus constraining b_2 to be less than 0).

All analyses were all carried out in the R programming environment (version 3.4.4) and all code is available at github.com/SimonCMills/mean-variance. Models were implemented in *Stan* (version 2.17.0) via *rstan* (Carpenter *et al.* 2017) and *brms* (Bürkner 2017).

4.4 Results

Including standard deviation terms (both as an interaction with mean temperature and as a main effect) improved the predictive capacity of models across the vast majority of species, with 25 out of 32 species having ΔWAIC<0 in both models that controlled for additional covariates and those that did not (Figure 3). The magnitude of improvement varied substantially across species, and in many cases the model improvement was quite minor, such that only 17 of 32 (53%) of species had less than 5% of the ΔWAIC posterior >0 (for both corrected and uncorrected models; i.e. indicating that SD term inclusion significantly improved model performance). For the remaining 15 species, where the ΔWAIC posterior substantially overlaps 0, the inclusion of SD terms did little to improve model predictive capacity and there was relatively little to distinguish the predictive capacity of this model from that of the more parsimonious model that contains just the average monthly temperature.

The specific coefficient estimates for SD-terms were quite variable across species, with SD effects reflected in both the intercept- and interaction-terms (Table 1 and Table S2). There was no clear pattern to the values that the individual coefficient estimates take, with no clear covariation between coefficient estimates and voltinism, mean-temperature effect, or the timing of the focal period (spring, summer, autumn, or winter; Figure S4). Further, coefficient estimates for both the main SD effect and the mean:SD interaction are clustered around zero, with no general tendency towards being positive or negative.

The biological significance of including SD effects can however be quite substantial. For example, in small tortoiseshell *Aglais urticacae*, inter-annual population growth is considerably sensitive to variation in SD, and variation in the width of the thermal distribution can drive substantial variation around the mean-only predicted growth rates (comparison between points and black line). For two populations experiencing an identical mean temperature (e.g. 0, centred scale), one could be experiencing a substantial decline (predicted growth rate = 0.75) while the other could be experiencing a substantial increase in population size (predicted growth rate > 1.25), depending on the SD-value for that month (Figure 4). For a species with more moderate model improvement from SD-terms, such as small heath, *Coenonympha pamphilus*, or small skipper, *Thymelicus sylvestris,* these effects are less pronounced, but the predicted growth rate can still vary markedly across the range of SDs (Figure 4). By contrast, for a species' model that is not substantially improved by addition of SD terms, like the dingy skipper, *Erynnnis tages*, there is little variation in inter-annual population growth that is not captured by the monthly mean alone (Figure 4). Looking across all species (Figure S3), there is relatively little in the way of consistent pattern, with some species showing enhanced sensitivity to temperature with increasing SD, while some display the opposite pattern of association.

Daily temperature models in which the population response is an average across individual daily exposures varied in their ability to explain population growth relative to other models (Figure 5), but overall tended to do less well than the phenomenological model with monthly mean and SD terms. For 15 species, neither the daily temperature model nor the mean and SD model significantly outperformed a mean-only model. Of the remaining 17 species that mean and SD models significantly improved on mean-only models, just 7 of these also had daily temperature models that were significantly better than mean-only models (Figure 5). Thus, overall, daily temperature models typically performed less well than models containing monthly mean and SD terms. Given the types of functional form observed in Figure S3, it is not overly surprising that these models do not perform well, due to the diversity of responses observed across species, and the fact that many of them would not obviously be explicable with a log-quadratic functional form. We did not explore more complex functional forms beyond the quadratic model, and it is therefore important to note that more complex forms may better explain variation in abundance.

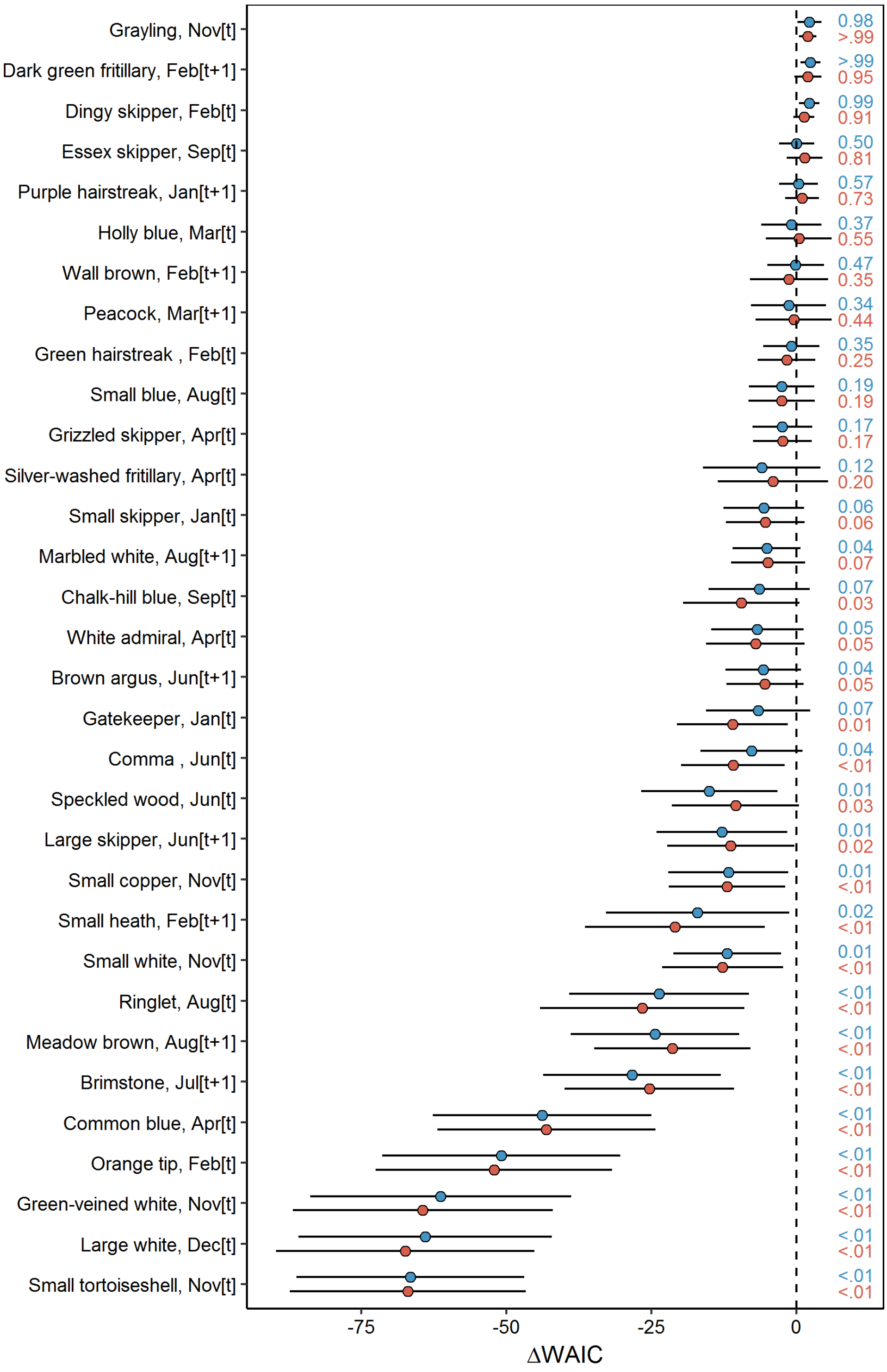

Figure 3 ΔWAIC scores for each species (Point-estimates and 95% credible interval), for comparison between a model that contains no SD terms and the model that contains SD terms. Negative values indicate model improvement, and the numbers on the right hand side indicate the proportion of the ΔWAIC posterior density > 0. Red points and text indicate models that do not control for Easting, Northing, and elevation, while blue indicate those that do. The temporal period of each species' focal weather variable is given alongside each species'

name, indicating the month, and whether this falls in year *t* (the year of the first count) or year *t+1* (the year of the second count).

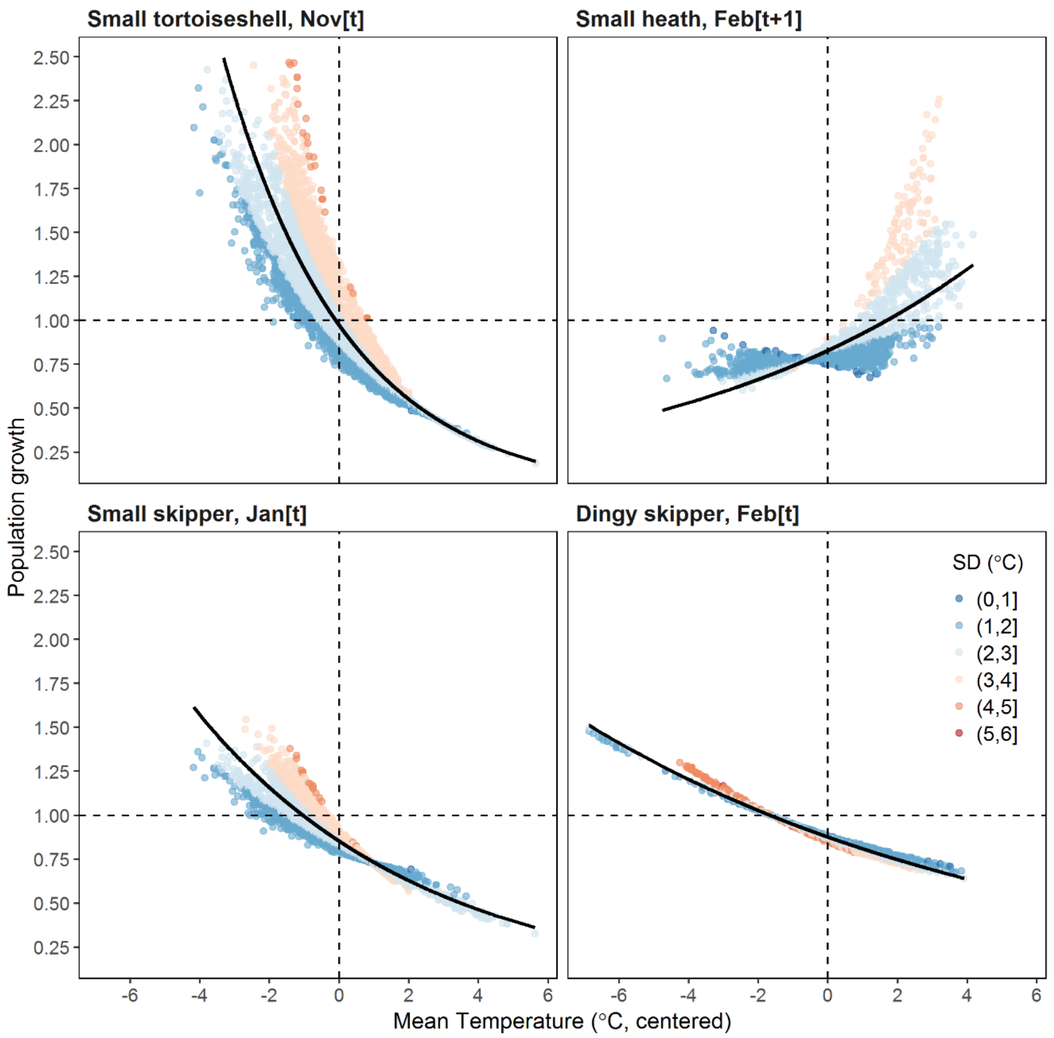

Figure 4 Predicted population growth rates with varying mean temperature and standard deviation of temperature for four selected butterfly species. Growth rates are measured as N[t+1]/N[t] when N[t] is fixed at each species' median abundance (across entire dataset), with a value of 1 indicating no population change. The overlaid black line is the predicted growth rate in a model that contains only the mean temperature effect (centred at 0) and does not contain SD terms. Each point is the model-predicted growth at an observed monthly mean, coloured by the standard deviation of temperature in that month (colours are discretised purely for visualisation purposes, but were modelled continuously). The four species are selected to show a range from one for which SD most improved model performance (small tortoiseshell),

through to a species for which SD-terms did not improve model performance (dingy skipper; Figure 3). The full set of species plots (n=32) are given in Figure S2.

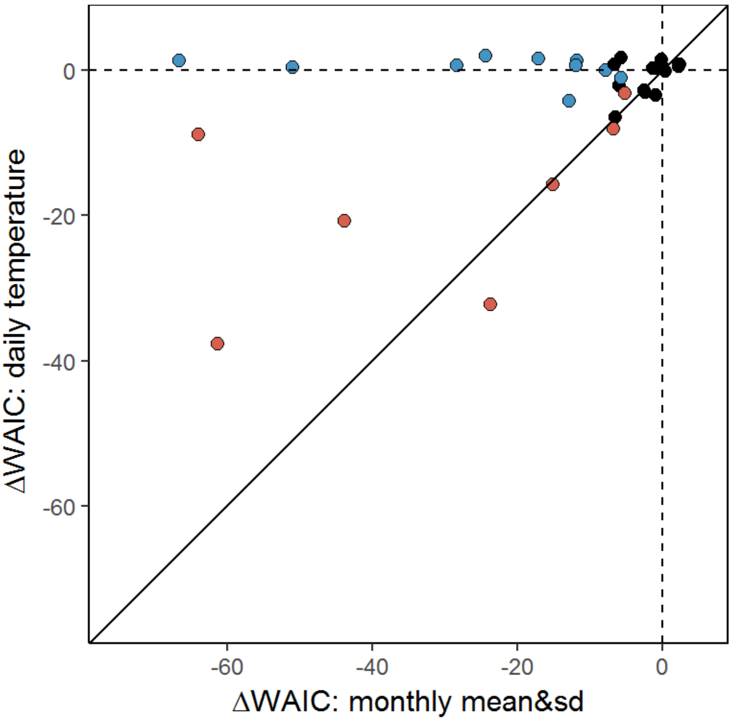

Figure 5 ΔWAIC scores for each species and modelling approach (y axis: daily temperature model; x-axis monthly mean&sd model that includes SD as both a main effect and interaction term). Values in the bottom left quadrant (i.e. ΔWAIC: daily temperature or ΔWAIC: monthly mean&sd are <0) are species for which either the daily temperature model or the phenomenological model containing SD terms had better model predictive power relative to a model that contains a mean temperature variable only. Points that are in the bottom left quadrant, but are above the 1:1 line, show less model improvement in the daily temperature model than in phenomenological model. Conversely, points that are in the bottom left quadrant, but are below the 1:1 line indicate species in which the daily temperature model performance was better than the phenomenological model performance. Point colour indicates degree of model improvement (relative to the mean-only model). Black indicates that neither the daily temperature nor the phenomenological model is significantly better than the mean-only model ("significantly better" defined as <5% of the posterior >0). Blue indicates that just mean&SD models were substantially better than mean-only models, while red indicates that both sets of models were significantly better than mean-only models. The fact that most points are above the 1:1 line, and there are a lot of blue-shaded points is due to daily temperature models tending to perform less well

than the phenomenological models. Figure S3 displays ΔWAIC scores for daily temperature models in the same format as in Figure 3

.

Table 1 Coefficients for temperature terms and summary statistics for models predicting population growth rate containing Mean monthly temperature, SD of monthly temperature and the interaction between the two. The 95% credible intervals for model coefficients are in parentheses, and bold font indicates where these do not overlap 0. Mean and SD variables are both centred, and coefficient values for the main effects can therefore be interpreted as the effect when the other variable is at its mean. Species are ordered according to ΔWAIC score. Note, models were also fitted with additional control variables relating to position in geographic range, and summary statistics for these can be found in Table S2

Species	**Month**	**Mean °C**	**SD °C**	**Mean °C:SD °C**	**R^2**	**pWAIC**	**ΔWAIC**	**RMSE**
1. Small tortoiseshell, *Aglais urticae*	Nov[t]	**-0.28 (-0.31, -0.26)**	**0.22 (0.18, 0.27)**	**-0.08 (-0.12, -0.04)**	0.39	-66.6	<.01	1.16
2. Large white, *Pieris brassicae*	Dec[t]	**-0.19 (-0.21, -0.17)**	**-0.20 (-0.24, -0.17)**	**0.05 (0.02, 0.09)**	0.46	-64	<.01	1.04
3. Green-veined white, *Pieris napi*	Nov[t]	**-0.14 (-0.16, -0.11)**	**-0.19 (-0.22, -0.15)**	-0.01 (-0.04, 0.02)	0.39	-61.3	<.01	0.94
4. Orange tip, *Anthocaris cardamines*	Feb[t]	**-0.06 (-0.08, -0.05)**	**-0.16 (-0.19, -0.12)**	**-0.02 (-0.04, -0.01)**	0.41	-50.9	<.01	0.91
5. Common blue, *Polyommatus icarus*	Apr[t]	**0.30 (0.27, 0.32)**	**-0.07 (-0.14, -0.01)**	**-0.20 (-0.24, -0.16)**	0.42	-43.8	<.01	1.10
6. Brimstone, *Gonepteryx rhamni*	Jul[t+1]	**0.08 (0.06, 0.09)**	**0.15 (0.10, 0.19)**	**-0.05 (-0.08, -0.02)**	0.37	-28.3	<.01	0.78
7. Meadow brown, *Maniola jurtina*	Aug[t+1]	**0.07 (0.06, 0.08)**	**0.05 (0.03, 0.08)**	**0.05 (0.03, 0.06)**	0.27	-24.4	<.01	0.61
8. Ringlet, *Aphantopus hyperantus*	Aug[t]	**-0.04 (-0.06, -0.02)**	**-0.10 (-0.16, -0.04)**	**-0.05 (-0.08, -0.02)**	0.25	-23.7	<.01	0.85
9. Small white, *Pieris rapae*	Nov[t]	**0.17 (0.15, 0.19)**	0.00 (-0.05, 0.06)	**0.06 (0.03, 0.09)**	0.45	-12	0.01	1.06
10. Small heath, *Coenonympha pamphilus*	Feb[t+1]	**0.06 (0.04, 0.09)**	**0.08 (0.00, 0.15)**	**0.12 (0.08, 0.16)**	0.17	-17.1	0.02	0.89
11. Small copper, *Lycaena phlaeas*	Nov[t]	**0.14 (0.12, 0.17)**	**0.08 (0.02, 0.15)**	**0.06 (0.02, 0.09)**	0.39	-11.7	0.01	1.05
12. Large skipper, *Ochlodes venata*	Jun[t+1]	**-0.13 (-0.15, -0.11)**	0.02 (-0.02, 0.06)	**-0.08 (-0.12, -0.05)**	0.30	-12.9	0.01	0.94
13. Speckled wood, *Pararge aegeria*	Jun[t]	**-0.09 (-0.10, -0.07)**	-0.02 (-0.05, 0.01)	**0.03 (0.02, 0.05)**	0.27	-15.1	0.01	0.70
14. Comma , *Polygonum c-album*	Jun[t]	**0.09 (0.08, 0.11)**	**-0.07 (-0.11, -0.04)**	-0.02 (-0.03, 0.00)	0.41	-7.8	0.04	0.92
15. Gatekeeper, *Pyronia tithonus*	Jan[t]	**0.08 (0.07, 0.09)**	**-0.06 (-0.09, -0.03)**	**-0.02 (-0.04, -0.01)**	0.23	-6.6	0.07	0.73
16. Brown argus, *Aricia agestis*	Jun[t+1]	**0.24 (0.20, 0.27)**	**-0.16 (-0.25, -0.06)**	-0.01 (-0.07, 0.06)	0.41	-5.7	0.04	1.14

17. White admiral, *Limenitis camilla*	Apr[t]	**-0.11 (-0.13, -0.08)**	**-0.10 (-0.16, -0.05)**	-0.00 (-0.03, 0.03)	0.33	-6.8	0.05	0.91
18. Chalk-hill blue, *Polyommatus coridon*	Sep[t]	**0.22 (0.18, 0.26)**	**-0.21 (-0.34, -0.09)**	**-0.17 (-0.25, -0.09)**	0.23	-6.4	0.07	0.93
19. Marbled white, *Melanargia galathea*	Aug[t+1]	**0.13 (0.11, 0.15)**	**-0.10 (-0.17, -0.03)**	-0.03 (-0.08, 0.01)	0.19	-5.2	0.04	0.82
20. Small skipper, *Thymelicus sylvestris*	Jan[t]	**-0.16 (-0.19, -0.13)**	**0.07 (0.01, 0.12)**	**-0.07 (-0.12, -0.02)**	0.24	-5.7	0.06	1.18
21. Silver-washed fritillary, *Argynnis paphia*	Apr[t]	**0.22 (0.19, 0.25)**	-0.08 (-0.18, 0.02)	**-0.15 (-0.22, -0.09)**	0.30	-6	0.12	0.85
22. Grizzled skipper, *Pyrgus malvae*	Apr[t]	**-0.13 (-0.16, -0.09)**	**-0.09 (-0.17, -0.02)**	0.03 (-0.04, 0.09)	0.34	-2.5	0.17	0.93
23. Small blue, *Cupido minimus*	Aug[t]	**-0.16 (-0.21, -0.11)**	**-0.18 (-0.31, -0.05)**	-0.03 (-0.10, 0.04)	0.27	-2.6	0.19	1.09
24. Green hairstreak , *Callophrys rubi*	Feb[t]	**-0.13 (-0.17, -0.10)**	0.02 (-0.05, 0.09)	**-0.07 (-0.13, -0.01)**	0.41	-0.9	0.35	1.00
25. Peacock, *Inachis io*	Mar[t+1]	**-0.18 (-0.20, -0.16)**	**0.04 (0.01, 0.07)**	**-0.04 (-0.07, -0.01)**	0.35	-1.4	0.34	0.81
26. Wall brown, *Lasiommata megara*	Feb[t+1]	**-0.17 (-0.21, -0.13)**	**-0.15 (-0.26, -0.04)**	-0.00 (-0.08, 0.07)	0.22	-0.2	0.47	0.99
27. Holly blue, *Celastrina argiolus*	Mar[t]	**0.21 (0.18, 0.24)**	0.02 (-0.06, 0.09)	0.04 (0.00, 0.08)	0.46	-0.9	0.37	1.20
28. Purple hairstreak, *Neozephyrus quercus*	Jan[t+1]	**0.06 (0.02, 0.11)**	0.05 (-0.07, 0.17)	0.03 (-0.03, 0.10)	0.40	0.3	0.57	1.10
29. Essex skipper, *Thymelicus lineola*	Sep[t]	**-0.14 (-0.21, -0.07)**	-0.06 (-0.18, 0.06)	0.04 (-0.06, 0.13)	0.30	0	0.50	1.29
30. Dingy skipper, *Erynnnis tages*	Feb[t]	**-0.08 (-0.10, -0.06)**	-0.02 (-0.07, 0.04)	-0.01 (-0.04, 0.02)	0.33	2.2	0.99	0.95
31. Dark green fritillary, *Argynnis aglaja*	Feb[t+1]	**-0.13 (-0.18, -0.09)**	0.03 (-0.05, 0.11)	-0.01 (-0.08, 0.06)	0.25	2.4	>.99	0.98
32. Grayling, *Hipparchia semele*	Nov[t]	**-0.11 (-0.17, -0.05)**	-0.06 (-0.25, 0.12)	-0.06 (-0.18, 0.06)	0.23	2.2	0.98	0.94

4.5 Discussion

We find that the predictive capacity of population growth rate models is enhanced when they include information on the range of thermal conditions that a population is exposed to (the standard deviation of daily temperatures). Models that include thermal standard deviations can vary substantially in the predictions that they make, compared to those that contain monthly mean temperature only, improving our ability to explain observed variation in population growth. Interestingly, however, a daily temperature model in which the effects of thermal variation arise through the simple accumulation of exposures on individual days within a given month performed much more poorly, and tended to be limited in their capacity to explain population growth. This discrepancy between the two modelling approaches suggests that the link between temperature variation over short time-scales and change in abundance may be complex and requires further work to characterise. Overall, these findings suggest that models of population growth that do not consider thermal variation acting at fine temporal scales may often overlook biologically relevant effects, and fit into a growing body of work that highlights the limitations of using coarse climatic averages to understand population change (McInerny & Purves 2011; Maclean *et al.* 2016; Suggitt *et al.* 2018), and the importance of more fully characterising the exposures that a population directly experiences (Sunday *et al.* 2014; Vasseur *et al.* 2014).

While our results suggest that fine-scale thermal variation occurring at sub-monthly intervals can be important to consider, it is not clear how fine-scale the temporal-resolution needs to be before there are no further improvements in model performance. Our thermal distributions were parameterised using daily temperature means, but these themselves average across even finer-scale variation in temperature. Thermal events that occur hourly or even sub-hourly intervals may play a role in determining organism performance (Scheffers *et al.* 2014), and it is thus plausible that there is fine-scale thermal variability that is relevant to population performance but is not captured by our models. Additionally, while our approach was to calculate standard deviations of daily temperatures occurring within each month in order to broadly quantify the width of the thermal distribution, these do not quantify other variation in distribution that might occur, such as skew. These other measures of the thermal distribution can also alter the response function (Vasseur *et al.* 2014), and it is therefore possible that our results here overlook further subtleties in the effect that the full thermal regime has on population growth.

Given that thermal variation at sub-monthly intervals appears important, a natural question is: why not model daily temperatures directly? Our results suggest that we should be considering thermal variation that occurs at these time-scales, but also that it is not clear how daily temperature exposures accumulate to drive variation in population change. We observe both a diversity of SD associations, with the effects of standard deviation variables being reflected in both main effects and interaction terms across different species, with the direction of these effects showing further substantial variation across species. This variety of response suggests that any single functional form may be limited in its capacity to explain all of them.

It is particularly intriguing that in some cases the daily temperature model in which the overall population response is simply the average across daily exposure events does a reasonable job of explaining population growth in some species, but performs worse (sometime very poorly) in most species. Given the simplicity of this model- which assumes that the TPC is symmetrical, it is not entirely surprising, as this functional form does not have the flexibility to capture the majority of observed responses. Averaging across a quadratic-type TPC could cause the intercept-term to vary, but could not generate interaction effects between the mean and standard deviation (see Figure 4, Lawson *et al.* 2015). However, the effects of standard deviation are, for many species, reflected in the interaction-terms. For a daily-temperature model to generate this form of association, we would need to consider a more complex functional form, specifically one in which the second derivative is not constant.

Perhaps more importantly than these questions about the shape of the TPC, the limited performance of the empirical model suggests that the TPC itself may vary within a species. Such intraspecific variation would not be captured by any model that assumes a fixed TPC and this is therefore a likely cause of the results we observe here.

The question is what factors might cause the TPC to alter? One potential mechanism is that the TPC is modified by the availability of microclimates, which can act to modify the temperatures that a population is directly exposed to. Both topography and habitat can alter temperatures at fine spatial scales, and can generate substantial microclimatic heterogeneity within a small radius of a site (Suggitt *et al.* 2011; Maclean *et al.* 2016). If there is a wide availability of microclimates, populations are likely to be buffered from climatic effects as they can minimise exposure to sub-optimal conditions by preferentially selecting for microclimates that maximise performance (Kearney *et al.* 2009). As a consequence, the thermal response of a population is likely to vary depending upon the availability of microclimates (Oliver *et al.* 2015). A recent analysis of UK Lepidoptera finds substantial reduction in extinction risk when the availability of local thermal microhabitats is considered (Suggitt *et al.* 2018). However, these results could arise either due to a subset of populations being able to persist in sub-regions of a coarse grid-cell, or through locally-acting buffering effects that allow populations to persist in situ. The latter is a particularly interesting prospect as it suggests a strong role for local features to adjust exposure and thus modify long-term persistence in the face of climate change. Extending the models that we apply here to consider interactions with landscape variables would enable an assessment of the importance of local factors in modifying thermal response and would thus be an interesting next step.

Finally, it is important to note that there are a number of aspects of thermal regime that we do not consider, but that are likely to be important for population regulation. Most obviously, both the duration of exposure and sequence of exposure events can alter how organisms respond to thermal conditions (Sinclair *et al.* 2016). From *in vivo* studies of organism performance, it is well understood that duration of exposure dramatically modifies the effects of temperature on organisms, and temperatures that are tolerable in the short-term can be lethal over longer time-frames (Rezende *et al.* 2014). This can occur both through a simple physiological response, and also due to chronic impairment of organism function, for example, as might occur over multiple days of poor weather which prevent foraging or other functions necessary to survival

(Robinson *et al.* 2007). Similarly, the sequence of events may modify response, for example as occurs through acclimation or acclimatisation to thermal conditions (Dowd *et al.* 2015). Both of these mechanisms amount to there being non-independence between individual exposure events with the response to the current thermal challenge depending upon the history of prior exposures. While these complexities represent difficult modelling challenges (Sinclair *et al.* 2016), the apparent importance of thermal variation in temperature at fine-temporal scales suggests that these also represent important avenues of exploration.

Here we find that variation in temperature at fine-temporal scales is relevant to understanding inter-annual population growth rate. Theoretically such effects are well understood, but, to date, have had relatively little empirical demonstration (though see Paaijmans *et al.* 2010) and, to our knowledge, have not been documented in butterflies previously. Our results identify a role for both variation in temperature as well as the upper and lower extremes of the thermal distribution in regulating populations (McDermott Long *et al.* 2016), both of which are increasingly the focus of research efforts (Thompson *et al.* 2013). While developing a stronger understanding of the mechanisms that drive these responses is an important next step, our results show that even relatively simple additions to the model structure, such as including SD-interactions can substantially enhance the predictive capacity of models.

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4.7 Appendix

Abundance (or fitness) varies across a thermal gradient according to the Gaussian function, *g(T; optimum, scale)*, multiplied by a constant (=100) . Across all panels in Figure 1, the scale of the response function is set to 5, with the optimum moving from 20, to 15, to 10, moving from left to right. If the realised abundance response, $\bar{g}$, is just the average across the abundance response at shorter time-scales, then abundance varies according to:

$$\bar{g}(\mu, \sigma) = \int g(T) \times pdf(T, \mu, \sigma)$$

Where $pdf(T, \mu, \sigma)$ is the probability of observing a particular temperature, given μ and σ. Assuming that temperatures are normally distributed, the realised temperature response changes with varying mean μ and standard deviation σ according to the curves displayed in Figure 1a.

Alternatively however, if $g(T)$ itself varies across different thermal regimes, i.e. as μ and/or σ change so does *g*, then this link between response to finer-temporal scale thermal events and the overall realised response no longer applies. This might occur in a number of ways, for example, due to physiological adaptation such as hardening, sequence of thermal events, duration of exposure, or if an extreme exposure results in widespread mortality or otherwise impaired population function. These all have the effect of altering the TPC, such that the above equality no longer correctly characterises the realised population response.

The specific example that we use (in Figure 1b) is when an extreme exposure causes local extirpation, such that the TPC outside of this extreme exposure no longer applies (as there is not a population there to experience it). In this case, the expected abundance response, $\bar{g}$, is a mixture of populations that were exposed and thus extirpated, and populations that were not exposed and thus the TPC still applies. The relative proportions of these two components depends on the probability of exposure, with overall response being the sum of $g_1(T) \times p_{exposure}$ and $g_2(T) \times (1 - p_{exposure})$. As $g_1(T)$ is simply 0 (as the population no longer exists), and $g_2(T)$ is identical to $g(T)$ this simplifies to:

$$\bar{g}(\mu,\sigma) = \int g(T) \times (1 - p_{exposure}(\mu,\sigma)) \times pdf(T,\mu,\sigma)$$

Now the realised population response diminishes with increasing probability of an extirpation event occurring. For the purposes of illustrating these changes we use an exposure threshold of 21°C, so that it lies slightly beyond the range of temperatures that a population reared at $\sigma = 0$ experiences. The inclusion of this extirpation threshold drives the differences between panels (a) and (b) in Figure 1. For the code used to implement this, see: https://github.com/SimonCMills/mean-variance/tree/master/scripts.

4.8 Supplementary material

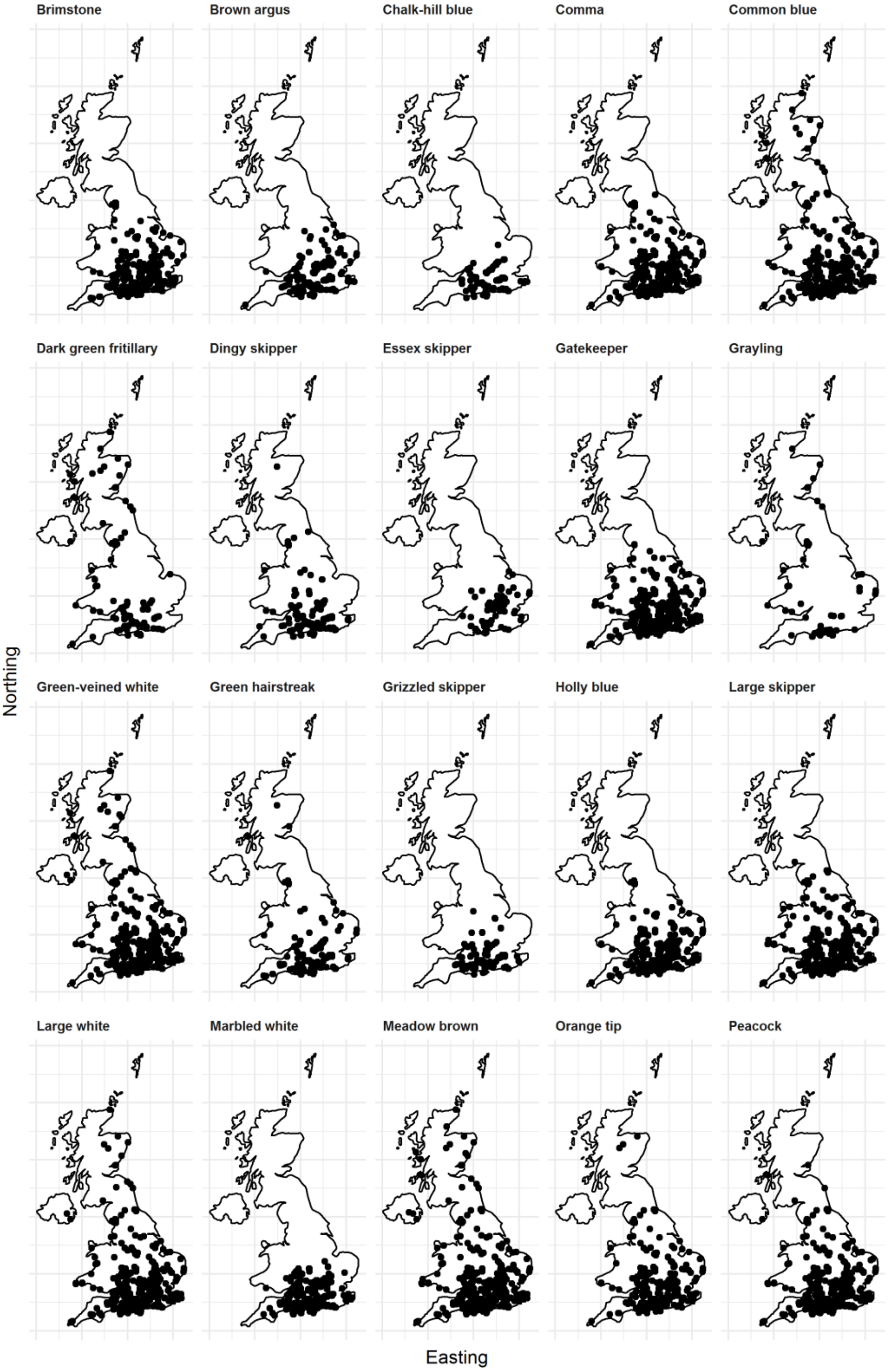

Figure S1 Continued overleaf.

Figure S1 Retained sites for individual species.

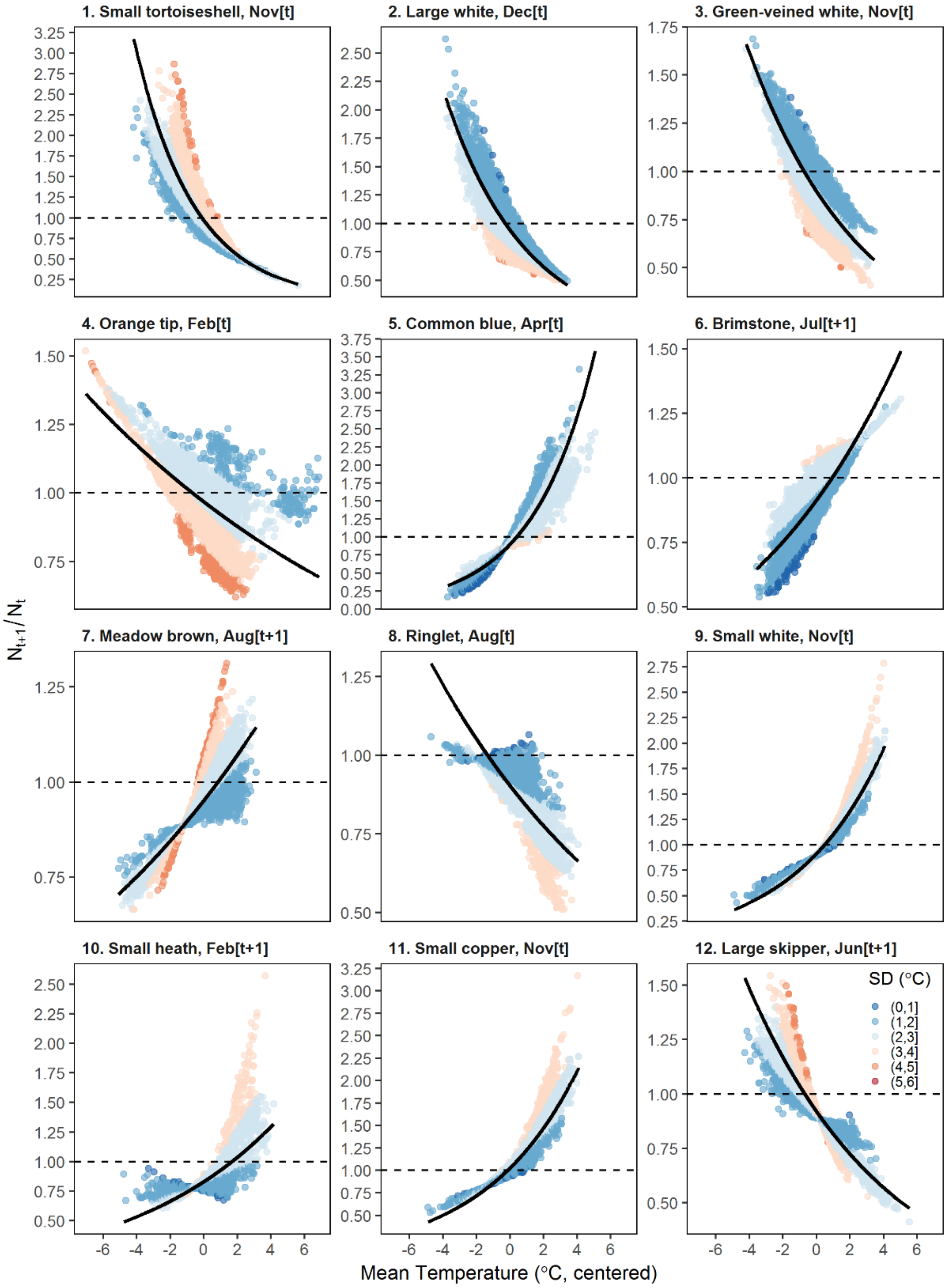

Figure S2 continued overleaf

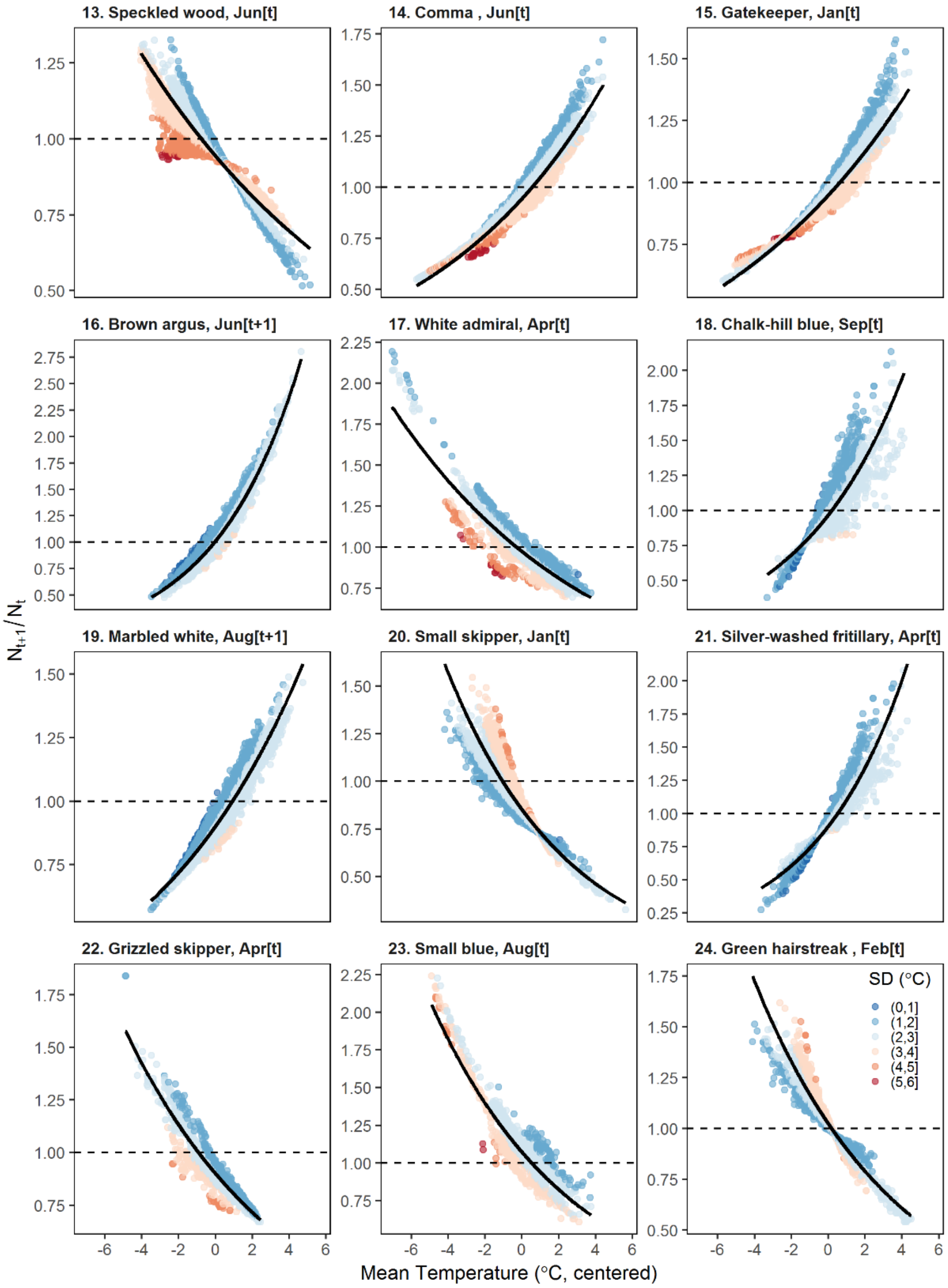

Figure S2 continued overleaf

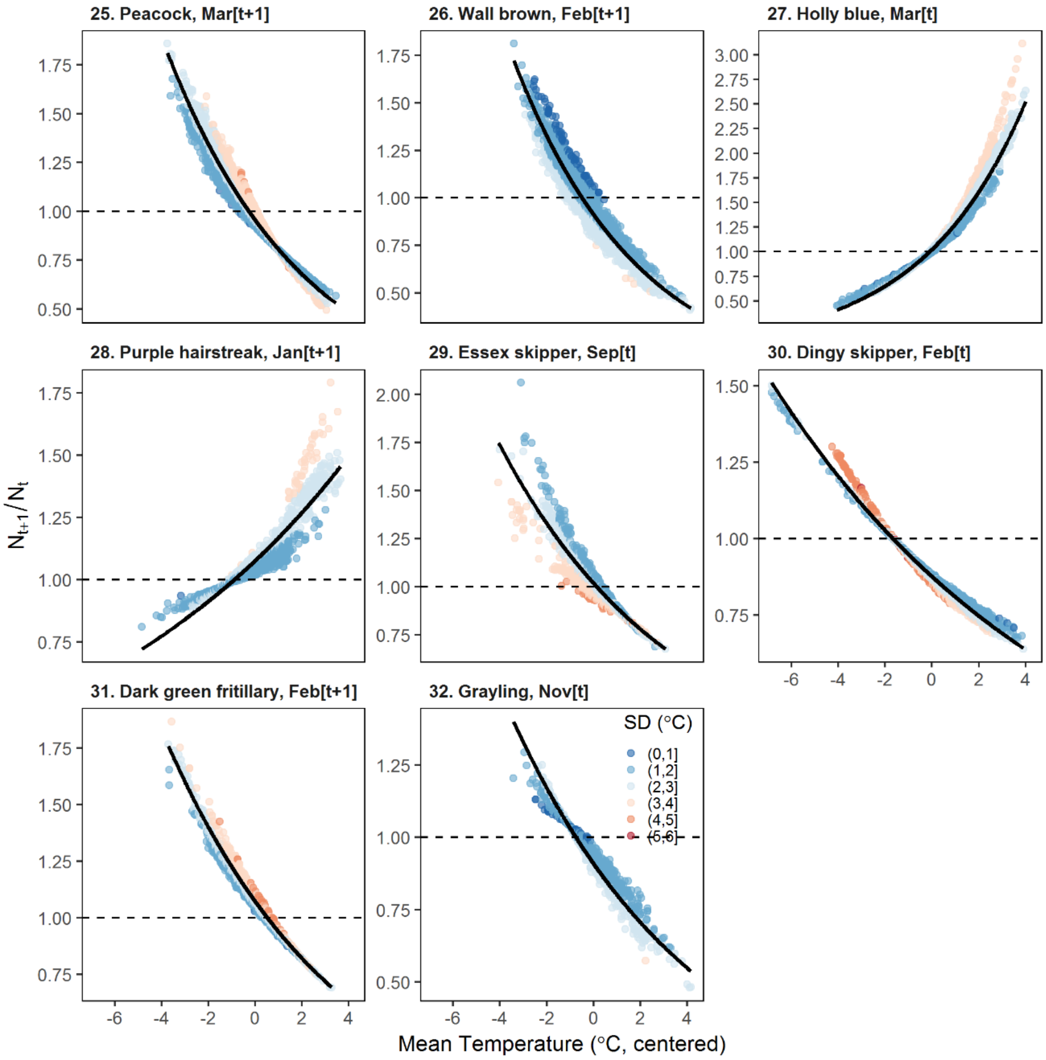

Figure S2 Predicted population growth rates with varying mean temperature and standard deviation of temperature for all species. Growth rates are measured as N[t+1]/N[t] when N[t] is fixed at each species' median abundance (across entire dataset), with a value of 1 indicating no population change. The overlaid black line is the predicted growth rate in a model that contains only the mean temperature effect (centered at 0) and does not contain SD terms. Each point is the model-predicted growth at an observed monthly mean, coloured by the standard deviation of temperature in that month (colours are discretised purely for visualisation purposes, but were modelled continuously). Species are ordered by ΔWAIC score.

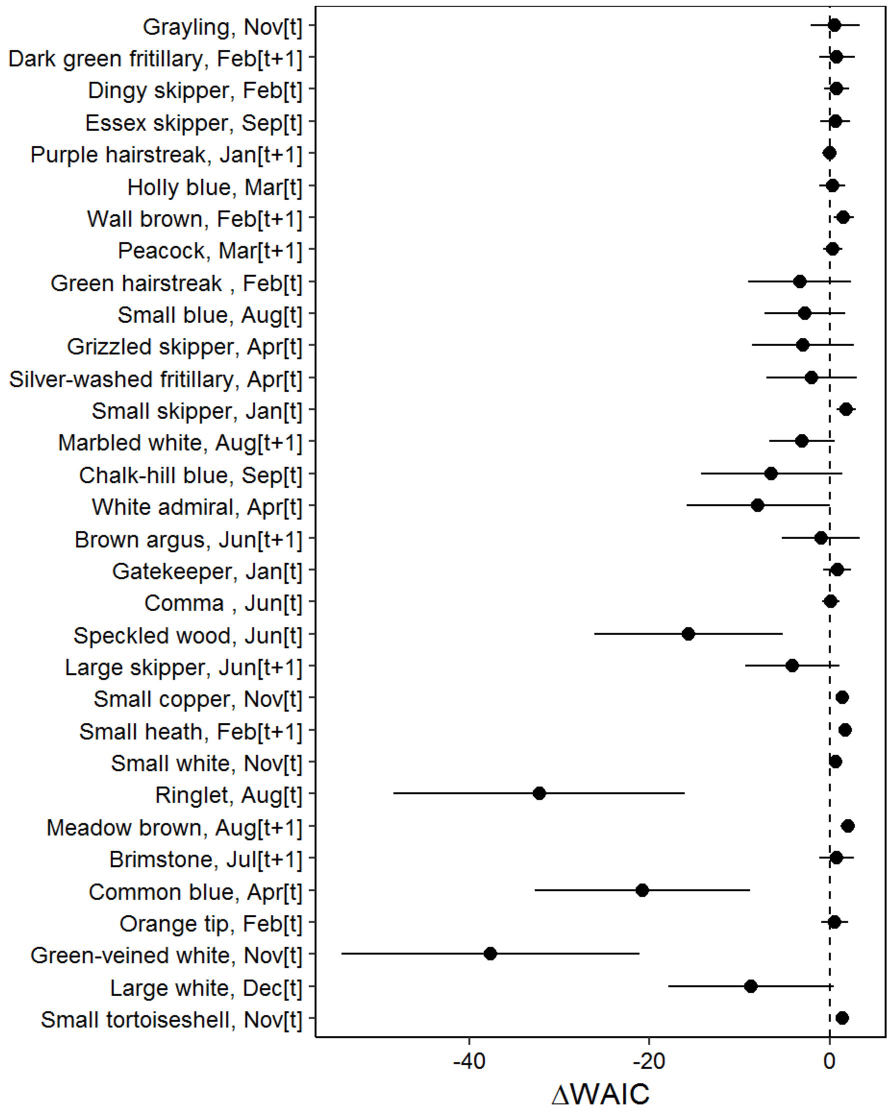

Figure S3 ΔWAIC scores for each species (Point-estimates and 95% credible interval), for comparison between daily temperature model and the model that monthly temperature model. Negative values indicate model improvement in the daily temperature model relative to the Mean-only model. The temporal period of each species' focal weather variable is given alongside each species' name, indicating the month, and whether this falls in year *t* (the year of the first count) or year *t+1* (the year of the second count). Ordering is retained from Figure 3.

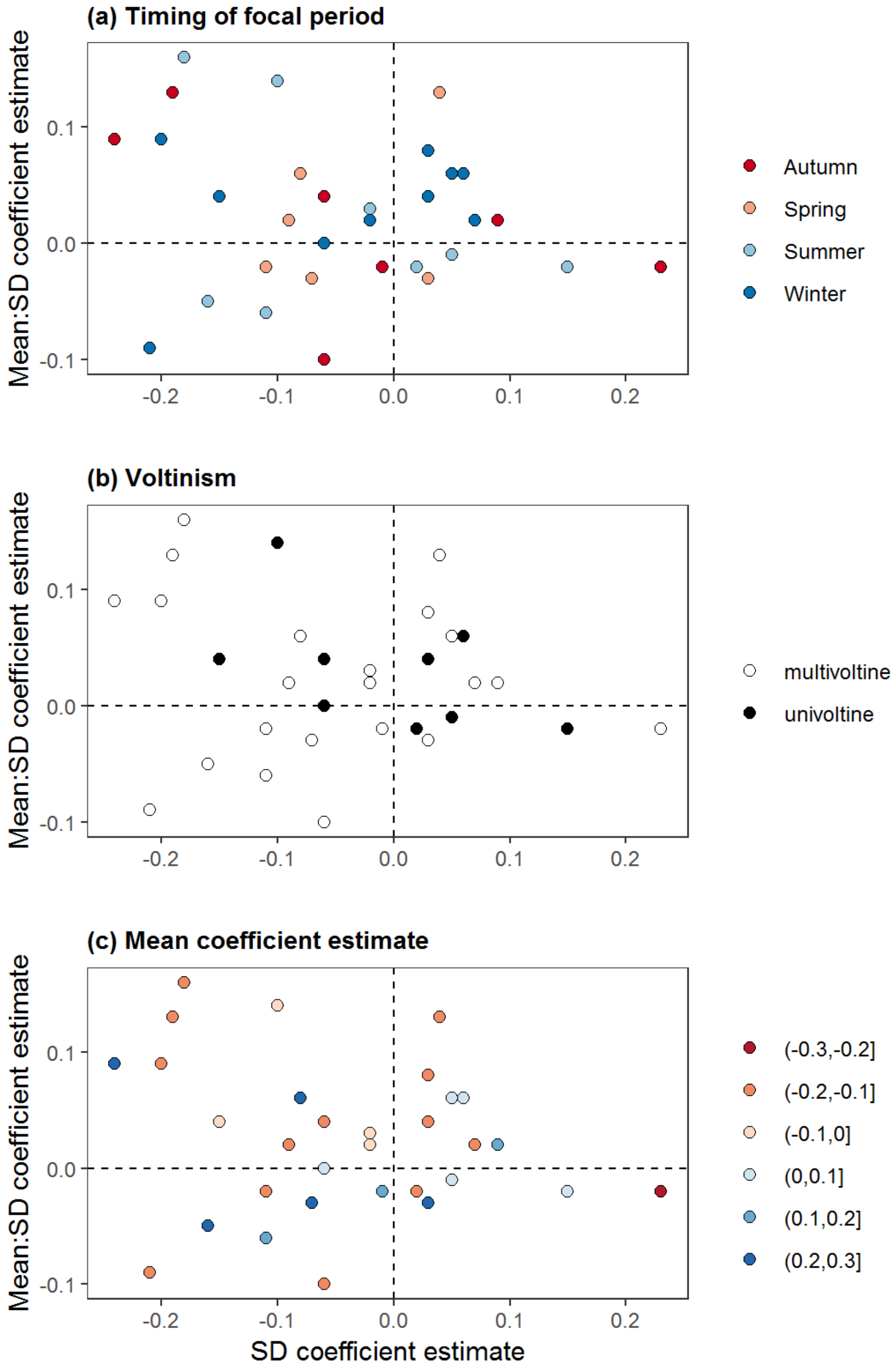

Figure S4 Coefficient estimates for SD main effects and mean:SD interaction terms across species. Points are coloured by (a) the timing of the focal period, (b) voltinism, and (c) by the value of the mean-temperature coefficient.

Table S1 Number of datapoints, number of sites, and year range, by species.

Species	N(obs.)	N(sites)	First year	Last year
Meadow brown, *Maniola jurtina*	8025	459	1974	2016
Large white, *Pieris brassicae*	7504	430	1974	2016
Small white, *Pieris rapae*	7379	424	1974	2016
Gatekeeper, *Pyronia tithonus*	7098	398	1974	2016
Green-veined white, *Pieris napi*	7008	397	1974	2016
Large skipper, *Ochlodes venata*	6904	393	1974	2016
Small tortoiseshell, *Aglais urticae*	6796	394	1974	2016
Common blue, *Polyommatus icarus*	6795	393	1974	2016
Speckled wood, *Pararge aegeria*	6661	384	1974	2016
Peacock, *Inachis io*	6637	388	1974	2016
Comma , *Polygonum c-album*	6365	362	1974	2016
Ringlet, *Aphantopus hyperantus*	5829	332	1974	2016
Brimstone, *Gonepteryx rhamni*	5740	336	1974	2016
Small copper, *Lycaena phlaeas*	5690	334	1974	2016
Orange tip, *Anthocaris cardamines*	5076	304	1974	2016
Small skipper, *Thymelicus sylvestris*	4992	296	1974	2016
Small heath, *Coenonympha pamphilus*	4519	265	1974	2016
Holly blue, *Celastrina argiolus*	4473	290	1974	2016
Marbled white, *Melanargia galathea*	4285	250	1977	2016
Brown argus, *Aricia agestis*	2950	178	1977	2016
Dingy skipper, *Erynnnis tages*	2182	136	1977	2016
Green hairstreak , *Callophrys rubi*	2157	135	1975	2016
Silver-washed fritillary, *Argynnis paphia*	2152	128	1977	2016
Wall brown, *Lasiommata megara*	2138	128	1974	2016
Dark green fritillary, *Argynnis aglaja*	1865	114	1977	2016
Chalk-hill blue, *Polyommatus coridon*	1725	96	1977	2016
Grizzled skipper, *Pyrgus malvae*	1711	111	1974	2016
White admiral, *Limenitis camilla*	1660	92	1974	2016
Purple hairstreak, *Neozephyrus quercus*	1600	99	1974	2016
Grayling, *Hipparchia semele*	1148	67	1977	2016
Essex skipper, *Thymelicus lineola*	1019	71	1977	2016
Small blue, *Cupido minimus*	952	58	1977	2016

Table S2 Coefficients for temperature terms and summary statistics for models predicting population growth rate containing Mean monthly temperature, SD of monthly temperature and the interaction between the two. The 95% credible intervals for model coefficients are in parentheses, and bold font indicates where these do not overlap 0. Mean and SD variables are both centred, and coefficient values for the main effects can therefore be interpreted as the effect when the other variable is at its mean. Species are ordered according to ΔWAIC score. These coefficients are for models that fitted additional control variables.

Species	Month	Mean °C	SD °C	Mean °C:SD °C	R^2	pWAIC	ΔWAIC	RMSE
1. Small tortoiseshell, *Aglais urticae*	Nov[t]	**-0.28 (-0.31, -0.26)**	**0.23 (0.18, 0.28)**	-0.02 (-0.09, 0.05)	0.39	-67	<.01	1.16
2. Large white, *Pieris brassicae*	Dec[t]	**-0.19 (-0.21, -0.17)**	**-0.21 (-0.24, -0.17)**	**-0.09 (-0.16, -0.02)**	0.46	-67.4	<.01	1.04
3. Green-veined white, *Pieris napi*	Nov[t]	**-0.13 (-0.16, -0.11)**	**-0.19 (-0.22, -0.15)**	**0.13 (0.05, 0.21)**	0.39	-64.4	<.01	0.94
4. Orange tip, *Anthocaris cardamines*	Feb[t]	**-0.06 (-0.08, -0.05)**	**-0.15 (-0.18, -0.11)**	0.04 (-0.03, 0.12)	0.41	-52.2	<.01	0.91
5. Common blue, *Polyommatus icarus*	Apr[t]	**0.30 (0.28, 0.32)**	**-0.08 (-0.15, -0.02)**	0.06 (-0.03, 0.16)	0.42	-43.1	<.01	1.1
6. Brimstone, *Gonepteryx rhamni*	Jul[t+1]	**0.08 (0.06, 0.10)**	**0.15 (0.10, 0.19)**	-0.02 (-0.10, 0.07)	0.37	-25.4	<.01	0.78
7. Meadow brown, *Maniola jurtina*	Aug[t+1]	**0.07 (0.06, 0.08)**	**0.05 (0.03, 0.07)**	-0.01 (-0.05, 0.04)	0.27	-21.4	<.01	0.61
8. Ringlet, *Aphantopus hyperantus*	Aug[t]	**-0.03 (-0.05, -0.01)**	**-0.10 (-0.16, -0.04)**	**0.14 (0.08, 0.21)**	0.25	-26.6	<.01	0.85
9. Small white, *Pieris rapae*	Nov[t]	**0.16 (0.14, 0.19)**	-0.01 (-0.06, 0.05)	-0.02 (-0.10, 0.05)	0.45	-12.8	<.01	1.06
10. Small heath, *Coenonympha pamphilus*	Feb[t+1]	**0.07 (0.04, 0.10)**	0.05 (-0.02, 0.13)	0.06 (-0.00, 0.12)	0.17	-21	<.01	0.89
11. Small copper, *Lycaena phlaeas*	Nov[t]	**0.15 (0.12, 0.17)**	**0.09 (0.02, 0.15)**	0.02 (-0.07, 0.11)	0.39	-12	<.01	1.05
12. Large skipper, *Ochlodes venata*	Jun[t+1]	**-0.13 (-0.15, -0.11)**	0.02 (-0.02, 0.06)	-0.02 (-0.07, 0.04)	0.3	-11.3	0.02	0.94
13. Speckled wood, *Pararge aegeria*	Jun[t]	**-0.09 (-0.10, -0.07)**	-0.02 (-0.05, 0.00)	0.03 (-0.02, 0.07)	0.28	-10.5	0.03	0.7
14. Comma , *Polygonum c-album*	Jun[t]	**0.09 (0.08, 0.11)**	**-0.08 (-0.11, -0.04)**	0.06 (-0.00, 0.11)	0.41	-11	<.01	0.92
15. Gatekeeper, *Pyronia tithonus*	Jan[t]	**0.08 (0.07, 0.09)**	**-0.06 (-0.09, -0.03)**	0.00 (-0.03, 0.04)	0.23	-11.1	0.01	0.73
16. Brown argus, *Aricia agestis*	Jun[t+1]	**0.24 (0.21, 0.27)**	**-0.16 (-0.26, -0.06)**	-0.05 (-0.20, 0.09)	0.41	-5.4	0.05	1.14
17. White admiral, *Limenitis camilla*	Apr[t]	**-0.11 (-0.13, -0.08)**	**-0.11 (-0.17, -0.06)**	-0.02 (-0.13, 0.09)	0.33	-7.1	0.05	0.91

18. Chalk-hill blue, *Polyommatus coridon*	Sep[t]	**0.22 (0.18, 0.26)**	**-0.24 (-0.37, -0.12)**	0.09 (-0.03, 0.20)	0.24	-9.5	0.03	0.93
19. Marbled white, *Melanargia galathea*	Aug[t+1]	**0.14 (0.11, 0.16)**	**-0.11 (-0.17, -0.04)**	**-0.06 (-0.12, -0.01)**	0.19	-4.9	0.07	0.82
20. Small skipper, *Thymelicus sylvestris*	Jan[t]	**-0.16 (-0.18, -0.13)**	**0.07 (0.01, 0.12)**	0.02 (-0.04, 0.09)	0.24	-5.4	0.06	1.18
21. Silver-washed fritillary, *Argynnis paphia*	Apr[t]	**0.22 (0.19, 0.25)**	-0.07 (-0.16, 0.03)	-0.03 (-0.12, 0.06)	0.31	-4.1	0.2	0.85
22. Grizzled skipper, *Pyrgus malvae*	Apr[t]	**-0.13 (-0.16, -0.09)**	**-0.09 (-0.16, -0.02)**	0.02 (-0.09, 0.14)	0.34	-2.4	0.17	0.93
23. Small blue, *Cupido minimus*	Aug[t]	**-0.16 (-0.21, -0.11)**	**-0.18 (-0.32, -0.05)**	**0.16 (0.02, 0.31)**	0.28	-2.6	0.19	1.09
24. Green hairstreak , *Callophrys rubi*	Feb[t]	**-0.13 (-0.17, -0.10)**	0.03 (-0.04, 0.10)	0.04 (-0.07, 0.15)	0.41	-1.7	0.25	1
25. Peacock, *Inachis io*	Mar[t+1]	**-0.18 (-0.20, -0.16)**	**0.04 (0.01, 0.07)**	**0.13 (0.08, 0.19)**	0.35	-0.5	0.44	0.81
26. Wall brown, *Lasiommata megara*	Feb[t+1]	**-0.16 (-0.20, -0.12)**	**-0.20 (-0.32, -0.09)**	**0.09 (0.02, 0.17)**	0.22	-1.3	0.35	0.99
27. Holly blue, *Celastrina argiolus*	Mar[t]	**0.21 (0.18, 0.24)**	0.03 (-0.05, 0.11)	-0.03 (-0.10, 0.04)	0.46	0.4	0.55	1.2
28. Purple hairstreak, *Neozephyrus quercus*	Jan[t+1]	**0.07 (0.03, 0.11)**	0.06 (-0.07, 0.18)	0.06 (-0.10, 0.22)	0.41	0.9	0.73	1.1
29. Essex skipper, *Thymelicus lineola*	Sep[t]	**-0.13 (-0.20, -0.06)**	-0.06 (-0.17, 0.05)	0.04 (-0.11, 0.18)	0.3	1.4	0.81	1.29
30. Dingy skipper, *Erynnnis tages*	Feb[t]	**-0.08 (-0.10, -0.06)**	-0.02 (-0.08, 0.03)	0.02 (-0.11, 0.15)	0.34	1.3	0.91	0.95
31. Dark green fritillary, *Argynnis aglaja*	Feb[t+1]	**-0.13 (-0.17, -0.09)**	0.03 (-0.04, 0.11)	0.08 (-0.06, 0.22)	0.27	1.9	0.95	0.98
32. Grayling, *Hipparchia semele*	Nov[t]	**-0.12 (-0.18, -0.05)**	-0.06 (-0.26, 0.13)	-0.10 (-0.29, 0.08)	0.24	1.9	>.99	0.94

Chapter 5:

General discussion

Monitoring schemes, as the name suggests, were largely developed to fulfil a need to monitor the state of our nature (Pollard & Yates 1993; Gregory *et al.* 2005; Dennis *et al.* 2013; Inger *et al.* 2015). In this regard, they have been tremendously successful, providing some of the strongest evidence of the systematic changes afoot in our European populations of birds and butterflies (Fox *et al.* 2011a; Inger *et al.* 2015), and contributing directly to red-list assessments of population health (Fox *et al.* 2011b). Understandably, as these datasets have grown in size, interest has turned to harnessing the power of these datasets- namely their substantial spatial, temporal, and taxonomic extents- to ask questions not only about whether population change is occurring, but what the drivers of population change might be.

In this regard, there have also been some notable successes, particularly when factors associated with population change have large effects. The dramatic declines of birds in our agricultural landscapes are self-evident in these datasets, for example (Gregory *et al.*, 2007; Birdlife International, 2013) and evidence of this form is central to mobilising conservation efforts and further work to understand the causes of these declines (e.g. Bradbury *et al.* 2003). Long-term population trend has been linked with a range of other life-history (Jiguet *et al.* 2007) and functional or climatic traits (Jiguet *et al.* 2010). Further, Stephens *et al.* (2016) identify broad congruence between regional population trajectories and the climatic suitability trend (CST) of species distribution models, suggesting a role for climate in driving long-term population trend. It is important to note that, unlike the fairly clear-cut example of population declines in farmland birds, and, to a lesser extent, woodland birds, these latter associations typically have smaller effect sizes and are thus somewhat more equivocal. For example, though Stephens *et al.* (2016) uncover a statistically significant association between CST score and regional population trend, there is substantial variation in regional population trend is not explained by CST, and instead is captured by the random-effect terms of the model (Stephens *et al.* 2016 Supp. Info.). These caveats aside, however, studies such as these do appear to identify reasonably sizeable associations between long-term trend and a range of other factors.

More recently, attention has turned to relating between-year changes in abundance to various environmental drivers, across a range of spatial scales (Jørgensen *et al.* 2015; Pearce-Higgins *et al.* 2015; Bowler *et al.* 2018). This class of questions are likely to be more difficult still. Inter-annual growth is driven by a great many factors, and, as discussed in chapters I and III, are likely to be typified by low signal to noise ratios. Taken in aggregate, the results of this thesis suggest that there are currently some difficulties in linking variation in inter-annual growth to environmental drivers with these datasets. Importantly however, these difficulties are not irresolvable, and I suggest some opportunities for future work on population dynamics that uses these datasets. There is a distinction to be made between birds and butterflies, due to both taxonomic differences and the substantial differences between sampling strategies employed by the different types of monitoring scheme. While the general suggestion from this work is that signals of weather can be more readily observed in the butterfly datasets than in the bird datasets, it is difficult to identify the precise cause of this. On the one hand, the relative demographic simplicity of butterfly populations may render weather drivers more easily resolvable (as populations do not have a complex structure). On the other, butterfly abundance indices have far less measurement error, as the derived abundance index is informed by a lot of counts over the course of the season, rather than just a few. Consequently, differences in the measurement process alone would be expected to drive differences in the apparent signal of weather. I expand on these points further below, and also discuss the more general themes of the thesis, broadly grouping them as: unquantified measurement error (section 5.1), issues with statistical significance (section 5.2), and characterising weather drivers and model generality (section 5.3). I finish with some general conclusions (section 5.4).

5.1 Measurement error (the observation process)

> *The data we deal with are bad, scarce, and derived. They're bad: they have tremendous measurement error, they have no nice sampling design, and they're often just opportunistic. [..] They're highly derived, in the sense that the things that you collect and measure are not the entities that*

> *are theoretically nominated and important. You have to do some post-processing and you need a really nice measurement model to do these things. It's nothing like an agricultural trial.*
>
> Richard McElreath, presenting at StanCon Helsinki, 2018

Complications introduced by measurement error in the analysis of time-series are well understood, and have been widely discussed within population ecology, particularly in the context of detecting density-dependence (DD; Dennis *et al.*, 2006; Freckleton *et al.*, 2006; Knape, 2008; Knape & de Valpine, 2012). The existence of measurement error (i.e. when the correspondence between observed abundance and 'true' abundance is not 1:1), is particularly problematic for the estimation of DD terms, as measurement error causes bias in DD estimates (Knape & de Valpine 2012). For estimating the effects of environmental variables, measurement error is less of a problem, so long as there is not strong temporal autocorrelation in these variables (Lindén & Knape 2009). In the absence of strong temporal autocorrelation in the environment ($r > 0.7$), models that assume process error, but not measurement error (i.e. the models applied throughout this thesis), will have coefficient estimates that are unbiased and have confidence intervals with correct coverage (Lindén & Knape 2009).

While, on the face of it, this might suggest that there may not be too much of a problem with measurement error for the purpose of estimating environmental effects, there are a few important complications introduced by the measurement process. Most importantly, these issues all arise due to the fact that currently the relative contribution of measurement error to observed variation in abundance is not known. However, if the contribution of measurement error to observed variation was addressed, these problems would be resolved, and work to address this question therefore offers substantial opportunity to enhance our ability to tackle questions about inter-annual growth with these datasets.

The consequence of unquantified measurement error is that it is difficult to establish whether or not observed effects are effects that we, as ecologists, should be interested in. When coefficients occur on scales that are readily interpretable (i.e. that have an intuitive meaning), low model explanatory capacity is not necessarily a critical problem. In these cases, an intuitive coefficient can be interpreted as 'meaningful', with reference to other potential effect sizes, despite the fact that it might explain a small proportion of the variation in the response variable. For example, consider the 76.5% reduction in species richness and 39.5% reduction in total abundance observed in highly degraded habitats (Newbold *et al.* 2015). These associations are intuitively meaningful, and are interpretable in the absence of any information about explanatory capacity. The problematic case is when a coefficient estimate does not have an intuitive meaning, and in the absence of further contextualisation we cannot say anything about the importance of its effects.

To pick an example from chapter II, for Orange Tip *Anthocharis cardamines* in the 41°-43° latitudinal band (largest effect in the first row of Table 2.S2), we observe a standardised coefficient estimates of 0.54 (±0.17) for pre-flight period temperature ($P<0.01$). This implies that across the 95% range of that environmental variable, we travel from a population growth rate of 35%, to a population growth rate of 294%. This seems like quite a substantial amount of variation in population growth across the range of this variable. If, however, we consider the effect of pre-flight period temperature in the 51° - 53° latitudinal band, at the same level of statistical significance ($P<0.01$), the effect is 0.05 (±0.01), implying variation in population growth of 91% to 110%. Does this represent a meaningful association with pre-flight period temperature? Probably not, but it's difficult to say. These sorts of coefficient estimates bracket two ends of a spectrum between estimates that are quite substantial and estimates that it is difficult to express much enthusiasm about. For more intermediate values it is even more difficult to say whether these represent meaningful drivers of change in these populations.

In cases such as this, explanatory capacity offers a straight-forward solution: if a variable substantially enhances our capacity to explain variation in response, then we should retain it if we wish to explain observed phenomena (Knape & de Valpine 2011). Coefficients can be entirely without intuitive meaning, but, if they appear to be very important for explaining observed phenomena, then on this basis alone they can be judged as important (as they substantially enhance our ability to explain the behaviour of a given system). The ability to make these judgements breaks down however, once the measurement process contributes substantially to variation in the response variable. Now, there might be a variable that does a very good job of explaining variation in the underlying 'true' variation, but that explains little of the observed variation in response due to the substantial noise contributed by the measurement process. When there is substantial unquantified measurement error and coefficients do not take on readily interpretable values (or, do not have extremely large effect sizes), it becomes very difficult to establish whether observed effects represent meaningful associations that we should be interested in.

A second issue introduced by low model explanatory capacity is to do with making predictions. Low explanatory capacity implies the majority of processes that cause variation in abundance are not present within the model. Forecasts should thus be treated with little faith, as the contribution of these unmodelled factors evidently far outweighs the contribution of those within the model, and it is not reasonable to assume that modelled variables will vary in isolation. Small changes in unmodelled factors are likely to have far more substantial effects on population growth than those included within the model and models that explain a low proportion of the variation are thus not terribly useful in a predictive role. Clearly, however, unquantified measurement error makes such an assessment difficult.

Measurement error is thus a substantial problem in the context of these datasets and these models. Indeed, if there is a single take-home message from this work, it is that, in order to maximally harness these datasets to understand inter-annual variation in abundance, then there needs to be a greater focus on the process of measurement, and, specifically, work needs to be done to establish the contribution of measurement error to observed variation in abundance. This particularly applies to the bird datasets, but can, to a lesser extent, also be raised in the context of the butterfly datasets. Fortunately, however, some relatively simple steps offer much opportunity to address these issues.

What might be done to address the issue of measurement? In the context of the butterfly datasets, it is fairly straight-forward. The sampling process is already extensive, consisting of many counts over the course of the season which contribute to an abundance index (that corresponds to the area under the flight curve, at a particular site). The method described by Dennis et al. (2013) generates a site-level point-estimate for this coarse measure of abundance, and confidence intervals for this are obtained via bootstrap. However, these bootstrap estimates are computationally intensive, to the extent that they cannot be calculated by default alongside the point-estimate (Dennis, E., pers. comm.). This is unfortunate, as these estimates both could be included in a weighted regression, so that high-quality estimates had relatively more influence relative to poor, but also these intervals tell us something about the sampling variation generated by this measurement process. In principle, this information would give some indication as to the relative contribution of this measurement process to observed variation in abundance. It is likely that this would be readily achievable via MCMC methods such as Stan or JAGS, or perhaps via INLA.

With regards to the bird monitoring datasets, it will be more difficult to obtain estimates of measurement error to observed variation in population growth as it will require additional sampling (beyond what is already done) to address. Specifically, it requires replicated sampling over a period that the population can be assumed to be closed (i.e. over the course of a few days) to quantify how much variation arises simply from the measurement process. Depending on the precise causes of measurement error, additional permutations may be required. For example, if observer experience or habitat type were deemed to be important contributors to measurement variation, then a sampling design that allowed for these influences to be directly assessed would need to be developed. There is relatively little work that directly addresses this issue; Freckleton *et al.* (2006) however, identify the potential of this approach. Due to the availability of a dataset in which there was replicated sampling, they were able to address the contribution of different sources of error to abundance measures for five species in the UK Common Birds Census (a scheme that predates the current UK BBS, based on territory mapping). They found in four out of five cases that census error contributed substantially to variation in population size, and measurement error can substantially exceed the underlying process variation.

Clearly, insisting that what is currently a single site-visit becomes three (or more) site-visits (as recommended by Brian *et al.* 2010; Knape *et al.* 2013) is likely unfeasible. Further, reallocating volunteer effort towards more surveys but at fewer sites would not fit with the main aims of these monitoring programmes, which is to track long-term change across wide spatial extents. However, just addressing this question at a much smaller subset of sites would allow for inference to be made more widely. For example, a relatively small study across just a few sites would move us from the very speculative position we are currently at -'we know measurement error exists, but not how much'- to a situation in which we have some idea as to the relative importance of this process. Further, different schemes do vary somewhat in their specific design - e.g. point counts vs. line transects etc.- and getting a better handle on the implications of these sampling designs would be a great help both when it comes to amalgamating multiple different schemes into a single dataset, as well as identifying optimal survey designs from the variety that are currently employed.

5.2 Model comparison in the large-N context

It is important to briefly address the role of statistical significance (or any other form of model comparison) in the context of these large-N monitoring datasets.

With increasing sample sizes it becomes increasingly possible to discriminate between competing explanations for observed phenomena. Model comparisons (or, equivalently, comparing certain regions of parameter space) will increasingly differentiate between models that might only marginally differ in their ability to explain variation in response (or, equivalently, their fit to the data). This is not inherently a problem - in fact it is an entirely desirable quality- but it means that identifying model differences becomes very easy when the sample size is large. Working with the bird monitoring datasets, effects that only marginally depart from 0 will frequently have an absolute t-value of >2. However, as discussed above, it is difficult to see how such a marginal coefficient estimate can represent an important association. Some additional context can be gleaned from the coefficients for lag-1 DD terms. These, often, have an absolute t-value of >150, and, in this context observing a t-value >2 starts to seem quite negligible. Extremely large t-values, or statistically significant t-values on seemingly marginal coefficient estimates is simply a function of there typically being in excess of 1×10^4 observations for a given species in the bird monitoring datasets.

In the absence of coefficients that are readily interpretable, and very marginal explanatory capacities, there should be scepticism of evidential claims based solely on statistical significance or any other form of model comparison. In the absence of being able to state the importance of a particular variable for explaining 'true' variation in abundance (due to unquantified measurement error), the case must be made on the biological implications of a particular coefficient value. Assessments of statistical significance should not be used to justify the importance of a particular association (as this is not what a *P*-value is designed to do). As discussed in the previous section, the most fruitful course of action will likely be to address the issue of measurement error, and, in the meantime, assess the importance of particular variables based on their biological implications.

5.3 Model complexity: characterising weather drivers, and general vs. unique trade-offs

> *For population ecology, the wedding of long-term studies with theory forces scientists to juggle two apparently incompatible aims: to understand any system, we need to appreciate its idiosyncrasies; to encompass broad patterns, we need to extract generalities. The current challenge to time series analysis and ecological theory is, thus, to simultaneously accommodate and transcend the details of natural history.*
>
> Bjørnstad & Grenfell, 2001

The question of "how complex should a model be to understand population change" is a further question that has frequently arisen in the course of this thesis, as well as one that has been widely discussed in the literature on population dynamics (Lawton 1999; Bjørnstad & Grenfell 2001; Coulson *et al.* 2001). It is fairly obvious that there are trade-offs between complex site or case-specific models and models that apply more generally and can be applied across large geographic and temporal extents (Bjørnstad & Grenfell 2001; Godfray & Rees 2002). However, the precise form of these trade-offs is less clear. Phenomenological models do appear, in general, to be fairly limited in their ability to explain inter-annual variation in population growth (Chapter II, III, IV; Coulson *et al.* 2001; Hallett *et al.* 2004; Knape & de Valpine 2011; Boggs & Inouye 2012), and there is thus some suggestion that, in order to understand inter-annual growth rate responses, more information is required than exists in simple time-series of population abundance (Knape & de Valpine 2011). Importantly, such a perspective precludes a macroecological approach to understanding drivers of inter-annual growth, and suggests that generalised, multi-species inferences about how populations will respond to climate change may simply be an unattainable goal.

A further perspective that I have been aware of is that weather drivers may just be inherently complex, high-dimensional sets of interacting and potentially non-linear effects. Indeed, it's very easy to find large sets of variables that might plausibly be involved in population regulation (Grosbois *et al.* 2008). However, if drivers of population growth are inherently this complex then there are necessarily severe limitations in our ability to understand the influence of weather on population growth rates, as responses of this form defy any simple approximation. The criticism that we didn't look at enough variables to conclude that it is difficult to explain variation in population growth with large sets of weather drivers (chapter III) is thus not reasonable. If drivers are really of this form then, necessarily, models will have a low capacity to predict variation in population growth, and adding large sets of variables and their interactions into the mix will not change this. This perspective further flies in the face of evidence from detailed demographic studies which typically uncover fairly simple low-dimensional associations with weather (Coulson *et al.* 2001, 2005; Dybala *et al.* 2013; Cleasby *et al.* 2017).

This criticism suggests an additional problem in how we approach questions regarding drivers of population dynamics. If the existence of strong prior notions about the importance of weather in determining population dynamics generates an asymmetry in how authors respond to the results of subsequent research, then a misleading picture of the importance of these factors is created. By iteratively adding more predictors and tweaking the model formulation until a result that more comfortably sits with our prior beliefs is arrived at, we misrepresent the underlying evidence for a particular phenomenon. This mechanism has been referred to as the garden of forking paths (Gelman and Loken, 2013), and its consequences are equivalent to those of the file-drawer problem, in which the results of a line of research influence the likelihood of it being published or otherwise disseminated (Rosenthal, 1979).

While it is probably premature to give up on the macroscale approach entirely, we should be concerned about the low explanatory power these approaches seem to have at present. Simply accepting that phenomenological models will necessarily have low explanatory power but we should stick with them anyway does not seem a particularly tenable position; rather, we should seek to develop a stronger understanding of the trade-offs between model complexity (and, consequently, data requirements) and model explanatory capacity, as well as work to identify generalities in response, both across taxonomic groupings, and also across spatial gradients. One particularly important question to ask in the context of climate change, for example, regards the extent to which there are generalities in population response to weather, and how these vary spatially.

Niche concepts lead us to expect that the direction of effect of weather associations will vary spatially, but also suggest a common form for these associations. At a warm range-edge for example, warming would be expected to drive declines in abundance as a species is shifted further away from its optimum. Conversely at a cold range-edge, warming would correspond to a species being shifted closer to its optimum. Niche theory thus gives us the backbone of a model. If we expect that there is just a single optimal position along the temperature axis, we can specify that population response has to be either unimodal (with declines to either side), or monotonically increasing or decreasing (if you are observing just the edges of a niche, rather than the turning point). In chapter IV I incorporated this theoretical expectation by forcing the log-quadratic term to take a negative value by assigning a zero prior to values above 0. However, this is not an ideal approach as the association is still forced to have a particular functional form (in this case the Gaussian). Others have opted for a more flexible approach in which the response function is a constrained spline, that has the unimodal or monotonic properties described above, but allows for substantial flexibility in the precise shape of the association (Beale *et al.* 2014).

However, this approach explicitly assumes that there is minimal intraspecific variation in order to assume a shared functional form across a species as a whole. If it is the case that response that is constructed for a species as a whole is in fact better understood as a 'smoothing across' different response curves at the sub-species level, the assumption that populations would respond in a particular way to future events becomes problematic. Consider, for example, the Ringlet butterfly *Aphantopus hyperantus*. In this species (as well as a number of other butterfly species), populations at the warm range edge exhibit aestivation behaviours that allow them to tolerate the warmest conditions during the summer months. In the absence of this behaviour they would likely be unable to tolerate the warmest, driest conditions and populations would consequently become extinct.

A key question is: when we observe how populations in this region respond to variation in environmental conditions, is this response representative of how another population elsewhere in the distribution would respond to increasingly warm and/or dry summers? As the UK summers become warmer and drier, would ringlets in the UK be able to exhibit the same aestivation behaviours that we observe in Spain? If it is the case that this behaviour needs to first migrate here from Spain, then the predicted response to a changing climate will be dramatically different than if they can already respond this way *in situ*.

This question is not unique to butterflies, and applies to many taxa such as plants and birds. In birds for example, blackbirds similarly exhibit marked variation in a variety of traits across their range extent. Morphologically, birds are significantly larger in Scandinavia than they are in central Europe, and in turn are significantly smaller at their warm range edge in Spain (Svensson, 1992). Behaviourally they also vary, with the insulation of blackbird nests showing a strong association with temperature of nest location (Mainwaring *et al.* 2016). These traits substantially alter the thermodynamics of the individuals that make up a population and would therefore be expected to affect how a given population would respond to a particular temperature event. The lability of these traits thus becomes a central question in forecasting population responses to climate change. Developing a firmer understanding of how population responses to weather are maintained across the range of a species is thus central to generating sensible forecasts of population response to changes in climate, and this is an important avenue of future work (Valladeres *et al.* 2014).

5.4 Concluding remarks

In this thesis I address several questions about the role of weather in regulating European populations of birds and butterflies, using monitoring datasets from 11 countries across Europe. There are three main findings from this work. Firstly, the importance of weather for driving temporal variation in abundance appears to vary across the range, with weather appearing relatively more important towards latitudinal range edges. This suggests that that weather and climate may represent limiting factors in these regions, and that it is in these regions that we expect to observe the earliest and most substantial consequences of climate change. Secondly, thermal variation at relatively fine temporal scales appears to be involved in population regulation, and including terms that quantify this variation in population growth rate models enhances their ability to explain variation in population growth for UK butterflies. This finding suggests substantial opportunity to improve upon pre-existing approaches through relatively straight-forward tweaks to the model formulation. The final finding is that greater caution is required in our conclusions about the importance of weather for regulating populations. This applies in particular to birds, where it has been particularly difficult to identify weather associations that drive meaningful variation in abundance, but can also be applied, to a lesser extent, to butterflies. It appears that, when using long-term monitoring datasets, weather terms typically display a limited capacity to explain population growth, with the consequence that there is substantial residual variation in population growth not explained by modelled variables. On the basis of these results, I recommend that, if these datasets are to be used to assess drivers of inter-annual growth, further work needs to be done to address the issue of measurement error (which will require additional data collection). In the absence of this, the ability to make robust and meaningful inference from these datasets is, in my opinion, somewhat limited. Overall, I hope that these represent useful contributions to the literature on population dynamics, and that they have in some small way advanced how we approach and think about questions to do with population regulation.

5.5 References

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