Life in a changing world:
climate change impacts on common European birds

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Declaration

I, Nina Margaret M^{c}Lean, hereby state that the work presented in this thesis is original. I am the senior author and principal contributor of all the chapters. The four chapters are co-authored by my main supervisor, Martijn van de Pol. Chapter 1 is additionally co-authored by Callum Lawson who contributed to the idea development and revisions. Dave Leech collated and provided the empirical data for Chapters 1 and 4. Henk van der Jeugd collated and provided the empirical data for Chapters 2-4, and Chris van Turnhout for Chapter 3. All three contributed to revisions and interpretation. Jonathan Lefcheck contributed to the analysis and revisions in Chapter 3. Loeske Kruuk contributed to idea development and interpretation in Chapter 4.

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Abstract

Anthropogenic climate change is predicted to be a major cause of extinctions. Therefore, a major aim of climate change ecology is to understand how species are being impacted and identify which species are most at risk. However, the ability to make these broad generalisations requires large-scale comparative analyses based on appropriate assumptions. This thesis investigates how European birds respond to changes in climate, the validity of several common assumptions, and identifies which species or populations are most at risk based on multiple long-term datasets.

Our understanding of how different responses relate and how they affect population persistence is lacking. A conceptual hierarchical framework is introduced in chapter one to better understand and predict when climate-induced trait changes (phenology or physiology) impact demographic rates (survival or reproduction), and subsequently population dynamics. I synthesise the literature to find hypotheses about life-history and ecological characteristics that could predict when population dynamics will likely be affected. An example shows that, although earlier laying with warmer temperatures was associated with improved reproduction, this had no apparent effect on population trends in 35 British birds. Number of broods partly explains which species are most at risk of temperature-induced population declines.

It is often assumed that populations within species respond similarly to climate change, and therefore a single value will reflect species-specific responses. Chapter two explores inter- and intra-specific variation in body condition responses to six climatic variables in 46 species over 21 years and 80 sites. Body condition is sensitive to all six variables (primarily in a non-linear way), and declines with warmer temperatures. I find that species signals might not exist as populations of the same species are no more alike than populations of different species.

Decreased body condition is typically assumed to have detrimental consequences on species' vital rates and population dynamics, but this assumption has rarely been tested. Expanding on chapter two, chapter three shows that temperature-induced declines in body condition have no apparent consequences on demography and population dynamics. Instead, temperature has strong effects on reproductive success and population growth rates via unknown traits and demographic rates.

Much of the literature investigating climatic impacts assumes that temporal trends accurately reflect responses to climate change, and therefore investigate trait changes over time. In chapter four, I use two long-term datasets to demonstrate that, for four different types of trait responses, trait variation through time cannot be assumed to be due to warming. Non-temperature causal agents are important in explaining temporal trends, often resulting in reinforced effects. Consequently, the roles of climatic and non-climatic effects need to be understood to better predict those species most at risk.

This thesis lays the foundations for more holistic climate change research that encompasses relationships among multiple response types, species and populations. Such knowledge will be vital for future conservation efforts.

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Introduction

Anthropogenic greenhouse gas emissions have been increasing at a rapid rate since the pre-industrial era and are now at higher levels than ever before. This has resulted in a range of impacts on our climate, including sustained increases in atmospheric and sea surface temperatures, reduced amounts of snow and ice, and rising sea levels (IPCC, 2014). Changes in the global climate are already affecting the natural world, with changes in biodiversity and shifting ecosystems, but also impacting human well-being and economic welfare (Williams *et al.*, 2008). Even if policies were instituted globally to slow or prevent any further increases in CO_2 emissions, surface temperatures are still projected to continue rising, extreme heat wave and precipitation events are expected to become more intense and frequent, and sea levels will continue to rise (IPCC, 2014).

Climate change is already being found to have a range of effects on organisms (Walther *et al.*, 2002). Responses include changes in phenology (i.e. the timing of events; Parmesan & Yohe, 2003), and physiology (e.g. body size or condition; Ozgul *et al.*, 2010; Gardner *et al.*, 2011; Goodman *et al.*, 2012), shifts in distributions (Chen *et al.*, 2011), behavioural patterns (e.g. behavioural thermoregulation; Glanville & Seebacher, 2006), life-history traits (e.g. length of gestation period; Clements *et al.*, 2011), demographic rates such as survival and reproduction (e.g. adult survival; Leech & Crick, 2007), population growth rates (Stephens *et al.*, 2016) and changes in communities and ecosystems (Gilman *et al.*, 2010). From a conservation point of view, one of the most pressing concerns relates to predicted increases in extinction events in the near future as a result of anthropogenic climate change (Thomas *et al.*, 2004). Up to one in six species are predicted to suffer an increase in risk of extinction as a result of future global temperature increases (Urban, 2015). Thomas *et al.* (2004) suggested that between 25-37% of latitudinally restricted species will likely be committed to extinction by 2050. Already, hundreds of species of plants and animals globally have experienced localised extinctions due to changes in the climate (Cahill *et al.*, 2013).

Understanding how organisms are responding to climate change, why species differ in their sensitivity, and predicting which species, habitats and ecosystems are most at risk are all fundamental aims of climate change ecology (Buckley & Kingsolver, 2012). Consequently, the identification of traits or characteristics that can help to predict which species or populations might be more at risk is of key importance (Williams *et al.*, 2008; Diamond *et al.*, 2011). The ability to generalise which species or populations are most at risk is particularly vital for species about which we have limited knowledge. Being able to generalise by extrapolating to less well-studied species is crucial because for most species, the required data to make an independent assessment is lacking (Foden *et al.*, 2013; Pearson *et al.*, 2014).

There are many difficulties currently surrounding our ability to describe broad-scale patterns in responses across populations and species, and to then reliably predict which groups are more at risk. For instance, in order to answer these questions, long-term biological datasets with different types of responses (including information on timing of events, physiology, survival and abundance) across multiple sites are often required. Comparative analyses are essential for generalising the impacts of climate change across regions and taxa. As the importance of long-term monitoring programs is increasingly recognised, large-scale datasets are increasingly common and accessible (Greenwood, 2007; Kluen *et al.*, 2017). Moreover, a significant amount of work in the past decade reporting effects of specific climate variables on phenotypic traits or demographic rates across a range of taxa, means that comparative analysis are now possible (Végvári *et al.*, 2010; Buckley & Kingsolver, 2012).

Another difficulty in our ability to identify broad-scale patterns and make reliable predictions is that many studies make a range of implicit assumptions that can amplify uncertainty and influence the reliability of observed trends or predictions (Wiens *et al.*, 2009). For example, the vast majority of ecological climate change research focusing on the direct effects of climate on trait responses (such as phenology) typically assumes that climate-induced trait changes will have consequences for survival, reproduction and population dynamics. However, this assumption has only more recently begun to be explicitly tested (Wilson & Arcese, 2003). Studies also tend to make a number of assumptions regarding which climatic variables are important and over what timeframes, and whether climatic effects are linear or non-linear (van de Pol *et al.*, 2016).

In this thesis, I utilise several long-term monitoring datasets to investigate how common European bird species are responding to changes in the climate, and which species or populations are most at risk. I consider the validity of several common assumptions, such as whether changes in phenology or physiology have consequences on demographic or population dynamics, whether there is a species signal, or alternatively, whether populations of the same species respond as differently as populations of different species, and if trends over time accurately reflect climate change responses.

Natural resource managers attempt to prioritise efforts based on how climate change will affect population size and persistence (Miller-Rushing *et al.*, 2010). Rather than consider how population dynamics are affected by climate, many studies focus on a variety of other types of trait responses, such as phenology, physiology or life-history responses. Many of these studies assume that these trait responses result in changes in demographic rates (e.g. survival or reproductive success) and ultimately lead to population-level responses (e.g. population growth rate, local extinction risk). In Chapter 1, I use a conceptual hierarchical framework to better understand and help predict the situations in which changes in phenotypic traits and demographic rates resulting from climate change will have the strongest consequences for population dynamics. Under this hierarchical framework, a change in the local climate can impact the trait level, which may in turn affect demographic rates, and subsequently population dynamics. I synthesise the literature to find testable hypotheses about life-history and ecological characteristics that could predict the situations in which climate-induced trait responses will likely affect population dynamics. Additionally, I examine a 48 year data set on 35 bird species found in the United Kingdom, to provide a quantitative example of how such *a priori* hypotheses can be tested for the long-standing question: “when do climate-induced changes in timing of egg-laying affect reproduction and population growth?”

It is generally assumed that different populations within a species will have similar responses to climate change. As a result, single values of sensitivity are typically used to reflect species-specific responses. There is some evidence in the literature that suggests a strong species signal might exist for phenological changes (Rubolini *et al.*, 2007; Thackeray *et al.*, 2016), but we have no indication as to whether this might hold true more generally for other types of climate responses (Malyshev *et al.*, 2016), particularly for key state variables such as body condition, growth or vital rates (reproduction, survival) that determine the population responses relevant for conservation. In Chapter 2, I examine an extensive 21-year data set on 46 common passerine species from 80 constant effort sites in the Netherlands to investigate whether generalising climatic responses in body condition to a single value for a species is meaningful by comparing the relative amounts of within- to among-species variation. Body condition (mass corrected for size; i.e. amount of fat reserves) is a key state variable, yet the impacts of climate changes on body condition have been less well studied than responses in phenology and range shifts (Gardner et al., 2011). To date, there are no projections for how body condition is likely to change under future climate scenarios, and the time periods (e.g. winter, spring) during which climate has the strongest impact on body condition are rarely systematically tested and remain poorly understood (Gardner et al., 2014; van de Pol et al., 2016). Finally, typically only linear responses have been considered, so it is unclear as to whether body condition responses might be non-linear (but see Yom-Tov et al., 2006; Salewski et al., 2010). Using this extensive dataset, I address these questions.

The majority of the literature investigating the consequences of changes in body condition is unrelated to climate (although see Gardner *et al.*, 2016). In general, decreased body condition is considered to reduce survival and reproduction, as it is typically associated with poor foraging conditions (Bergan & Smith, 1993; Naef-Daenzer *et al.*, 2001; Møller & Szép, 2002; Harding *et al.*, 2011; Aubry *et al.*, 2013; Krams *et al.*, 2013; Paquette *et al.*, 2014). However, there are some scenarios in which decreased body condition could be advantageous and lead to higher survival and reproduction, such as reduced energy expenditure, reduced predation and improved flight capabilities (Covas *et al.*, 2002; Senar *et al.*, 2002; Quillfeldt *et al.*, 2006; Rogers, 2015). In Chapter 3, I use the framework developed in Chapter 1 to quantify the effects of temperature-induced changes in body condition on annual survival and reproductive success, and the subsequent impact on the population growth rate. Further, I examine inter- and intra-specific variation at each level of the hierarchy, and whether life history and ecological characteristics can explain these relationships.

Another limitation in the field of climate change ecology is that much of the literature investigating the effects of climate change on organisms does not directly relate climate variables to changes in traits such as phenology. Instead, they assume that temporal trends accurately reflect responses to climate change, and therefore investigate trait changes over time. The decision to relate systematic variation in traits through time rather than directly to climate relies on three important assumptions: that other non-climatic causal agents are not changing over time, that climate affects the trait of interest, and that the climate experienced by the organism or system is changing over time. Non-climatic effects, such as habitat loss, modification or degradation, pollution, spread of invasive species, loss of keystone species, spread of diseases or overexploitation may also be changing over time (Edinger *et al.*, 1998; Wilcove *et al.*, 1998; Mora *et al.*, 2007; Brook, 2008). We currently have little understanding of how strongly such non-climatic causal agents contribute to temporal trends and what their combined effects with climate might be, or how this might vary for different traits. In Chapter 4, I explore whether changes in four commonly examined trait responses (lay date, body condition, fledglings per breeding attempt and proportion of juveniles) over time can be assumed to be driven by warming temperatures. It is important to know the contributions, magnitude and directions of both non-climatic and climatic causal agents, not only to improve our predictive models, but to develop appropriate conservation management strategies (Parmesan & Yohe, 2003; Wright *et al.*, 2009).

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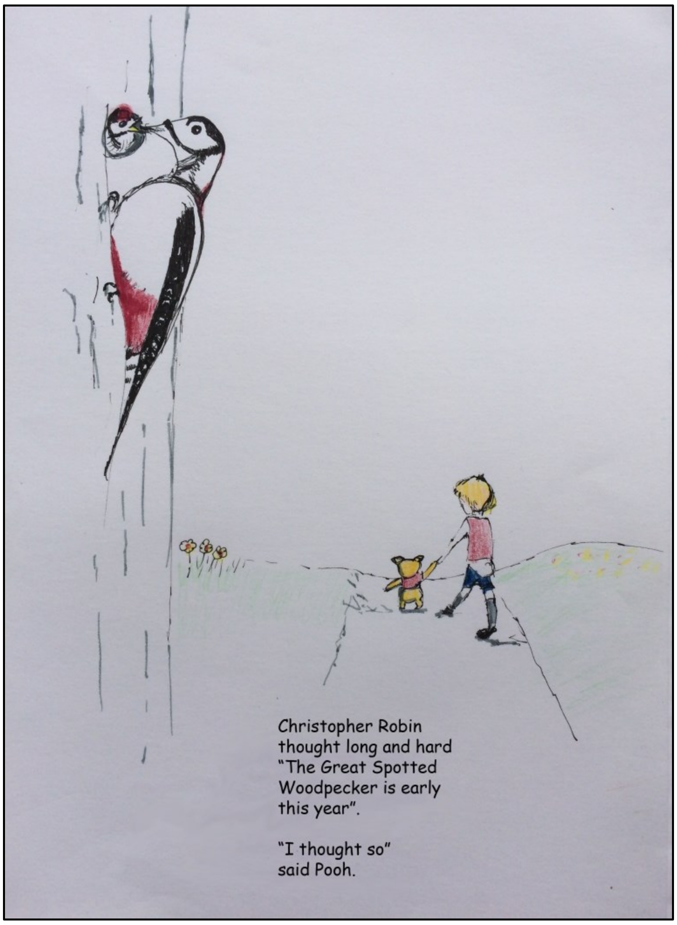
Chapter 1

Predicting when climate-driven phenotypic change affects population dynamics



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Abstract

Species’ responses to climate change are variable and diverse, yet our understanding of how different responses (e.g. physiological, behavioural, demographic) relate and how they affect the parameters most relevant for conservation (e.g. population persistence) is lacking. Despite this, studies that observe changes in one type of response typically assume effects on population dynamics will occur, perhaps fallaciously. We use a hierarchical framework to explain and test when impacts of climate on traits (e.g. phenology) affect demographic rates (e.g. reproduction) and in turn population dynamics. Using this conceptual framework, we distinguish four mechanisms that can prevent lower-level responses from impacting population dynamics. Testable hypotheses were identified from the literature that suggest life-history and ecological characteristics which could predict when these mechanisms are likely to be important. A quantitative example on birds illustrates how, even with limited data and without fully parameterised population models, new insights can be gained; differences among species in the impacts of climate-driven phenological changes on population growth were not explained by the number of broods or density-dependence. Our approach helps predict the types of species in which climate sensitivities of phenotypic traits have strong demographic and population consequences, which is crucial for conservation prioritisation of data-deficient species.

Introduction

Anthropogenic climate change is predicted to be a major cause of extinctions in the near future (Thomas *et al.* 2004). Consequently, natural resource managers and policy makers are interested in how climate change will affect population size and persistence and which species will be most affected (Miller-Rushing *et al.* 2010). However, much of the research on responses to climate change actually does not consider how population size, population growth rate or extinction risk varies as a function of climate. Instead, most studies tend to focus on a variety of other types of responses, most notably phenology (e.g. timing of migration or reproduction; Cotton 2003; Sherry *et al.* 2007), physiology (e.g. body size; Ozgul *et al.* 2010), behaviour (e.g. behavioural thermoregulation; Glanville & Seebacher 2006), life-history (e.g. length of gestation period; Clements *et al.* 2011) or demographic rates such as survival and reproduction (e.g. adult survival; Leech & Crick 2007). Understanding the climate sensitivities of these phenotypic traits and demographic rates is of interest in its own due to the insights into underlying processes, but will generally only be relevant for conservation if the effects of such changes are apparent at the level of population dynamics. This last step is typically assumed, but rarely explicitly tested. Consequently, the mechanisms causing climate-induced population changes are still poorly understood (e.g van de Pol *et al.* 2010).

The few empirical studies to have quantified how phenological, physiological or life-history responses to climate affect demographic rates or population-level responses have reported contrasting outcomes (e.g. Chase *et al.* 2005; Ozgul *et al.* 2010; Pearce-Higgins *et al.* 2009; Plard *et al.* 2014; Wilson & Arcese 2003; Wright *et al.* 2009). For example, earlier breeding increased the development rate of a yellow-bellied marmot (*Marmota flaviventris*) population which increased reproductive output, leading to a rapid increase in population size (Ozgul *et al.* 2010). Conversely, earlier breeding in song sparrows (*Melospiza melodia*) increased reproductive output, but had little effect on the population size (Wilson & Arcese 2003). It is now clear that climate-induced changes in phenotypic traits or demographic rates affect population dynamics in some species but not in others (Dunn & Møller 2014; Miller-Rushing *et al.* 2010; Reed *et al.* 2013a; Robinson *et al.* 2014); yet, for any given species, there remains little basis for predicting which of these outcomes is most likely.

Progress can be made by studying the mechanisms that determine whether phenotypic traits or demographic rates impact population dynamics, and linking such mechanisms to species' life-history and ecological characteristics (Miller-Rushing *et al.* 2010). For example, changes in adult survival tend to have stronger effects on the population dynamics of long-lived species than of short-lived species, suggesting that longevity might be used to predict when climate effects on survival will translate to population growth (Jenouvrier *et al.* 2009; Sæther & Bakke 2000; Sandvik *et al.* 2012). Such information is potentially of great value to biodiversity conservation, because practitioners could use species characteristics to prioritise conservation efforts towards those most likely to be at risk of climate change. Being able to generalise by extrapolating to less well-studied species is crucial, because for most species the required data to make an independent assessment is lacking (Foden *et al*. 2013; Pearson *et al.* 2014).

Here, we use a hierarchical framework to better understand and help predict the situations, populations and species in which climate-driven changes in phenotypic traits and demographic rates will have the strongest consequences for population dynamics (Ådahl *et al.* 2006; Jongejans *et al.* 2010; Morrison & Hik 2007). Using this conceptual framework, we identify four mechanisms that could prevent changes in traits and demographic rates from affecting population dynamics. We then synthesise the literature to find testable hypotheses about life-history and ecological characteristics that could either strengthen or weaken these mechanisms in different species or populations. Subsequently, we illustrate with a quantitative example on 35 British bird species how such *a priori* hypotheses can be tested for the long-standing question, when do climate-induced changes in timing of egg-laying affect reproduction and population growth (Dunn & Møller 2014; Reed *et al.* 2013a ; Wilson & Arcese 2003). Importantly, our approach can use existing empirical data to give key new insights into how changes in lower-level responses impact population responses in different species, even without knowledge about all factors and pathways affecting population dynamics and the need to construct population matrix models.

Hierarchical framework

The many types of responses to changes in climate mentioned in the Introduction can be categorised into hierarchical levels, from trait-level responses to demographic- and population-level responses (Fig. 1). Under this hierarchical framework, a change in the local climate can impact the trait-level, which in turn can affect demographic rates, and subsequently population dynamics. The decomposition of population responses into contributions from different underlying elements is a powerful quantitative and analytical tool to better understand how population dynamics respond to climatic variation (Ådahl *et al.* 2006; Jongejans *et al.* 2010; Morrison & Hik 2007; Nichols & Hines 2002). Decomposition approaches are well established in theory on demographic population matrix and integral projection models (Easterling *et al.* 2000). We propose–and later illustrate with a quantitative example–that even in cases where not all information is available to construct population models, this conceptual framework and decomposition approach (building on Nichols & Hines 2002) can still be used to test key hypotheses (see Box 1 for limitations). Furthermore, the strength of each of the underlying relationships can be easily estimated from empirical data (Box 1).

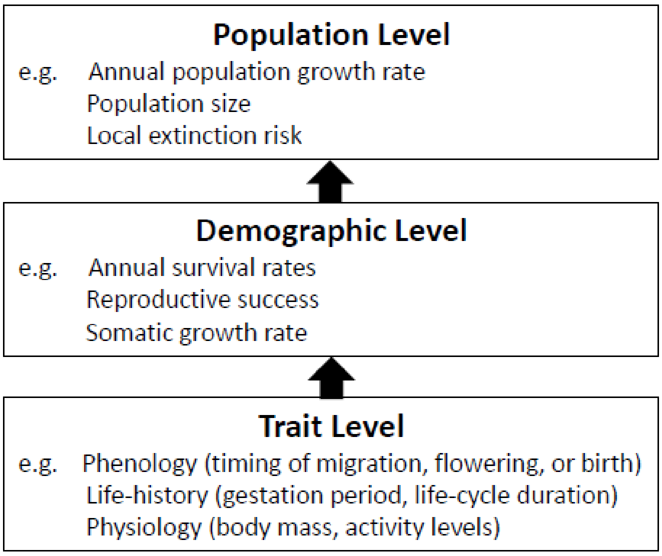

Figure 1 Hierarchical levels of responses to climate change. Changes at the trait-level can impact demographic rates, which can subsequently impact population dynamical parameters.

The hierarchical framework and decomposition of pathways allows us to identify four types of mechanisms that could prevent a change in trait from impacting the population-level (although it should be noted that the conceptual framework could be extended to consider responses at other levels, such as genetic- or metapopulation-levels, as well as non-climatic environmental variables).

Single pathway mechanisms

We can begin by considering climate responses within a *single pathway*. In order for changes in climate to result in a population-level response (expressed as dP/dC_1 in equation 1; Fig. 2ai and 2aiii), three processes need to occur: (i) a change in climate (C_1) must impact the trait (T_1), (ii) the change in trait must impact the demographic rate (D_1), and (iii) the change in demographic rate must impact the population parameter (*P*; i.e. $dT_1/dC_1 \neq 0$, $dD_1/dT_1 \neq 0$ and $dP/dD_1 \neq 0$). When this occurs, there will be observable relationships between trait and climate; demography and climate; and population and climate (Fig. 2aii).

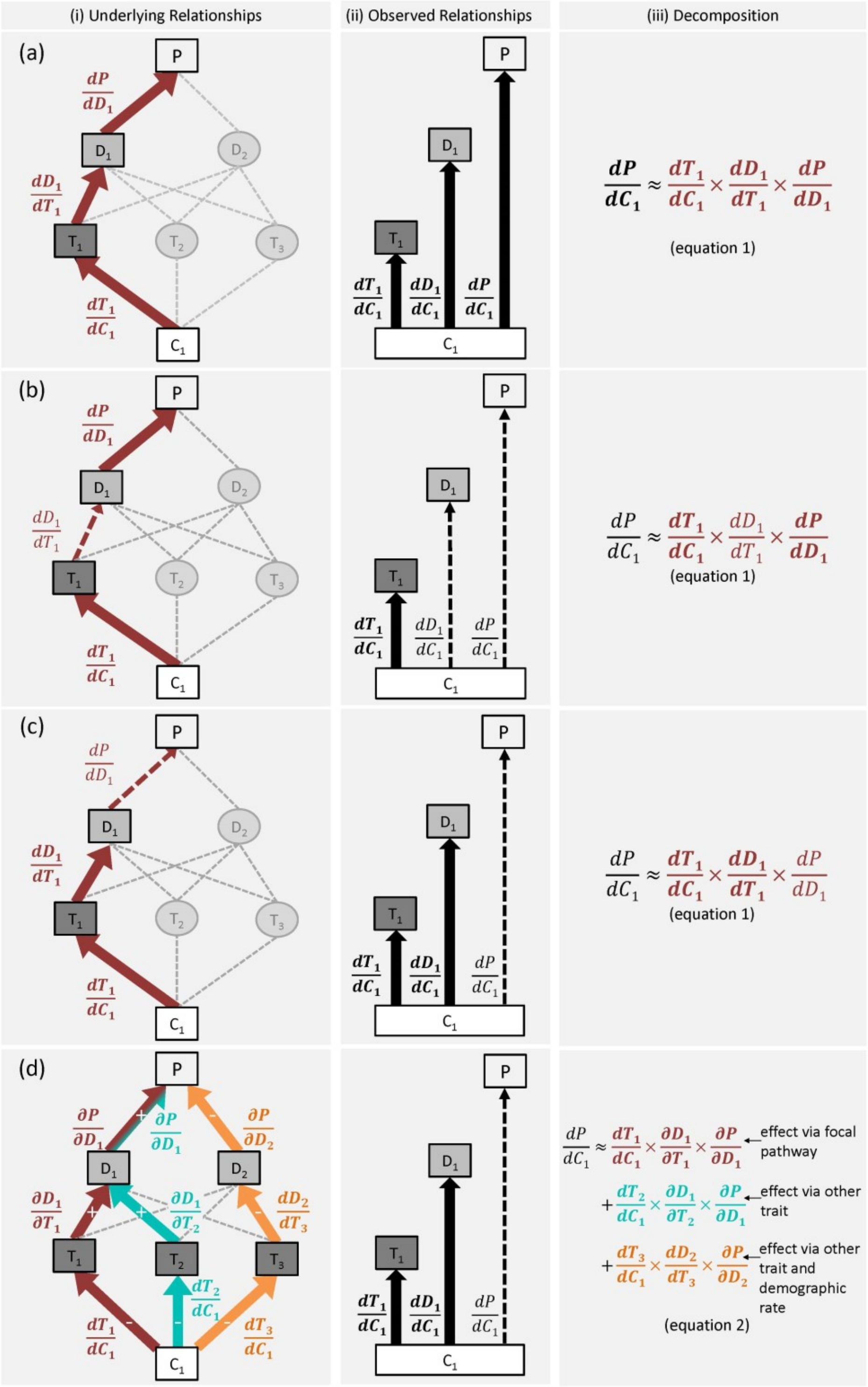

Figure 2 Hierarchical framework showing the relationships between the different hierarchical levels through which a climate variable (C_1) can affect population dynamics; via a trait (*T*), a demographic rate (*D*) to a population parameter (*P*). Horizontal panel **(a)** shows strong relationships between each level, **(b)** shows a weak relationship between trait and demography, **(c)** shows a weak relationship between demography and population, and **(d)** shows multiple pathways each with strong relationships that

counteract (+/- signs) and thus result in no observable impact to population dynamics. The vertical panels show **(i)** the underlying relationship: thick arrows represent strong and dashed arrows weak relationships between levels (dashed grey lines show other possible connections between unobserved traits and demographic rates shown as circles), **(ii)** the observable relationships that would be detected between climate and each of the three response variables in the hierarchy (thick arrows show direct observable relationships and dashed arrows weak relationships)., and **(iii)** the decomposition of the relationships; the change in population from a small change in climate ($\frac{dP}{dC_1}$) is the product of each of the underlying relationships between climate, trait and demography. Please note that in Equation 1, the full derivative terms $\frac{dP}{dC_1}$ and $\frac{dT_1}{dC_1}$ represent the absolute change in population (P) and a trait (T_1), respectively, associated with small changes in climate (C_1). By contrast, in equation 2 we are interested in how multiple pathways are influenced by a change in climate and their overall effects on the population-level, and thus relationships reflect partial derivatives, e.g. $\frac{\partial P}{\partial D_1}$ & $\frac{\partial P}{\partial D_2}$, where relationships are estimated in one pathway while accounting for effects of other pathways.

Population responses cannot always be predicted based on the observed changes in traits or demographic rates alone. Assuming that climate has an effect on a trait, there are two non-mutually exclusive mechanisms that could prevent a population response from occurring. Firstly, the change in trait has no, or little effect on the demographic rate (i.e. $dD_1/dT_1 \approx 0$; Fig. 2b). In this case, even if there was a strong relationship between demography and population growth, there would not be an observable relationship between climate and demography or climate and population (Fig. 2bii). Secondly, the change in demographic rate has no or little effect on population dynamics (i.e. $dP/dD_1 \approx 0$; Fig. 2c). As a result, there would not be an observable relationship between climate and population growth (Fig. 2cii).

Multiple Pathway Mechanisms

Even when the relationships within a single pathway are exactly known, changes in climate variables might also affect other traits or demographic rates, causing the population response to a given climate variable to be stronger or weaker than expected (i.e. multiple pathways; Fig. 2d). There are two non-mutually exclusive mechanisms that could either strengthen or weaken a population response. Firstly, a single climate variable could affect population dynamics via multiple traits and/or demographic rates, resulting in multiple pathways (Fig. 2di). Secondly, multiple climate variables could influence the same trait (Kruuk *et al.* 2015) or demographic rate (Rudolf & Singh 2013), or influence otherwise unaffected traits. Multiple pathways and climate variables can result in stronger, reinforced (Gibbs *et al.* 2012; Scherber *et al.* 2013), or weaker, counteracted responses than expected when the effects of a single climate variable are considered in isolation (Larsen *et al.* 2011; Leuzinger *et al.* 2011). Therefore, accounting for their combined effects can be necessary to explain observed changes in population dynamics (Stopher *et al.* 2014). The climate sensitivity of population dynamics (dP/dC_1) might therefore not be accurately predicted by considering a lower-level response ($dD_1/d\Delta C_1$ or dT_1/dC_1) from a single pathway alone (Fig. 2diii).

Hypotheses based on species characteristics

Having established four mechanisms by which a climate-induced change in a trait may or may not affect population dynamics, the key challenge is now to understand whether species' life-history and ecological characteristics can predict when these mechanisms are likely to play an important role. Comparative methods are a valuable and widely-utilised approach for identifying species characteristics that help explain species declines or extinctions (Buckley & Kingsolver 2012; Cardillo *et al.* 2005; Fisher & Owens 2004). However, these approaches often rely on explanatory characteristics that have not always been derived *a priori*, that do not have clear underlying biological mechanisms or have expectations for the direction of their effects (but see e.g. Sandvik & Erikstad 2008). To this end, we identified testable hypotheses from the literature suggesting life-history and ecological characteristics that might explain when changes in traits or demographic rates are likely to have further consequences, and if their effects are likely to be reinforced or counteracted from multiple pathways or climate variables (Table 1; See Appendix 1 for methods). These hypotheses are applicable for a broad range of taxa and can be tested in future comparative analyses to determine whether or not they would make useful predictor characteristics.

Some of the hypotheses identified had been thoroughly researched and were based on quantitative evidence, while other hypotheses were based on single-sentence suggestions or speculations, or patterns that we then translated into a potential hypothesis. Some hypotheses specifically concerned one species or group, yet we framed these hypotheses as general as possible. Our aim here was not to determine how well supported or likely these hypotheses were, but to overview the characteristics that might explain variation among species in population response for future comparative analyses.

Box 1 Quantifying pathways from data, limitations and alternative approaches

A decomposition approach requires one to estimate the full and partial derivatives shown in Figure 2 from data. These derivatives reflect the effect sizes of traits, demographic rates, and population growth rates to each other (e.g. how much reproductive success changes per lay date), and to climate (e.g. how much egg-laying date changes per degree Celsius). We assume that changes in the climate, traits and demographic rates are relatively small, such that we can characterise the relationships between these variables as being roughly linear. Structural equation models are a suitable tool as they allow one to estimate all these relationships (i.e. slopes) in a single model. They also allow for distinguishing indirect from direct effects; i.e. estimating the partial derivatives of the focal pathway using partial regression coefficients, while statistically controlling for the effect of climate via another direct pathway, and vice versa (see worked example section & Fig. 3; Pugesek *et al*. 2003). In some cases it could also be possible for changes in climate to directly impact the demographic-level (e.g. climate affecting annual survival). However, we generally consider that these effects occur indirectly through underlying changes in a (unknown) trait (e.g. body condition).

Although our hierarchical framework is inspired by demographic theory on matrix population and integral projection modelling, we do not use population models to estimate the relationships between climate, demographic and population growth rates. A population modelling approach could have been possible and even more powerful, but it requires relatively complete data on all demographic rates, which is often unavailable for many species. Our statistical approach of calculating the dependency of annual realised population growth rate directly from the population size time series has the advantage that it can still produce new key insights into the importance of certain climate-trait-demography pathways for population dynamics, with fewer assumptions needed to be made (e.g. about the st(age)-dependency of the demographic rates determining the lifecycle structure). A drawback of this purely statistical approach is that it cannot easily deal with species with strongly st(age)-structured lifecycles, such as delayed reproduction and other sources of time lags that can cause short-term population-level responses to climate change being weak (Robinson *et al.* 2004).

Responses to changes in climate (or trait/demographic rate) are not only affected by changes in mean conditions, but also by (interannual) variation in conditions (Boyce *et al*. 2006). Climatic variability can potentially even alter the effects of changes in the mean climate (Lawson *et al*. 2015). The magnitude and direction of the impact of variation in climatic conditions depend directly on the curvature of the relationships (quantifiable by the second derivative; Ruel & Ayres 1999), and can also be predicted by species characteristics (Lawson *et al*. 2015). However, it is not straightforward to extend our hierarchical approach to include variability at the levels of vital rates and traits, as the effect of variability in the traits and vital rates affecting population growth rate not only depend on the second derivative of the relationship but also on the covariance patterns among traits and vital rates (Barraquand & Yoccoz 2013). Thus, it requires predicting both the means and variances of the variables at each level and the covariances between them (Barraquand & Yoccoz 2013; Lawson *et al.* 2015). Additionally, the theory describing exactly how covariance patterns determine the impact of variability requires further theoretical development (Lawson *et al.* 2015).

Nonetheless, we would like to emphasise that effects of climatic variability on responses are negligible as long as responses are roughly linear or there is little climatic variability, in which case solely focussing on changes in climatic means is sufficient. Although responses would be non-linear when populations are experimentally exposed to the full range of climate (e.g. populations cannot grow in extreme cold or heat), on a local scale in the wild, responses can often be treated as linear because populations exhibit much less curvature when only a small part of the climatic range is experienced. The validity of these assumptions regarding linearity and variability can be tested by re-fitting each of the relationships in the hierarchy with flexible functional forms that allow for non-linear effects (e.g. using generalised additive models, GAMs; Wood 2006), and then calculating how much the mean response is altered by the inclusion of variation in the explanatory variable. If the mean response differs substantially, this suggests that the effects of climate variability may need to be explicitly incorporated into predictions of the response to climate change.

Single pathway hypotheses

We identified many explanatory characteristics from the literature that could explain interspecific variation in the strength of the relationship between trait- and demographic-level responses (Table 1a). Most explanatory characteristics were specific to certain types of traits, including phenology, body mass and sex ratio skews. For example, species may be more likely to experience strong demographic responses from phenological changes if they live in seasonal habitats, because changes in timing could result in mismatches with important resource peaks (Both *et al.* 2010). Species that reproduce only once a year are hypothesised to have stronger reproductive responses to phenological changes than species that breed multiple times throughout the year, because there is a higher risk that all of their offspring will be born during a period that lacks important resources (Jiguet *et al.* 2007).

One hypothesis was broadly applicable to many types of trait changes. Specialist species that are dependent on single hosts or specific or seasonal resources are expected to have stronger relationships between traits and demographic rates because their resources are more constrained compared to generalists. For example, phenological shifts are likely to have stronger impacts on demography for specialist species that depend on a particular resource which is only available for a specific time, while generalists are more likely to be able to switch to other resources to meet their needs (Miller-Rushing *et al.* 2010).

We also identified many explanatory characteristics that could explain species variation in the strength of the relationship between demographic- and population-level responses (Table 1b). Analyses of the varying contributions of demographic rates to population dynamics are common (Heppell 1998; Heppell *et al.* 2000; Sæther *et al.* 1996; Sæther & Bakke 2000; Silvertown *et al.* 1993). Species' life-history characteristics are believed to strongly influence these relationships. Specifically, changes in adult survival have stronger impacts on population dynamics in species that are long-lived, experience late maturation or produce few offspring compared to species that are short-lived, experience early maturation or produce many offspring. By contrast, changes in reproductive success will tend to have much stronger effects on population dynamics in short-lived than in long-lived species (Sæther & Bakke 2000).

Table 1 Hypotheses from the literature (with invoked life-history and ecological explanatory characteristics) to explain differences among species in **(a)** the strength of the relationship between trait- and demographic-level responses, **(b)** the strength of the relationship between demographic- and population-level responses, and **(c)** how likely a species is to have a single climate variable affect multiple traits or demographic parameters that reinforce or counteract higher-level effects. The first column differs slightly for each section, such that it specifies the trait **(a),** demographic rate **(b)**, or whether the pathways are likely to strengthen (reinforce) or weaken (counteract) the higher-level response **(c)**.

(a) Trait	Explanatory characteristic	Hypotheses: A stronger relationship exists between trait- and demographic-level rates in species or populations that …
Any trait	Specialisation / Resource dependence	are specialists, dependent on a single host species or a specific or seasonal resource, as they are limited by other species and/or resources, whereas generalists are not constrained to the same extent [1-5].
Phenology	Habitat seasonality / Resource duration	live or breed in strongly seasonal environments or rely on narrow food peaks for breeding, as an increased probability of mismatches between important events (e.g. reproduction) and important resources can have strong repercussions [5, 6-10].
Phenology	Breeding seasonality	have temporally well-defined (non-opportunistic) breeding seasons, as changes resulting in timing outside of the season are likely to be costly (e.g. mismatches or unfavourable conditions) [11]. However, [11] also found that this relationship can potentially also be strong in year-round breeders.
Phenology	Annual number of reproductive events	reproduce once a year, as there is a higher risk of mistiming their single breeding event [12]. However, species with multiple reproductive events could also benefit if the time between reproductive events is extended and this improves survival [5].
Phenology	Degree of parental care	have extensive parental care, as a change in reproductive timing can affect the period of parental effort and daily work rate (affecting parental survival) [13].
Phenology	Income/capital breeder	rely on resource intake during breeding rather than stored resources (e.g. fat, food source), as they are strongly constrained by the availability of high quality resources [14].
Body size	Seasonally forced life-history	have a seasonally forced life-history (e.g. fixed size at age of maturity), as not being a certain size at a given time (e.g. life-stage transitions) may require a growth rate out of proportion to food availability, coming at a cost of sacrificing reserves or future reproductive success. By contrast, in non-seasonally forced environments, individual growth rates can vary proportionately with food availability leading to, for example, more flexible ages of maturation [15].

Sex ratio skew	Sperm storage	are unable to store sperm, as they are more dependent on encountering and mating with scarce males and are consequently more susceptible to reproductive isolation [16].
Sex ratio skew	Reproductive strategy	are unable to mate with multiple individuals [16], as some individuals of the more common sex will not be able to reproduce.
Sex ratio skew	Male aggression	have high male aggression, as a male biased population exacerbates the occurrence of aggression, which may lead to social dominance, reproductive suppression, infanticide or sexual coercion [17].
(b) Demo-graphic rate	**Explanatory characteristic**	**Hypotheses:** **A stronger relationship exists between demographic- and population-level rates in species or populations that …**
Survival	Longevity / age of maturation / fecundity	are long-lived, late maturing or have low numbers of offspring [14, 18-23, but see 24, 25], as the population growth rate is more sensitive to changes in survival in such species.
Reproduction	Longevity / age of maturity / fecundity / semelparity	have low survival rate, short generation times, early maturation, high numbers of offspring or only reproduce once in their lifetime [20-23, 25-27], as the population growth rate is more sensitive to changes in reproduction in such species.
(c) Pathways' interaction	**Explanatory characteristic**	**Hypotheses:** **A higher likelihood of a single climate variable affecting multiple traits or demographic rates in species or populations that…**
Reinforced	Intermittency of reproduction	cannot skip or alter their reproductive strategy during unfavourable conditions, as such species are more likely to experience decreases in both survival and reproductive success, which will result in stronger population-level declines. By contrast, species that can skip reproduction will experience declines in reproductive success, but not in adult survival [4, 28-30].
Reinforced	Reliance on susceptible habitat types	rely on susceptible habitat types such as ice/snow or water bodies for multiple functions. For example, in some species, the loss of ice substrate or water bodies can impact multiple critical functions, such as resting, reproduction, molting, food availability, development, phenology, risk of desiccation and migration ability [31-36].
Reinforced/ Counteracted	Ectothermy / poikilothermy	are ectothermic/poikilothermic, as changes in temperature affect many processes such as hearing, development, activity, immune responses [37-38].
Reinforced	Food limitation	are food limited, as this may lead to trade-offs between traits or demographic rates, such as between growth and reproduction or between fecundity and future survival [15,39-40].
Counteracted	Strength of density-dependence	experience strong density-dependent regulation. For example, reduced annual fledgling production from changes in phenology can be counteracted by increased post-independence survival of offspring [10].

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Multiple pathways hypotheses

Using single pathway characteristics alone will not always be enough to accurately predict how a climate-induced change in trait will affect population dynamics because the population response could also be affected by other pathways. Therefore, in addition to determining the strength of relationships within a single pathway, we also identified testable multiple pathway hypotheses from the literature suggesting life-history and ecological characteristics that might explain when changes in traits or demographic rates are likely to be reinforced or counteracted at higher levels. These multiple pathway effects are classified into two mechanisms: (i) those due to multiple traits and/or demographic rates being affected by a single climate variable (Table 1c), or (ii) due to multiple climate variables.

One species characteristic that could explain when the effects of a change in trait or demographic rate are likely to be reinforced by another pathway is physiology. A change in climate could be more likely to affect multiple traits in species that are ectothermic or poikilothermic as many processes improve with temperature (e.g. development, digestion, activity). As a result, demographic-level effects may be stronger than would be expected when looking at a single trait.

As another example, it has been proposed that species that do not skip reproduction during unfavourable conditions (which could induce trait changes such as decreased body mass) are more likely to experience declines in both survival and reproductive success, therefore reinforcing the effects of climate at the population-level. Species that can skip reproduction, on the other hand, may experience greater declines in reproductive success but reduced declines in adult survival (Jenouvrier *et al.* 2005).

Another characteristic that could explain when the effects of a change in trait or demographic rate are likely to be counteracted by another pathway is the degree of density-dependence. Species in which density has a strong impact on population dynamics might have weaker population responses from changes in demographic rates than species with weak impacts of density. Although the above explanation may suggest density-dependence to be a single-pathway hypothesis, typically at least two demographic rates are involved, with the effect of climate on one demographic rate having knock-on effects on a second demographic rate. For example, in some birds a change in egg-laying phenology reduces annual fledgling production, which then increases post-independence survival of offspring due to decreased competition, such that there are virtually no population consequences of the phenological change (Reed *et al*. 2013a). As a result, the population-level effects are weaker than expected from looking at a single pathway alone. It should be noted that this hypothesis differs slightly from Fig. 2di, as the two counteracting vital rates are affected by each other, rather than both being independently effected by the change in the lower-level parameter.

To our knowledge hypotheses that explain when multiple climate variables (e.g. rain, temperature, humidity) either reinforce or counteract trait- or demographic-level effects have not yet been developed. However, two general areas could be of interest for future development of hypotheses. First, species that are sensitive to climatic and environmental disturbances in general could be expected to have multiple climate variables either reinforce or (depending on the specific effects of each variable) counteract population responses. For instance, larval or juvenile stages are typically less resilient to multiple environmental variables (Doyle *et al.* 2009), suggesting that species with long juvenile stages are more likely to be affected by multiple pathways. Weedy species or co-tolerant species, on the other hand, might be less likely to experience strong effects from multiple climate variables (Darling *et al.* 2013). Secondly, habitat characteristics might be important. For example, species living in regions or habitats that are dominated by a single climate variable might be less likely to experience other climate variables strongly influencing their population responses compared to species in habitats with no dominant climate variable. For instance, the dominant variable in arid environments –rainfall– has often been found to be the most biologically important climate factor in arid zone species, with other climatic variables having little importance (Altwegg & Anderson 2009; Lloyd 1999; Sæther *et al.* 2004). Additionally, the effects of climate change might be buffered for species in sheltered habitats (e.g. caves, deep sea and forests) or constructed or natural shelters (e.g. beaver lodge, tree hollows and burrows; Williams *et al.* 2008). These species are less likely to be impacted by multiple environmental variables because they are decoupled from prevailing climatic conditions and so the effects of those climate variables will be much weaker (Keppel *et al.* 2012). In comparison, species in exposed habitats could be affected by multiple climate variables that reinforce higher-level responses.

Testing hypotheses with data: a worked quantitative example

We conducted a worked example using data on 35 common British bird species over 48 years (1966-2013; BTO 2015) to (i) decompose how climate-induced changes in traits affect demographic rates and population dynamics (Fig. 3), and to (ii) test two hypotheses from Table 1. In many birds the timing of egg laying is under negative directional fecundity selection (‘earlier is better’; Brown & Brown 1999; Sheldon *et al*. 2003). Therefore, in our analysis we assessed the relationships within a single pathway, quantifying how temperature-induced changes in egg laying dates (trait-level) impact reproductive success (demographic-level; fledglings per breeding attempt) and how reproductive success in turn impacts the annual population growth rate (population-level; $r_t=\log(N_{t+1}/N_t)$). For each species, we first separately determined the time of year during which mean temperature best explained variation in mean laying date (see Appendix 1), using the R package *climwin* (Bailey & van de Pol 2015) and the Central England Temperature dataset (Parker *et al*. 1992). Subsequently, we used structural equation models (SEMs) for each species to derive the path coefficients among hierarchical levels (presented in Fig. 3i; see Appendix 1 for details). SEMs can simultaneously quantify the strength of relationships (partial regression coefficients) within the focal lay date pathway (called indirect effects in SEMs), while accounting for the effects of other pathways of temperature (called direct effects here, as we have not measured any other traits or demographic rates that could have mediated the effects of other pathways).

We tested whether the single pathway hypothesis, the 'annual number of reproductive events', explained whether temperature-driven phenology shifts affected demographic and population dynamics (Table 1a). We predicted that single-brooded species that exhibited a temperature-dependent change in egg-laying date would show a stronger response in terms of reproductive success than multi-brooded species, because there is a higher risk that all of their offspring will be born during a period that lacks important resources (Jiguet *et al.* 2007). We also tested the multiple pathways "strength of density-dependence" hypothesis (Table 1c) to investigate whether a second pathway could potentially be counteracting any population-level effects from changes in temperature (see Appendix 1 for details). Here, the expectation was that a given change in reproduction would have a weaker effect on the population growth rate in species with stronger density-dependence compared to weakly regulated species. This is because post-independence survival of offspring may decrease in more strongly regulated species due to increased competition, such that the population consequences of changes in phenology and fledgling productivity are dampened (Reed *et al.*, 2013a).

Decomposing the pathway

Of the 35 species studied, 27 laid their eggs earlier in warmer years. Each 1°C increase in mean temperature during spring (typically during March-May) was associated with individuals laying their eggs 3.8 days earlier on average (Fig. 3a; the remaining 8 species showed no clear relationship between lay date and temperature during any period and were excluded from further analyses; Appendix 1). Earlier egg-laying was associated with increased reproductive success in many species (Fig. 3b), such that those species that advanced their lay dates most in response to warming also experienced the greatest increases in reproduction (Fig. 4a; r^2=0.21; model 3 in Appendix 2 Table S1; removing the magpie from this analysis decreases the estimate from -0.032±0.011SE to -0.019±0.012SE (model 1 in Appendix 2 Table S3), suggesting that the magpie has a large influence but is not driving the entire relationship). Moreover, the total effects (see Fig. 3ii & 3iii) of temperature on reproductive success were well predicted by the (indirect) lay date pathway (Fig. 4b; r^2=0.41; model 1 in Appendix 2 Table S1). However, there was also an important direct effect of temperature on reproduction (the blue pathway in Fig. 3i; r^2=0.29). These results suggest that the effects of temperature on reproductive success are, for a substantial part, acting via the effects on the phenology of egg-laying (or via another correlated causal trait of which lay date is a proxy), but that another pathway mediated by an unmeasured trait(s) could also be important.

Although the effects of spring temperature on lay dates predicted the effect of temperature on reproduction well, they poorly predicted how temperature affected population growth rate (Fig. 4c; r^2=0.02, model 1 in Appendix 2 Table S2). Moreover, the total effects of temperature on the population growth rate were not explained by the (indirect) lay date and reproductive success pathway (Fig. 4d; r^2=0.00; model 2 in Appendix 2 Table S2; the removal of the redstart did not change this, see Appendix 2 Table S5). These results suggest that the strong effects of temperature on phenology and subsequently on reproductive success are not carrying through to the population growth rate, possibly due to unmeasured multiple pathways.

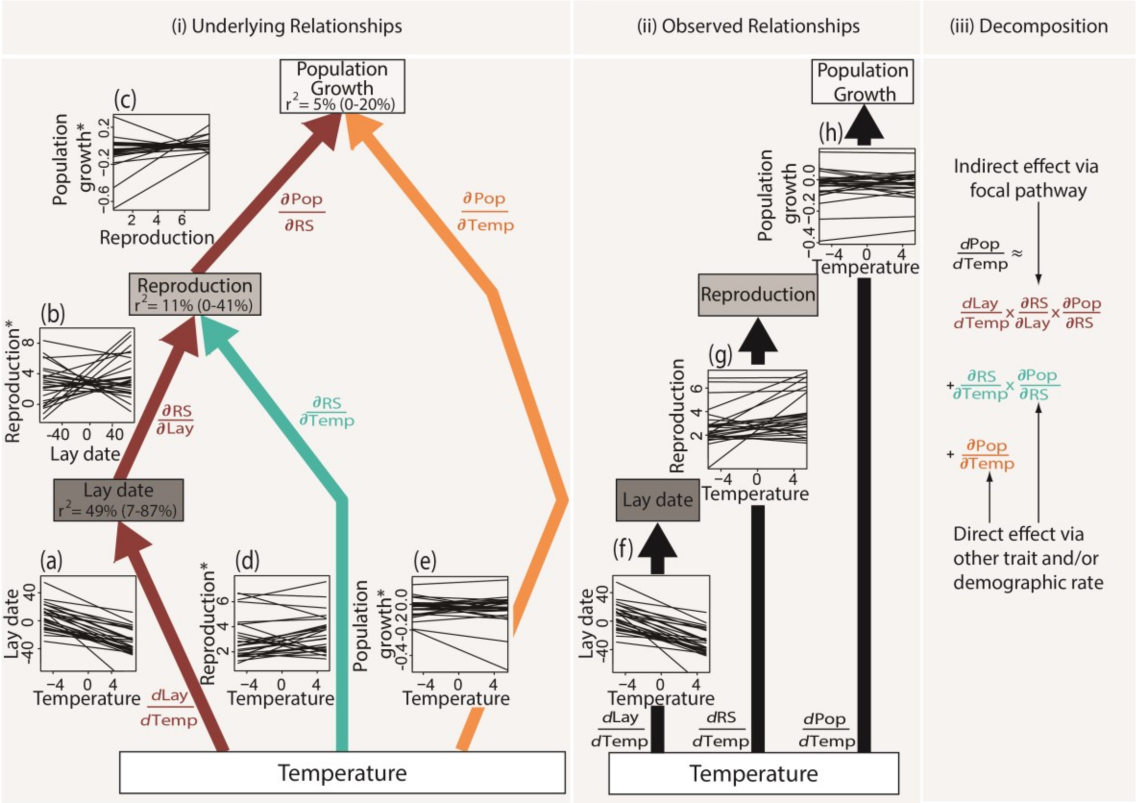

Figure 3 Decomposition of pathways by which climate-driven phenological change affects reproductive success and population growth rate in 27 bird species. Panel (i) “Underlying Relationships” displays the graphical model used in the structural equation analysis carried out on each species. The model includes the indirect effects of temperature on population growth rate via lay date and reproduction (the red, focal pathway), as well as the direct effects of temperature on reproductive success ($\frac{\partial RS}{\partial Temp}$; blue path) and on population growth rate ($\frac{\partial Pop}{\partial Temp}$; orange path). Plots (a)-(h) show the regression estimates for each path, with each line representing a different species. The r^2 values for each variable show the mean amount of variation explained by all pathways, and in parentheses the minimum and maximum r^2 values across all species. The * (as well as the ∂ symbol) denotes those dependent variables that have partial coefficients, where the slope represents the effect once the influence of the other variable is controlled for. Panel (ii) “Observed Relationships” shows the total effect (indicated as full derivatives) of temperature on lay date, reproduction and population growth rate, based on all direct and indirect effects. The total effect of temperature on reproduction is calculated as $\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} + \frac{\partial RS}{\partial Temp}$. Panel (iii) “Decomposition” shows how the total effect of temperature on the population growth rate is calculated. The direct effects act via some other unmeasured trait and/or demographic rate. Note that temperature and lay date are mean centred in (a)-(h).

Testing two hypotheses

Consistent with the ‘annual number of reproductive events’ hypothesis, we found that changes in lay date were more strongly associated with per nest reproduction in single brooders than in multi-brooders (difference of 0.03±0.01SE fledglings/day; r^2=0.24; 5.9 $AICc$ better than the null model). Notwithstanding, the number of broods was of relatively little use for predicting in which species temperature effects on phenology would have the strongest impacts on reproduction (Fig. 4a; ΔAICc = -3.8 model 2 vs. 3 in Appendix 2 Table S1). Despite this, we unexpectedly found that warmer temperatures were generally associated with increased population growth rates in multi-brooders, but decreased population growth in single-brooders (Fig. 4c; ΔAICc =5.3 model 3 vs. 0 in Appendix 2 Table S2). This suggests that spring temperature could be impacting the population growth rate of single- and multi-brooders via a pathway other than lay date and reproductive success. Thus, multi-broodedness may be a useful characteristic for predicting the impacts of global warming on population growth, but for reasons unrelated to the original hypothesis.

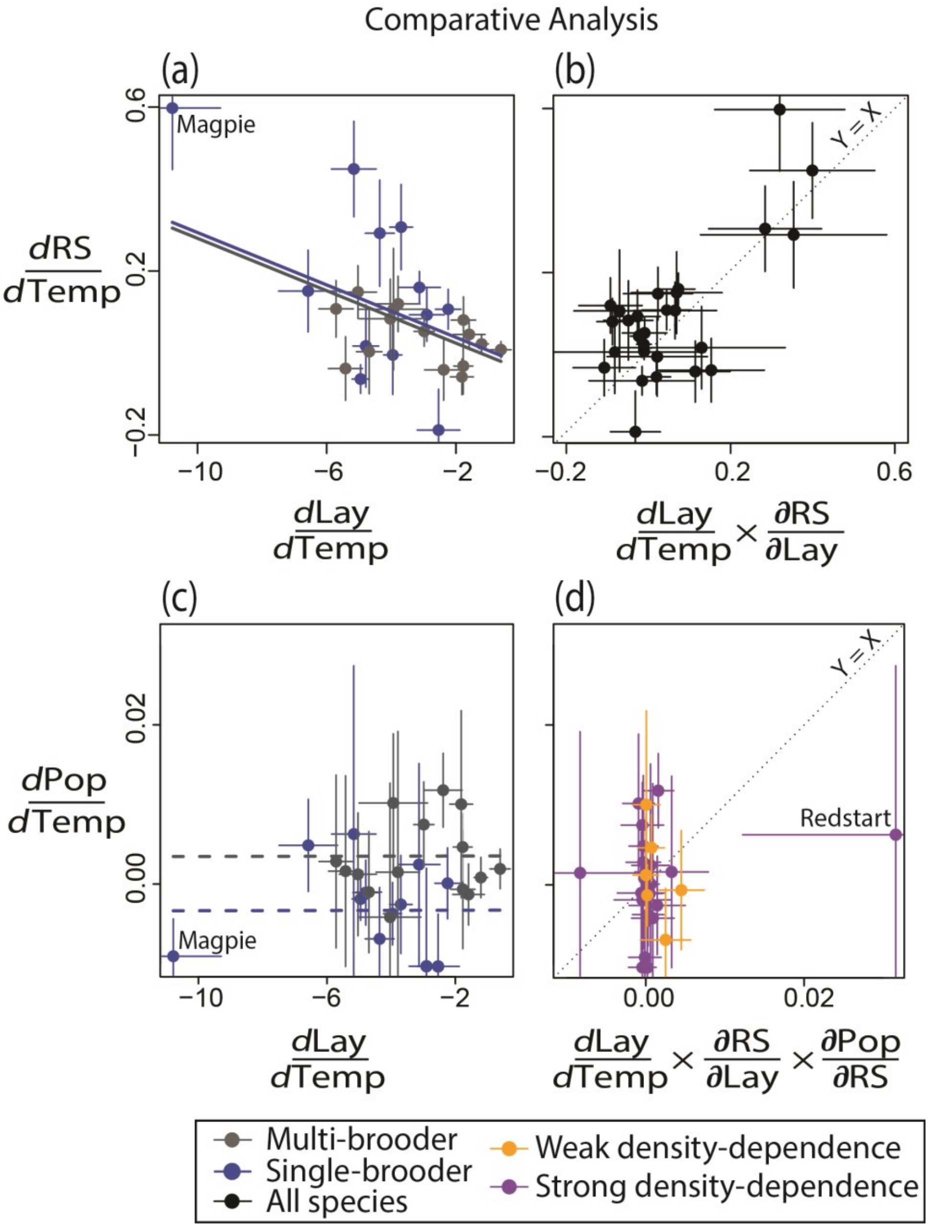

Figure 4 Comparative analysis of climate sensitivities of 27 bird species. Shown are the relationships between the total effects of temperature on **(a)** laying dates ($\frac{dLay}{dTemp}$) and reproductive success ($\frac{dRS}{dTemp}$), and **(c)** laying dates ($\frac{dLay}{dTemp}$) and the population growth rate ($\frac{dPop}{dTemp}$). While **(b)** shows the relationship between the multiplied regression slope estimates of temperature on lay date and lay date on reproductive success ($\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay}$; i.e. the indirect, focal pathway), with the total effect of temperature on reproductive success ($\frac{dRS}{dTemp}$), **(d)** shows the relationship between the multiplied slope estimates of the entire indirect pathway ($\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}$), with the total effect of temperature on population growth ($\frac{dPop}{dTemp}$). Note that if the effects of temperature on reproductive success **(b)** or the population growth rate **(d)** worked solely via the focal pathway, we would expect all values to fall on the dotted line Y=X.

We found no support for the density-dependence hypothesis, as the strength of density-dependence in population size did not help to explain variation among species in the strength of the population response to temperature (Fig. 4d; ΔAICc = 7.4 model 4 vs. 0 in Appendix 2 Table S2). Therefore, despite multiple pathways being a likely explanation for the strong effects of temperature on phenology and reproductive success not carrying through to the population growth rate in most species, density-dependence is unlikely to be the explanation behind that other pathway.

Discussion

We used a hierarchical framework to decompose and test when the impacts of climate on traits affected demographic rates and in turn population dynamics. This conceptual framework allowed us to distinguish four mechanisms that could prevent lower-level responses from impacting population dynamics. We identified testable hypotheses from the literature suggesting life-history and ecological characteristics that could predict when these mechanisms are likely to be important and in which species or taxa. We illustrated how empirical data could be used to (i) quantify the degree to which a strong climate sensitivity of a trait results in important demographic or population-level consequences, and (ii) test these hypotheses using a worked example on 35 bird species over 48 years in the United Kingdom. Future comparative analyses will be able to use the hypotheses and methods that we have presented to help improve our ability to predict which species or populations are most at risk from climate change.

Decomposition

Many studies assume that climate sensitivities of traits or demographic rates will have important population–and thus conservation—consequences. We discovered that although changes in laying dates from warmer temperatures are associated with improved reproductive success, this had no apparent effect on population trends. Furthermore, temperature effects on reproduction where mediated via laying date, but there was also an important direct effect of temperature on reproductive success that was mediated by an (unknown) trait other than laying date. This result emphasises that even if one finds that the climate sensitivity of a trait predicts the climate sensitivity at a higher level, this does not exclude the existence of multiple important pathways, and our framework allows decomposition of the contribution of different pathways even if not all relevant traits are measured.

It could also be interesting to investigate these relationships taking the reverse approach: quantify the direct effects of climate on the population-level and then investigate which traits and demographic rates are affected by the same climate variable and how much variance in the population-level response they explain. This reverse top-down approach allows one to focus on identifying the pathway through which the climate signal most important for the population-level works (i.e. via which trait(s) and demographic rate(s)). The top-down and bottom-up approaches may identify different climate variables as being important and answer different questions (How important is a pathway? vs. What is the most important pathway?), but are also complementary in that they can both be used to test hypotheses on which species characteristics best explain interspecific variation in climate sensitivity.

In studies in the wild, it is challenging to establish causality of a single pathway, and we cannot measure all pathways. Yet, if possible, it is important to consider multiple pathways and climate variables, as single pathway studies will over-estimate population responses if multiple effects counteract one another, or under-estimate if they reinforce climate effects (Larsen *et al*. 2011; Leuzinger *et al*. 2011). Patterns that can explain variation among species when including multiple pathways are also potentially the most relevant to real life scenarios. Of course, focusing on a single pathway or even relationships between two levels in the hierarchy will be useful to build our knowledge, as still very few studies have fully investigated single pathways from trait to population responses (but see Ozgul *et al*. 2010; Plard *et al*. 2014; Wilson & Arcese 2003).

Hypothesis testing

By utilising the framework, we found that analysing data from a single pathway can still provide information on multiple pathways. The associations between temperature on population growth were not well explained by the lay date to reproduction single pathway, suggesting that temperature may be impacting population growth via different traits or demographic rates. By testing the multiple pathway density-dependence hypothesis, it was possible to investigate whether another (unmeasured) demographic parameter was counteracting the effects of increased reproductive success from earlier egg laying on population growth. Strong density dependence has previously been found to prevent population-level responses from mismatches with breeding times and important food resources by reducing competition in one bird population (Reed *et al*. 2013a). However, the strength of density dependence was not effective in explaining variation in the effects of temperature on population growth. This suggest that either density dependence is not a general explanation for the absence of population responses to phenological changes among

British birds, or that methodological issues such as spatial scale have limited our ability to detect density-dependence.

Our framework can test in detail hypotheses about characteristics that can explain which species or populations are more likely to experience consequences of climate change at higher levels. Although the single pathway hypothesis that we tested (the annual number of reproductive events at species level) was only slightly useful for predicting responses in reproductive success based on changes in lay dates, we unexpectedly found it to be a useful species characteristic for predicting population responses to temperature. The population growth rate for multi-brooders increased under warmer temperatures, while single-brooders declined, a trend also found by both Dunn and Møller (2014) and Jiguet *et al*. (2007). Thus, the number of broods a species produces could be used to identify or predict which species are most at risk to be impacted by climate change due to changes in spring temperature. However, because we know that its predictive power did not stem from phenological effects on reproduction as hypothesised, there must be another reason. One reason could be that multi-brooding species are more likely to benefit from longer breeding seasons gained climate change (Dunn and Møller 2014). Despite its apparent effectiveness, we should be cautious about using the number of reproductive events to predict avian responses to temperature changes in other regions or species until future studies provide more insights into the mechanisms behind its effects.

The enormous number of papers in the past decade reporting an effect of a specific climate variable on a phenotypic trait or demographic rate across a range of taxa means that comparative analysis is already possible, with the aim of improving our understanding of which species are most climate-sensitive and why (Buckley & Kingsolver 2012; Végvári *et al*. 2010). Other existing large datasets to focus on could include temperature dependent changes in growth dynamics in plants (Mielikäinen & Sennov 1996; Pretzsch *et al*. 2014), calcification rates in corals (Madin *et al*. 2012), changes in body size (Ozgul *et al*. 2009; Ozgul *et al*. 2010) or timing of reproduction in mammals (Plard *et al*. 2014) and temperature-dependent sex-determination in reptiles (Schwanz & Janzen 2008). Even when studies do not have empirical data available on all three levels, analysis on only two levels can still be useful, as illustrated by our test of the multi-broodedness hypothesis that showed that the effect of temperature-driven changes in laydate on reproductive success were slightly stronger in single brooded species.

Challenges

Although many studies have suggested hypotheses for species characteristic that could explain differences in the links between demographic rates and population-level responses (Table 1b), hypotheses for the three other mechanisms were limited. In particular, there were very few hypotheses in the literature about which species are more likely to encounter reinforced or counteracted responses to changes in climate due to multiple pathways or climate variables. This suggests that when conducting comparative analyses it might be necessary to initially take an exploratory approach to find any characteristics that explain differences among species and then test these using independent data. For a characteristic to be effective, it would need to incorporate not only the likelihood of experiencing more than one pathway, but also that each of those pathways would have strong effects that flow up to higher hierarchical levels.

Noise from other unmeasured environmental variables affecting population dynamics can reduce the explanatory power (r^2) of the relationship between a change in the focal climate variable and the biological response. In such cases, the estimated strength of such relationships (as measured by the regression coefficient) should remain unbiased, but their associated uncertainty will increase (Hutcheon *et al*. 2010). However, measurement error in the explanatory variable – whether climate, trait, or demographic rate – can result in the strength of relationships being underestimated, such that they appear to be weaker than they truly are (regression dilution; Hutcheon *et al*. 2010). Detecting effects of traits on demographic rates can also be an issue of statistical power (Reed *et al.* 2013b), suggesting that it is more important to focus on effect size than statistical significance.

Non-additive effects among responses can increase the complexity of the relationships within the hierarchical framework, making relationships even more difficult to detect. If different pathways interact with one another to cause synergistic non-additive effects at the population-level, then the results can potentially be much stronger than if they were additive (Bansal *et al.* 2013). Additional non-climatic stressors can also interact with climatic variables: for instance, the combination of air pollution and drought results in extremely high mortality for a number of woodland species in Central Europe (Alexieva *et al.* 2003). Finally, climatic variability can also influence or even interact with changes in climate means (see Box 1; Lawson *et al*. 2015). Our dataset shows that it is feasible to decompose pathways and test hypotheses despite all these potential issues. This suggests that these problems are not insurmountable, and therefore, that clear biologically relevant conclusions are possible.

Conclusion

Given that climate impacts on traits do not always result in changes to population dynamics, future research should seek to understand how and when climate-mediated changes in traits will have strong impacts at the demographic- and population-level. To help achieve this, we firstly recommend further development of hypotheses that might predict for which species changes in traits or demographic rates will impact population dynamics. In particular, hypotheses about multiple pathways and climate variables are needed. Comparative analyses can subsequently investigate how climate is impacting the different levels of responses across regions and taxa and test these hypotheses. Our worked example illustrates that currently-available datasets, even those with incomplete demographic data (e.g. missing data on the adult survival pathway), are suitable for this purpose. Finding characteristics that can predict when climate-induced changes in traits or demographic rates are likely to have effects at the population-level will be important for the development of conservation strategies. This would be particularly effective for conservation of species in which we have limited knowledge (i.e. most species are data-deficient), as their climate sensitivity may be predicted based off their species characteristics, therefore helping to determine where to prioritise conservation efforts (Sæther *et al.* 1996).

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Appendix 1 - Methods

Literature Review

We conducted a search of the literature using ISI Web of Science (www.isinet.com) and Google Scholar (www.scholar.google.com) to find and categorise hypothesised explanatory characteristics. The search terms included various combinations of: “climate, climate change, climate change impact, phenology, sex-skew, body size, body mass, migration, physiology, demography, survival, reproductive success, fecundity, population, population trend, elasticity, sensitivity, counteract, reinforce, multiple climate variables, multiple climate factors, multifactor climate experiment, multiple climate change drivers, life history, traits and characteristics”. Relevant articles were initially identified based on their titles and abstracts and relevant citations within papers were also checked.

Worked Example

Climate Windows

The R package *climwin* (Bailey & van de Pol 2015) was used to find the time period during which mean temperature explained the most variation in mean lay dates (weighted by annual sample size) for each species. We looked at every possible combination of dates from a cut-off (37 days after the latest mean lay date across all years) back to 365 days ago.

The best window was selected (as judged by the lowest AICc value) and those temperature values were used in the subsequent analyses. There were, however, a couple of cases where the best model appeared to be a false positive resulting from the large number of windows being tested, because the next best models all suggested a very different time period. In this case, this model was disregarded and the best model from the different time period was selected. If there was no clear temperature window (following Bailey & van de Pol 2015, this was defined as (1) AICc values less than 10-15 better than the null model, (2) the better models suggest a large, seemingly random range of periods, or (3) the best window spans less than 10 days) that species was removed from any further analyses as we were only interested in those species that showed a lay date response to temperature.

Only 8 out of 35 species were not found to have temperature affect the date of laying, and were therefore excluded (Table S1). These species were often opportunistic species (e.g. doves and pigeons), or had small sample sizes. For the majority of species, mean spring temperature (roughly March-May) was the important climate factor for changes in lay date. Previous studies have identified similar windows using the same data but with different techniques

(Thackeray *et al.* submitted; Phillimore *et al.* submitted). Most temperature signals were as expected, with early breeders responding to earlier temperatures (e.g. robin) and long-distance migrants responding to later temperatures (e.g. redstart).

Table S1 The periods that mean temperature was calculated from for each species and whether they were included in any further analyses.

	Species	**WindowOpen**	**WindowClose**	**Included**
1	Blackbird	11-Mar	9-Apr	Yes
2	Blackcap	8-Mar	8-May	Yes
3	Blue tit	22-Mar	1-May	Yes
4	Chaffinch	7-Mar	10-May	Yes
5	chiffchaff	6-Mar	6-May	Yes
6	Coal tit	19-Mar	3-May	Yes
7	Dunnock	27-Mar	1-Apr	Yes
8	Garden Warbler	22-Mar	9-May	Yes
9	Great spotted woodpecker	14-Mar	29-Apr	Yes
10	Great tit	13-Mar	5-May	Yes
11	Jackdaw	17-Mar	25-Apr	Yes
12	Little owl	15-Feb	28-Apr	Yes
13	Magpie	5-Mar	31-Jul	Yes
14	Marsh tit	18-Mar	1-May	Yes
15	Mistle thrush	11-Mar	30-Mar	Yes
16	Nuthatch	11-Feb	1-May	Yes
17	Pied Wagtail	25-Mar	10-May	Yes
18	Redstart	9-Apr	2-Jun	Yes
19	Reed bunting	16-Jan	22-May	Yes
20	Reed Warbler	26-Jan	16-Jul	Yes
21	Robin	9-Feb	20-Apr	Yes
22	Sedge Warbler	8-Jan	10-May	Yes
23	Song thrush	18-Mar	31-Mar	Yes
24	Spotted flycatcher	27-Apr	3-Jun	Yes
25	Treecreeper	8-Mar	12-Jun	Yes
26	Whitethroat	14-Apr	2-Jun	Yes
27	Wren	14-Mar	28-May	Yes
28	Bullfinch	20-Feb	24-Feb	No
29	Collared dove	25-Mar	25-Mar	No
30	Corn bunting	7-Feb	28-Jul	No
31	Tawny Owl	24-Mar	24-Mar	No
32	Turtle dove	19-May	28-May	No
33	Woodpigeon	8-Sep previous year	15-Sep previous year	No
34	Yellow wagtail	15-Apr	9-May	No
35	Yellowhammer	30-Sep previous year	30-Sep previous year	No

Effect Size Calculations

We analysed annual estimates of mean egg laying dates, mean number of fledglings produced per breeding attempt (FPBA) and an index of population size on birds throughout the United Kingdom between 1966 and 2013 provided by the British Trust for Ornithology's Nest Record Scheme and the joint common bird census (CBC) and Breeding bird survey (BBS). The estimates of FPBA were not derived from direct observations, but rather as a function of maximum recorded brood size and egg and chick stage nest failure rates. As a consequence, these data do not take partial brood losses into account (Crick et al. 2003), so annual variation in breeding success may be under-estimated. However, FPBA is the standard productivity parameter used by BTO to identify temporal trends in breeding success (Baillie *et al.* 2014) and to explore the relationship between breeding success and population trajectory (e.g. Siriwardena *et al.* 2000; Finch *et al.* 2014; Morrison *et al.* 2015). The population values were an index (relative to an arbitrary value of 100 assigned for the population values in 2011) of population size, so they did not provide actual estimates of the numbers of animals, but rather the difference in population size compared to those in 2011. This rescaling has no effect on the estimates of population growth rate. We calculated the annual population growth rate as $r_t = \log\left(\frac{nt+1}{nt}\right)$, where n is the indexed annual population value. The corn bunting, great spotted woodpecker, marsh tit and little owl were all missing information for some of the 48 years.

We constructed structural equation models (SEMs) for each species individually. Each species had the same model (Fig. 3i presents the model used for this analysis) that partitioned the net effects of temperature on the three response variables into direct and indirect effects. The indirect pathway was the focal pathway by which temperature impacted population growth via laying date and reproduction. The direct and indirect path coefficients and bootstrapped standard errors from each species were used in subsequent comparative analyses. The temperature values for each window were mean centred for these analyses. Lay dates, FPBA and the population growth rate were approximately normally distributed within species. All SEMs fitted the data well (poor model fit was determined if the RMSEA value was greater than 0.06 and if CFI values were less than 0.95; Hu & Bentler 1999) with the exception of four species (the coal tit, dunnock, jackdaw and spotted flycatcher). We investigated these 4 species using linear regressions and in all cases there was at least one pathway that had a negative R^2 value because there was no clear trend (i.e. the fit was worse than fitting a horizontal line because the data were evenly spread). However, we decided to include these species in the comparative analysis because (1) their slope estimates could not be distinguished from zero, (2) their slope estimates were not very different to the estimates produced by the well fitted models, and (3) the comparative analysis results did not change when these four species were excluded.

To test the single pathway hypothesis, annual number of reproductive events, we used the information from Fergusson-Lees *et al.* (2011) on the number of broods of each species. Some single-brooded species are known to have replacement broods if their first attempt fails, but this was not taken into account in this analysis. To test the density-dependence multiple pathway hypothesis, we calculated the strength of density-dependence by linear regression of the population growth rate (r_t) over the population size in year t. In the analysis, continuous density dependent values were used, however, in order to visually represent their pattern in Figure 4d we designated each species to be either weakly density-dependent if their slope values were less than -0.0001, or strongly density-dependent if they were greater than -0.0001.

Species Comparison

The path estimates from the SEMs were used to compare the sensitivities across all of the species at each hierarchical level. Linear models weighted by the inverse of the estimated standard error of the regression coefficient were used to investigate patterns in sensitivities and the two *a priori* selected hypotheses, number of broods and density dependence (Table 1). We compared the linear models by using the second order Akaike's Information Criteria (AICc) scores. Models within 2 AICc units of each other were considered equally well supported (Burnham and Anderson 2002).

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Appendix 2 - Results

Table S1 Models investigating the variables that best explain the total effect of temperature on reproductive success among species. $\frac{\boldsymbol{dRS}}{\boldsymbol{dTemp}}$ refers to the total effect of temperature on reproductive success (all pathways are included), $\frac{\boldsymbol{dLay}}{\boldsymbol{dTemp}}$ refers to the effect of temperature on of lay date and the factor broods refers to whether species are single- or multi-brooders. The variable $\frac{\boldsymbol{dLay}}{\boldsymbol{dTemp}} * \frac{\boldsymbol{\partial RS}}{\boldsymbol{\partial Lay}}$ refers to the indirect pathway (i.e. the effect of temperature on reproductive success that is mediated by laying date) where $\frac{\boldsymbol{\partial RS}}{\boldsymbol{\partial Lay}}$ refers to the partial effect of lay date on reproductive success, holding temperature constant. The value 1 refers to an intercept only (null) model.

	Model	**Log-likelihood**	**AICc**	**ΔAICc**	**Weight**	**Estimate ± SE**	**R^2**
2	$\frac{dRS}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay}\right)$	24.1	-41.2	0.0	0.98	0.77 ± 0.18	0.41
1	$\frac{dRS}{dTemp} \sim \frac{dLay}{dTemp}$	20.1	-33.2	8.0	0.02	-0.03 ± 0.01	0.21
3	$\frac{dRS}{dTemp} \sim \frac{dLay}{dTemp}$ * broods	21.1	-29.4	11.8	0.00	-0.03 ± 0.02	0.20
0	$\frac{dRS}{dTemp} \sim 1$	16.4	-28.4	12.8	0.00	0.06 ± 0.02	

Table S2 Models investigating the variables that best explain variation in the effect of temperature on population growth rates among species. $\frac{dPop}{dTemp}$ refers to the total effect of temperature on the population growth rate (all pathways are included), $\frac{dLay}{dTemp}$ refers to the effect of temperature on of lay date, the factor broods refers to whether species are single- or multi-brooders and the factor density refers to the strength of density-dependence. The variable $\left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right)$ refers to the indirect pathway (i.e. the effect of temperature on the population growth rate via laying date and reproductive success) where $\frac{\partial RS}{\partial Lay}$ refers to the partial effect of lay date on reproductive success, holding temperature constant and $\frac{\partial Pop}{\partial RS}$ refers to the partial effect of reproductive success on population growth, holding temperature constant. The value 1 refers to an intercept only (null) model.

	Model	Log-likelihood	AICc	ΔAICc	Weight	Estimate ± SE	R^2
3	$\frac{dPop}{dTemp}$ ~ broods	105.0	-202.9	0.0	0.88	-0.006 ± 0.002	0.22
0	$\frac{dPop}{dTemp}$ ~ 1	101.0	-197.6	5.3	0.06	0.0005 ± 0.001	
1	$\frac{dPop}{dTemp} \sim \frac{dLay}{dTemp}$	101.8	-196.6	6.3	0.04	0.0007 ± 0.0005	0.02
2	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right)$	101.4	-195.7	7.2	0.02	0.15 ± 0.18	0.00
4	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right)$* Density	101.6	-190.3	12.6	0.00	-224.0 ± 521.1	0.00

Table S3 Models investigating the variables that best explain the total effect of temperature on reproductive success among species with the Magpie removed. See Table S2 for details.

	Model	Log-likelihood	AICc	ΔAICc	Weight	Estimate ± SE	R^2
2	$\frac{dRS}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay}\right)$	25.8	-44.6	0.0	0.98	0.63 ± 0.17	0.33
0	$\frac{dRS}{dTemp}$ ~ 1	20.0	-35.6	9.0	0.01	0.05 ± 0.02	
1	$\frac{dRS}{dTemp} \sim \frac{dLay}{dTemp}$	21.3	-35.5	9.1	0.01	-0.02 ± 0.01	0.05
3	$\frac{dRS}{dTemp} \sim \frac{dLay}{dTemp} *$ broods	21.7	-30.4	14.1	0.00	0.006 ± 0.03	0.00

Table S4 Models investigating the variables that best explain variation in the effect of temperature on population growth rates among species with the Magpie removed. See Table S3 for details.

	Model	Log-likelihood	AICc	ΔAICc	Weight	Estimate ± SE	R^2
3	$\frac{dPop}{dTemp} \sim$ broods	101.5	-195.9	0.0	0.80	-0.005 ± 0.002	0.18
0	$\frac{dPop}{dTemp} \sim 1$	98.3	-192.1	3.8	0.12	0.001 ± 0.001	
2	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right)$	98.6	-190.1	5.8	0.04	0.13 ± 0.17	0.00
1	$\frac{dPop}{dTemp} \sim \frac{dLay}{dTemp}$	98.3	-189.5	6.4	0.03	0.00008 ± 0.0007	0.00
4	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right) *$ Density	99.1	-185.2	10.7	0.00	-349.9 ± 503.4	0.00

Table S5 Models investigating the variables that best explain variation in the effect of temperature on population growth rates among species with the Redstart removed. See Table S3 for details.

	Model	Log-likelihood	AICc	ΔAICc	Weight	Estimate ± SE	R^2
3	$\frac{dPop}{dTemp} \sim$ broods	102.4	-197.8	0.0	0.96	-0.007 ± 0.002	0.30
0	$\frac{dPop}{dTemp} \sim 1$	97.3	-190.1	7.7	0.02	0.0003 ± 0.001	
1	$\frac{dPop}{dTemp} \sim \frac{dLay}{dTemp}$	98.3	-189.5	8.2	0.02	0.0007 ± 0.0005	0.03
2	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right)$	97.4	-187.7	10.1	0.01	-0.21 ± 0.56	0.00
4	$\frac{dPop}{dTemp} \sim \left(\frac{dLay}{dTemp} * \frac{\partial RS}{\partial Lay} * \frac{\partial Pop}{\partial RS}\right) *$ Density	98.1	-183.2	14.5	0.00	-71.9 ± 533.4	0.00

Chapter 2

High intra-specific variation in avian body condition responses to climate limits generalisation across species

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Abstract

It is generally assumed that populations of a species will have similar responses to climate change, and thereby that a single value of sensitivity will reflect species-specific responses. However, this assumption is rarely systematically tested. High intraspecific variation will have consequences for identifying species- or population-level traits that can predict differences in sensitivity, which in turn can affect the reliability of projections of future climate change impacts. We investigate avian body condition responses to changes in six climatic variables and how consistent and generalisable these responses are both across and within species, using 21 years of data from 46 common passerines across 80 Dutch sites. We show that body condition decreases with warmer spring/early summer temperatures and increases with higher humidity, but other climate variables do not show consistent trends across species. In the future, body condition is projected to decrease by 2050, mainly driven by temperature effects. Strikingly, populations of the same species generally responded just as differently as populations of different species implying that a single species signal is not meaningful. Consequently, species-level traits did not explain interspecific differences in sensitivities, rather population-level traits were more important. The absence of a clear species signal in body condition responses implies that generalisation and identifying species for conservation prioritisation is problematic, which sharply contrasts conclusions of previous studies on the climate sensitivity of phenology.

Introduction

A major aim of climate change ecology is to understand why species differ in their sensitivity to climate change and identify which species are most at risk [1]. To answer these questions, studies typically assume—sometimes explicitly, often implicitly—that climate responses from individual studies are representative for the species as a whole. For example, comparative meta-analyses often use values reported in local population studies to investigate interspecific variation in climate responses [e.g. 1–3], and the IUCN Red List uses evidence from studies on specific population(s) to argue that the species as a whole might be under threat from climate change [4]. Empirical studies on the effects of climate change rarely consider variability in responses among populations of the same species [5–7]. Typically a single value is used which is thought to adequately reflect species-specific responses to changing environments, essentially assuming that within-species variation is negligible [8–11].

However, is the concept of a species' climate response useful for generalisation and prediction? If responses to climate change vary substantially within species—which they often appear to do [12–19]—then generalising the response to a single species signal may not be accurate, nor meaningful. For instance, a single species signal would be unrepresentative if populations showed different climate-driven responses at their low-latitude range margin compared to their poleward range margins [11,20,21]. In such a situation it is important to properly account for this intra-specific variation when modelling environmental responses, as it can help us to understand the mechanisms underlying responses to environmental change, and to better predict their effects [8,10]. For instance, intraspecific variation can reduce the overall effects of climate change on the species because some populations may be less affected, essentially buffering the overall impacts [6,22,23]. This phenomenon is known as the portfolio effect, where spatial or genotypic diversity can dampen variation in total population abundance [24].

Identifying life-history and ecological traits that can explain and predict differences in sensitivities is currently of particular importance for making effective conservation and management decisions [1,25]. For most species, we lack the sufficient data to make reliable direct estimates of their climate sensitivities, and consequently nowadays conservation organisations often indirectly predict the climate sensitivities of data-deficient species based solely on their species traits [25]. However, when trying to make generalisations across species, few comparative studies consider variation among populations within species. When there is high intraspecific variation, species life-history traits (e.g. life-expectancy), which are the main focus of most comparative studies, are likely to be of little predictive power. Instead, if a species is not responding consistently across different populations, it suggests that local, population-specific traits (e.g. habitat type) could be more important.

In order to provide some yard-stick for what ‘a lot’ of intraspecific variation might be, and therefore when local rather than species traits might be more important, comparative analyses that include both intra- and inter-specific variation are needed. In such studies, it is possible to determine whether populations of the same species are more alike than populations of different species, suggesting a species signal exists [6,8]. Ample comparative studies exist that compare interspecific variation and quite some studies compare intraspecific variation of one or a few species [e.g. 12,13,16–18]. However, apparently there are so few species with sufficient intraspecific information [26] that intraspecific analyses of many species has seldom been achieved.

As far as we are aware, only three studies have systematically investigated the amount of within- to among-species variation in responses to climate change. Rubolini et al. [5] and Thackeray et al. [7] both found strong species-signals, with about 50% of the variance in observed changes in phenology attributed to differences among species (although the latter study did not explicitly interpret this result in the context of species signals). In contrast, Malyshev et al. [6] found that only roughly 10% of the variance was due to among-species variation in plant growth responses to drought and winter frost. Thus, the little evidence available in the literature suggests a strong species signal for phenological changes, but we have no indication as to whether this might hold true more generally for other types of climate responses, particularly for key state variables (body mass, growth) and vital rates (reproduction, survival) that determine the population responses relevant for conservation.

Body condition (mass corrected for size; i.e. amount of fat and protein reserves; [27]) is a key state variable that affects vital rates [28–31] and thereby is likely important for population dynamics [e.g. 32]. It is now becoming clear that body condition and mass of avian species around the world are changing substantially over time and with climate [28,29,31–39]. However, despite being identified as one of the three major responses to climate change, the impacts of climate on body condition (and body size) have been less well studied than responses in phenology and range shifts [40]. Of the few studies that investigate the relationship between temperature and body condition directly, warmer temperatures have often been found to result in decreased juvenile and adult body mass [28–30,34,41]. This can be either through indirect effects, as temperature can alter the amount of food resources available [30], or through direct effects on energetics [29,34,42]. However, we still do not have a good understanding of the mechanisms underlying environmentally-driven changes in body condition [43].

Despite the importance of body condition, our understanding of climatic effects on body condition is limited. The literature has mostly focused on temperature responses, but other climatic variables could also have important influences on body condition (see Box 1 for a description of other climate variables and potential underlying mechanisms). We also have little understanding of how the effect of climate on body condition varies among different populations. This is in part because the majority of research investigates changes over time, which makes general patterns difficult to interpret as the direction of changes will depend on the climate in the local region [43]. What's more, the time periods (e.g. winter, spring) during which climate has the strongest impact on body condition are rarely systematically tested and so are still poorly understood [43–45]. Typically only linear responses have been considered, so it is unclear as to whether body condition responses might be non-linear [but see 38,39].

As a result of this missing knowledge, there are currently no future projections for how body condition is likely to be impacted under future climate scenarios. Projecting the ecological responses of future climate changes using recent observed effects is now a major challenge in climate ecology [46]. As the climate is predicted to continue to change in the future, conservation plans and action will rely on our ability to accurately project impacts [47,48].

Here we use an extensive 21-year data set from 80 Dutch constant effort sites to investigate (1) how avian body condition responds to changes in climate, and (2) how consistent these responses are both across and within 46 common passerine species. We also project how species and populations are likely to change under future climate scenarios. We first test how sensitive species and populations are to six climate variables that we hypothesise as having important effects on body condition (temperature, rainfall, humidity, sunshine, daily temperature range (DTR) and wind speed; see Box 1), and determine the time period (testing all options over a full year) in which the effect is most marked. Subsequently, we integrate the sensitivities of populations and projected changes in climate to predict body condition responses to future climatic conditions in 2050. Second, we ask whether there is a species signal, or instead if populations of the same species respond as differently as populations of different species, by comparing the relative amounts of within- to among-species variation. We investigate whether species and population traits can explain variability in responses among species and populations. We predict that if intra-specific variation is high, species traits (e.g. life-expectancy) and phylogenetic distance (a proxy for unknown species traits) will be of less importance for predicting body condition responses to climate; rather population traits (e.g. habitat type) and geographic distance (closer sites are more similar) should be more appropriate.

Materials and methods

Body condition data for common Dutch bird species

Approval of the work by an ethics committee is not required for catching and banding birds in the Netherlands. Under Dutch law, catching and banding birds requires a banding license which each of the banders have obtained from the bird banding scheme. The Dutch constant effort site project has run over a period of 21 years at 80 field sites across the Netherlands ([49]; 1994-2014; see Fig S1 in Appendix 3 for map). The project followed a standardised protocol [50] where mist netting is carried out with a constant effort from the 12th April until the 14th August, 12 times per year. We focussed on 46 common passerine species of which in total 174,875 birds were caught. Not all sites collected observations over the 21 years of the study period (mean=10 years, range=1-21 years); 10 species were captured in less than 7 different sites, and for this reason excluded from any intra-specific analyses. Captured birds are ringed and morphometric measurements taken, including body mass (grams), wing length (maximum chord measurement; [51]), sex and age-class (typically juvenile or adult; based on the plumage of the bird). We estimated body mass corrected for size by taking the residuals from the linear regression of body mass on wing length; this means that our measure of body condition is more of a measure of body fat [27,29,31]. When investigating the effects of climate on body size or condition, wing length is generally thought to be the best single linear predictor of structural size for passerines [29,52]. Although wing length has been found to be affected by climate [for example 53], we found no change in wing length over the length of the study, suggesting that our measure of body condition was not affected by any changes in wing length.

Climatic data

Our knowledge of which climate variables are important for body condition is limited, as previous studies have mostly focused on the effects of temperature or , less frequently, rainfall [for example 28,29,33,34,37]. We suggest a number of plausible weather signal hypotheses (see Box 1). Consequently, we look at the effects of six climatic variables: daily windspeed (in 0.1 m/s), mean daily temperature (over 24 hours, °C), mean relative humidity (percent), longest possible daily sunshine duration (percent), daily sum precipitation (in 0.1 mm), and daily temperature range (DTR, difference in minimum and maximum daily temperatures in °C). Daily records of each of the six variables over the study period were available from the Royal Netherlands Meteorological Institute (KNMI) for 37 weather stations across the Netherlands. The biological data from each site was matched with the closest weather station (mean distance 17 km; see Table S2 in Appendix 3).

Climate projections were available for all climate variables except sunshine, based on a regional climate model from the Royal Netherlands Meteorological Institute (KNMI). We chose to use the most extreme of the four available climate scenarios (‘WH’), as the best case scenario is thought unlikely [54], but also because using a worst case scenario can be more useful for conservation decisions. The WH scenario assumes a high global temperature change (around 2°C by 2050) and strong changes in air stream patterns in the Netherlands [55]. Under this scenario, temperature and wind speeds are projected to increase across all seasons, while humidity is expected to decrease. Daily temperature ranges are projected to decrease in all seasons except summer where it increases. Conversely, rainfall is projected to increase in all seasons except summer where it decreases. We assumed that there would be little geographic variation in projected exposure across the small spatial scale of the Netherlands and therefore use the same climate exposure for all populations (i.e. the furthest sites are only around 250km apart, see Fig S1 & S3 in Appendix 3; [47]). For all climate variables except wind (for which only one annual estimate was available), we matched the projected exposure for each season (winter/ spring/ summer/ autumn) to the season when the climate window occurred (see later). In cases where the climate window spanned more than one season, we averaged those seasons’ projected exposures.

Box 1 Potential effects of various climate variables on body condition

A range of climate variables could impact body conditions of birds through both direct and indirect means. The bulk of the literature that investigates body condition responses to climate focuses on temperature, and to a lesser extent rainfall. Temperature could have direct effects on condition via a number of mechanisms. Temperature has a direct effect on their energetics [42]. Warmer temperatures can result in overheating or decreased foraging efficiency [28,76]. Birds might strategically down-regulate their body mass under warmer conditions (as they may not need as much body fat for warmth) which could reduce time spent feeding and improve flight performance [77,78]. Changes in rainfall can impact freshwater supplies, which can have consequences for hydration [28]. Changes in temperature and rainfall may have indirect effects on body mass through changes in food availability, perhaps through mismatches in peak food abundances [30,79] or by exacerbating parasites and diseases which impact on the health of birds [28].

However, other climatic variables could arguably also impact body condition. For instance, humidity can impact heat retention and fuel composition which can, in turn, impact lean mass [76,80]. Birds rely primarily on evaporative cooling from cutaneous and respiratory surfaces for heat dissipation, which is much less effective in high humidity [76]. Wind speed can have multiple effects on birds that may impact their body condition. Wind speed affects bird energetics [81,82], body temperature [83], field metabolic rate [81,82], it reduces thermal resistance of the feathers such that they change their orientation [82,84], and it affects the movement of migratory land birds. Strong wind has been found to have a negative impact on the body condition of chicks [81,82]. Alternatively, high wind speeds may allow some birds to fly faster and reach foraging sites more easily, resulting in increased body condition [85].

The amount of sunshine (i.e. cloudiness) may impact foraging behaviour, movement and body temperature. Exposure to bright sunlight might make birds easier to detect by predators, and visual glare could reduce their ability to monitor the environment effectively [82]. In cold environments, heat gain from solar radiation can reduce the costs of foraging [82]. However, Konarzewski & Taylor [81] found that sunshine did not impact chick mass in Little Auks, nor were feeding rates affected by cloud cover in Guillemots [86]. The consequences of changes in daily temperature range in endotherms are mostly unknown, but are most likely associated with increased thermal stress [87]. Increased temperature range can impact mortality, egg size and cost of energy expenditure [87,88].

Species and site trait data

We identified a number of hypotheses about species and population traits that could potentially explain differences in body condition responses to climate. We predict that if intra-specific variation is high, population-level traits will likely explain most variation. However, species-level traits may still be important for explaining some variation. We tested four species level (body size, migratory strategy, habitat preference and life-expectancy) and two site level hypotheses (habitat and population density), see Box 2 for rationale.

Furthermore, in the absence of other a priori hypotheses about explanatory traits, phylogenetic (or geographic) distances among species may be able to act as a proxy for predicting species' (or site) responses [56]. Phenotypic differences between species and populations are expected to rise over eco-evolutionary time, such that closely related species and proximate populations should respond more similarly to environmental change [1,57]. Similarly, geographic distance among sites could explain site-variation in body condition responses because closer populations are expected to have more similar environments, and thus geographical distance could be acting as a proxy for some unknown environmental variable [58]. We therefore examined whether phylogenetic (i.e. time of divergence in millions of years) and spatial (Euclidian in km) distance could predict the amount of dissimilarity in climate responses among species and sites.

Body size estimates were calculated as the mean body mass across all individuals for each species. Species' preferred habitat type was assigned into the categories urban (garden), woodland, wet (reed bed, wet scrub) and open (dry scrub) based on [59]. Life-span was adult life-expectancy, calculated as 1/adult annual survival. Population density was calculated as the number of individuals of the same species caught (per meter of net per day) for each site averaged across all years. Population habitat type needed to be grouped into wet (reed bed, wet scrub) or dry (dry scrub, garden, woodland) because some habitats were rare. To determine phylogenetic distance, we downloaded 1,000 different possible phylogenetic trees from a pseudoposterior distribution from birdtree.org [57,60] (Fig S7 in Appendix 3).

Box 2 Species and site level hypotheses to explain intra- and inter-specific variation in climate responses.

Species level hypotheses

1. Body mass responds differently to changes in climate in larger and smaller bird species. Body size affects a range of biological processes including water requirements, thermoregulation, energy and mass acquisition and utilisation rates [40]. Size plays an important role with climate, as smaller individuals are generally found at lower latitudes where climates are warmer (Bergmann's rule; [40, 89]).
2. Body mass responses differ among species with different migratory strategies (resident, short- and long-distant migrants). Environmental conditions can have stronger effects on migrants because they have a higher chance of mismatches with important resources [90–93]. Migratory species are also influenced by conditions in other areas [94]. Additionally, migrant species may be less likely to increase their body mass as increased fat can have strong negative effects during migrations [95].
3. A species' preferred habitat type could alter their physiological response to climate. Food availability might change if forest phenology is advanced, affecting invertebrate timing and availability [72,90,92]. Marshes or reeds are more stable because they grow throughout spring and summer [72]. Also, some habitat types might interact with climate by providing more refugia [90]. Forests can buffer extreme weather (i.e. windy conditions, shade), whereas marshland areas provide standing water but can fluctuate strongly with precipitation and temperature [90].
4. Species with different longevity may adopt different trade-offs when dealing with climatic impacts on body mass because life-expectancy can alter strategies under poor environmental conditions [96]. For instance, shorter lived species may require a growth rate out of proportion to food availability, as species that are under time pressure to attain a certain size at a given time will often sacrifice future fitness by growing out of proportion to resource availability [97]. Long-lived species might be more flexible as they do not need to put on the weight as quickly.

Site level hypotheses

1. Body mass responses may differ between habitat types (wet or dry) as changes in climate can affect freshwater supplies, making it difficult for birds to hydrate [28].
2. Population density could act as a proxy for site quality, where populations in better quality sites may be more resilient to changes in climate [28].

Statistical analyses

We explore avian body condition responses to changes in climate using species and site-specific sensitivity values (how strongly body condition is affected by a change in specific climate variables) and future projections (projected change in percent body condition by 2050 due to all climate variables combined) based on regional climate model projections [55].

Climate windows and signals.

The first step was to identify which climate variables impacted body condition, and over which periods. For each species and climate variable we performed a climate window analysis to identify the time period during which the variable explained the most variation in body condition, using the R package *climwin* (Fig 1 Step 2a; [61]). This allowed us to take an exploratory approach, as it considers all possible combinations of consecutive days for the whole year (i.e. the 365 days before the end of the sampling season on the 15th August) to identify the 'best' possible window (see Appendix 3 for details). As such, all time periods over all seasons (i.e. summer or winter etc.) were investigated. Randomisation techniques were used to assess the likelihood that the best time window is actually a spurious result of overfitting ([44]; see Appendix 3). We added the following predictor variables to these models (in addition to mean climate) to account for the confounding effects of age (juvenile or adult), sex (if identifiable for that species), day within the season, time of capture, and the random effect 'Individual ID' (some individuals were caught repeatedly). We investigated both linear and quadratic relationships between climate and body condition because we had no *a priori* reason to suspect the relationships would be linear.

As the *climwin* analysis tests only a single climate variable at a time, we combined the best windows of each climate variable into one model in order to account for the effects of multiple climate variables. We next included all climatic variables (grand-mean centred; and linear or quadratic) that were found to have a climate signal plus the baseline variables (age, sex, day within season, time, individual ID) into a single model explaining variation in body condition. For example, if a species was affected by all six climate variables, the full model would be:

$$\begin{aligned} Body\ Mass = {} & Temperature + Rain + Wind + DTR + Humidity + Sunshine + Age \\ & + Time + Time^2 + Season + Season^2 + Sex + (1|Individual\ ID) \end{aligned}$$

Model selection and averaging was used to determine which climate variables were important and to calculate parameter estimates after accounting for the other climate variables [62]. For species that were found to be affected by multiple climate variables, we compared models with every possible combination of those climate variables, while including the climate-unrelated explanatory variables (age class, observed sex, time, season and individual ID) in all models. We subsequently excluded climate variables if they were not present in any models within 2 delta AICc units of the best model [62], as this would suggest that their effects were of low biological relevance, or if they appeared to be uninformative ("hitchhiker") variables (Appendix 3 for definition; [63]). To calculate the model-averaged slope estimates for each site, an interaction term between the site and the climate variable was included.

Collinearity among climate variables (defined as r>0.6) was rare; collinear climate variables were always kept in the same models when testing the different combinations of variables (i.e. both always included or excluded from the same models). In this way, the effects of the two correlated climatic variables were always measured together, which yields unbiased parameter estimates ([64]; see Appendix 3 for details). We checked whether sensitivities to climate variables differed substantially between juveniles and adults, and between males and females, however there was no strong difference between groups, thus we only present results for adult females (see Appendix 3 for details). All models were fitted using the *lmer* function of the *lme4* package in the R statistical package [65] and the *MuMIn* package was used for model averaging and selection [66].

Climate Sensitivities

In order to compare linear and non-linear responses, we calculated a measure of "sensitivity" to each climate variable (Fig 1 Step 2a). Our measure of sensitivity was the tangent at the mean climate (i.e. the first derivative of the climate regression function or the local slope estimate at the mean value of the climate variable of interest; Fig S6 in Appendix 3; [67]). This gives the change in body condition (grams) per climate unit at the mean climate, or the climate sensitivity in average climatic conditions. By taking the slope at the mean climate we can investigate projections for the near future. The mean climate was calculated across all sites and years. We excluded any sites that were measured solely in years in which the climatic conditions were above or below the mean climatic conditions over the entire study period, as we did not want to extrapolate beyond the available data (10 sites on average across all species and climate variables, ranging from 0-58 sites). In order to compare climate sensitivities among species that differed in body size (i.e. a change of 1 gram would be quite different for larger or smaller birds), we used the percent change in body condition per climate unit.

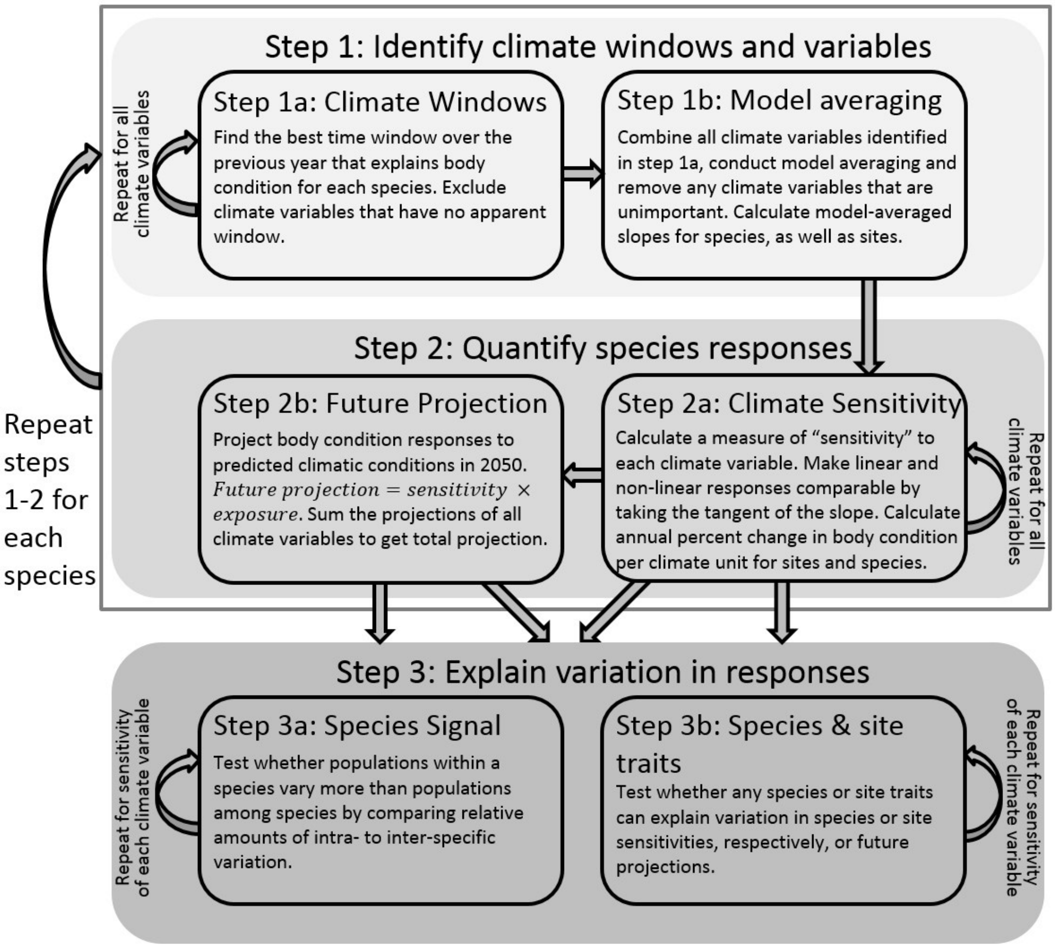

Figure 1 Conceptual diagram summarising the three main steps of the analyses: (1) identifying the climate variables that affect each species and over which time periods (i.e. climate windows), (2) quantifying species and population responses to climate, and (3) investigate inter and intraspecific variation in climate responses. Step 3a investigates the relative amounts of intra- and inter-specific variation to ask how consistent responses are and whether there is a species signal. While in step 3b, comparative analysis is used to test for any species or site traits (e.g. phylogenetic relatedness or habitat type) that explain differences among species or sites sensitivities and future projections. Steps 1 and 2 are carried out on each species individually, while in Step 3 all species are combined.

Future Projections

We projected the change in percent body condition (B) by 2050 by multiplying each species' sensitivity ($\frac{\partial B}{\partial C_i}$; change in condition per climate unit) with their projected exposure based on climate scenarios for 2050 ($\frac{dC_i}{dT}$; predicted change in climate over time). The sum across all climate variables gives the overall future projection estimate ($\frac{dB}{dT}$; change in condition over time due to the combined effect of all climate variables) (Eq. 1).

$$\frac{dB}{dT} = \sum_i \left(\frac{\partial B}{\partial C_i} * \frac{dC_i}{dT}\right) \qquad eqn\ 1$$

where B represents body condition; C_i the climate variable i, and T time. We calculated future projections to climate change for each site. For a single climate variable, their future projection could be small for several reasons. A species could be highly sensitive, but have only a small projected change in climate by 2050 (i.e. little exposure). Similarly, high exposure with low sensitivity will result in small future changes. When this occurs, the climate variable will have a low contribution to the overall future projection for the population or species.

Species Signal

To determine whether a species signal exists, we quantified the amount of among- and within-species variation in sensitivity and future projections. We ran an intercept-only mixed 'variance component model' model [68] with site-specific sensitivity estimates as the response variable (weighted by the inverse standard error of the sensitivities), and 'species' as a random intercept term. This was performed for each climate variable separately. To estimate the relative amount of variation in body condition response that was due to species differences, we compared the ratio of the among-species variation (estimate of the variance of the random effect 'species') to the total variation (the sum of the 'species' and residual 'population' variance estimate) [8,11]. This ratio can also be interpreted as the intra-class correlation coefficient (i.e. the similarity between the climate responses of populations of the same species; [68]). A value close to zero suggests that among-species variation is low, while population variation is high, indicating that a species signal might not be present (Fig 2). Alternatively, a value close to one suggests that the correlation between the climate sensitivity of two populations of the same species was much higher than the correlation between two populations of different species [8].

This method unfortunately introduces sampling variance into the residual 'population' variance estimate because it is carried out in two steps (uses model-based climate sensitivity estimates with varying levels of error as the dependent variable in a second model). However, this was unavoidable given that this analysis could not be carried out on the raw body condition response data due to the different climate variables, and also included linear and non-linear responses for each species. We took two steps to address this issue. First, each observed climate response was weighted by its uncertainty (1/standard error of response estimate) to reduce the inflating effect of sampling variance on the residual (population) variance. Additionally, we investigated the impact of sampling variance on response estimates by assessing whether a relationship existed between the number of years a site was sampled and how different (absolute deviation) each population was from the species mean. We conducted a quadratic regression on the absolute residuals over the number of years sampled and found no relationship between them (within 0.04 AICc units of the null model), suggesting that inflating effects of sampling variance on variance components were negligible.

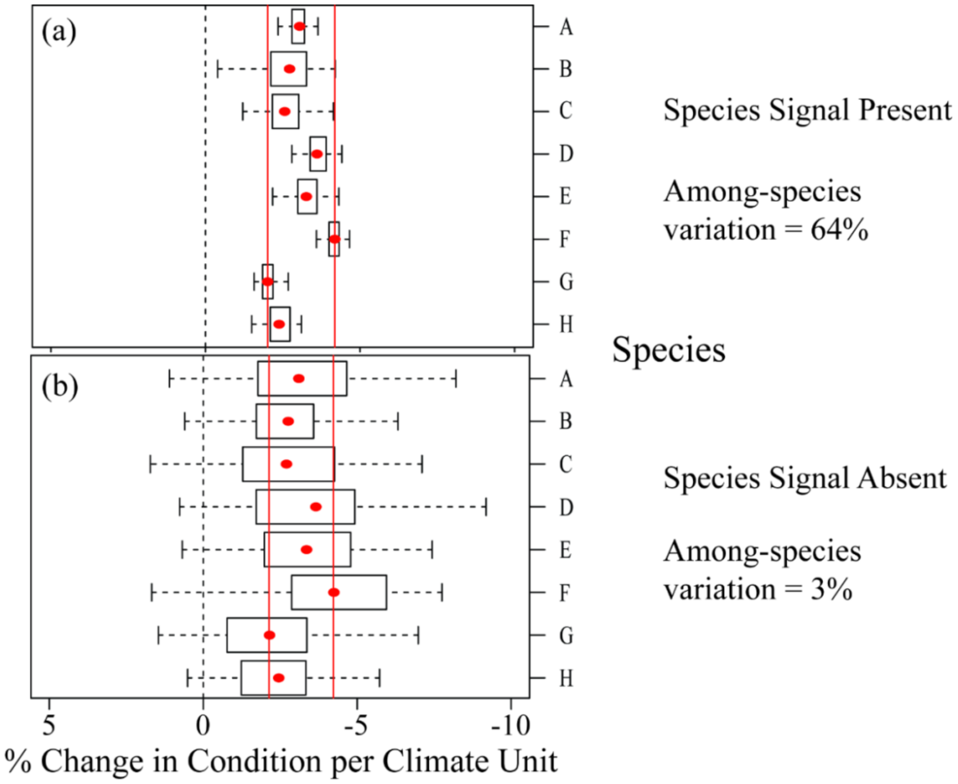

Figure 2 Illustration of hypothetical intra-specific and inter-specific variation in sensitivities to climate. Plot (a) shows an example where a species signal is present. Here, the correlation between the climate sensitivity of two populations of the same species is much higher than the correlation between two populations of different species. The percentage of among-species variation explained is 64%, which suggests that population variation is low compared to among-species variation. Plot (b) shows an example where a species signal is absent. Here, the correlation between the climate sensitivity of two populations of the same species is lower than the correlation between two populations of different species (i.e. population sensitivities within a single species vary just as much as much as population sensitivities among different species). As such, the percentage of among-species variation explained is a much smaller 3%. The sensitivity estimates for each species is shown by the red points, while the black boxplots show the distribution of population sensitivity estimates (intraspecific or among-site variation in climate sensitivity). The two red vertical lines show the minimum and maximum of the species' sensitivity estimates (i.e. the range of the red points).

Species and site traits

To investigate whether species and population traits can explain variability in responses, we ran a mixed model for each hypothesis (Box 2), with either sensitivities or overall future projections as the response variables, trait as the explanatory variable, and species as the random intercept term. All models were weighted by the inverse standard error of the sensitivities. We compared the AICc value of each to a null (intercept only) model. Pairwise phylogenetic and geographic distance were related to dissimilarity in climate sensitivity (the absolute difference in sensitivities between two species or sites), and phylogenetic distance was also related to whether species were impacted by the same climate variables (i.e. whether both species are affected by that climate variable, or if one species is affected by that climate variable, but the other is not) (see Appendix 3 for details). If the relationship between phylogenetic (or geographic) distance and dissimilarity is positive, more closely related (spatially proximate) species respond more similarly to climate variables.

Results

Climate sensitivities

In most bird species (39 of the 46), body condition (corrected for size) responded to at least one climate variable, with 34 species affected by multiple climate variables. No particular climate variable was clearly more important overall: out of 46 species, 19 were affected by temperature, 26 by rainfall, 21 by sunshine, 24 by humidity, 25 by wind and 24 by DTR (Fig 3). Temperature was associated with body condition in most species from early May to mid-July (spring-early summer), while wind speed had an effect around early January to mid-April (winter; Fig 3). The time periods for all other climate variables showed much less consistency. The majority of species showed non-linear relationships between body condition and climate: 50% of species showed quadratic responses to humidity, 57% to temperature, 71% to DTR, 80% to wind, 81% to sun and 92% to rain (Fig 3). The average R^2 value from the final model averaged across all species was 0.19 (1st quartile: 0.14, 3rd quartile: 0.24).

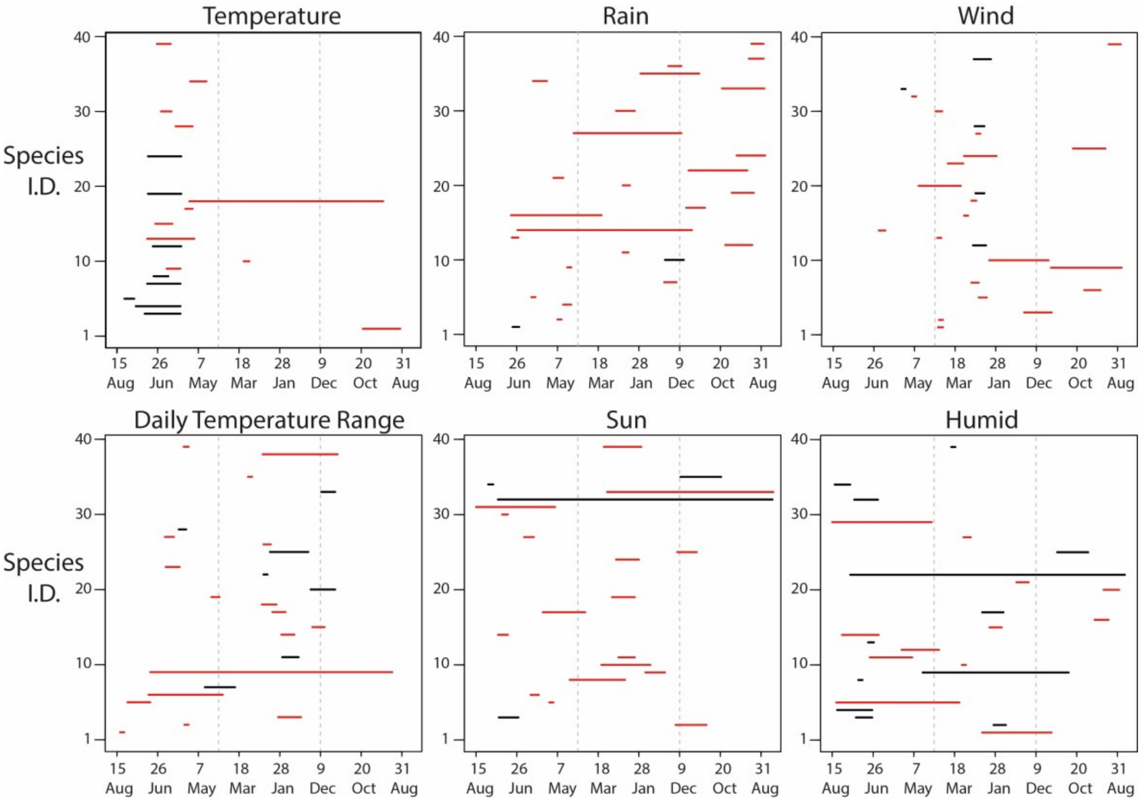

Figure 3 The time periods (or climate windows) over which climatic variables affected body condition. Windows can potentially start from the 15th of August back 365 days before. Red and black lines show whether the relationship is quadratic or linear, respectively. Specific species names can be seen in Table S2 in Appendix 4.

The only climate variables that showed moderately consistent responses in sensitivities across all species were temperature and humidity (Fig 4). Increased temperature was associated with a decrease in body condition for 84% (N=19) of species (on average -0.4% body condition /°C [95% C.I.= -0.7%, -0.2%]). Increased humidity was associated with increased body condition in 75% (N= 24) of species (on average 0.08% body condition /% humidity [95% C.I.= 0.003%, 0.15%]). Species sensitivities to each climate variable were not strongly correlated, as species that were highly sensitive to one climate variable were not likely to be highly sensitive to any other variables (max.|r|=0.52; Fig S2 in Appendix 4).

Sensitivities also varied substantially within species, with responses at different sites often ranging from positive to negative (Fig 4). Only a few species showed consistent responses among sites for specific climate variables. For instance, almost all sites of the European greenfinch *Carduelis chloris*, icterine warbler *Hippolais icterina* and short-toed treecreeper *Certhia brachydactyla* showed positive responses to humidity.

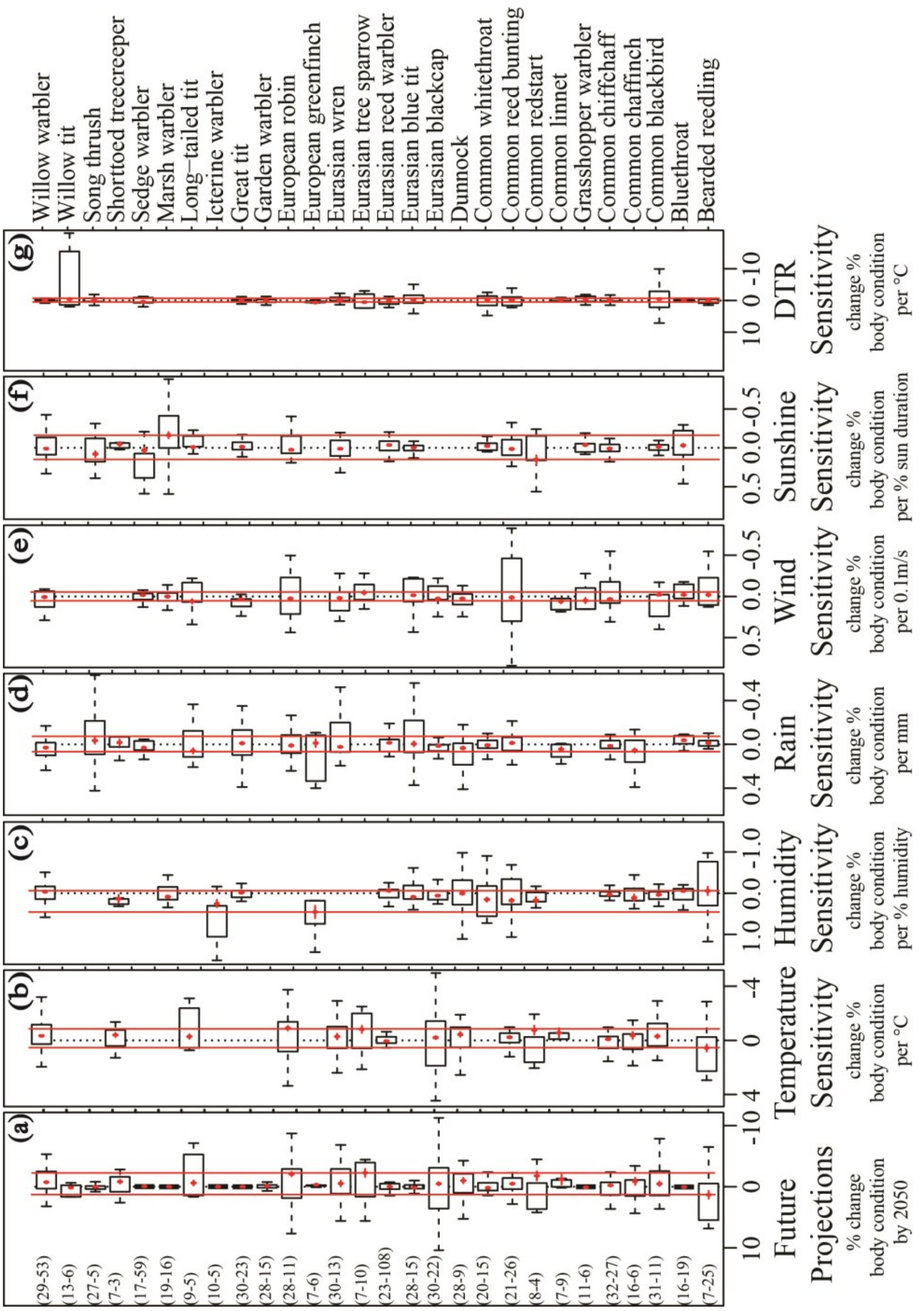

Figure 4 Interspecific and intraspecific variation in future projections (a) and sensitivity (b-g) of 29 bird species at 80 sites. The overall species' sensitivity (or future projections) are shown by the red points and lines (with standard error bars). The two red vertical lines show the minimum and maximum of the species' sensitivity estimates (i.e. the range of the red points). For each species, the intraspecific (among-site) variation in climate sensitivity (or future projections) is described by the black boxplots. Sample sizes are shown in brackets along the left side of the figure, with the first number showing how many sites were present followed by the average number of individuals per site per year.

Future Projections

We found that 62% (N= 39) of species are projected to decrease in body condition by 2050 due to the combined effect of all climate variables. Future projections ranged from 5% decreases to 1.3% increases in body condition by 2050 across all species. However, on average, total body condition is projected to decrease (0.4% ±0.2 SE). Although future projection estimates were made up of sensitivities and exposures to all climate variables, they were mainly driven by temperature (Fig 5), as overall projections were highly correlated to temperature projections (r=0.98). The projected changes in body condition due to other climate variables were all small, potentially due to smaller changes in these climate variables by 2050 compared to temperature.

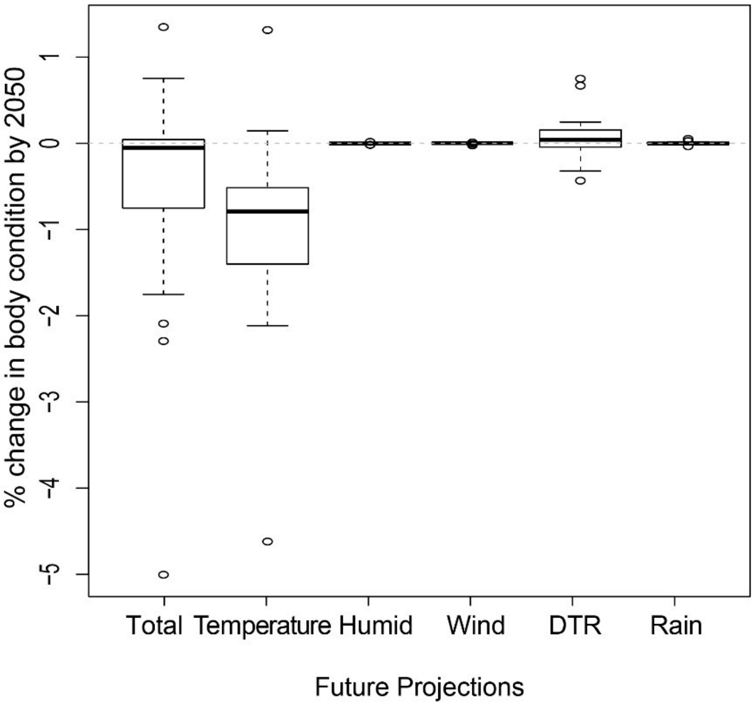

Figure 5 Boxplot of the projected change in percent body condition by 2050 (total future projections) and the contribution of each climate variable for all species for 39 passerine species. Total future projections is the sum of all climate projections.

Species signal

Intra-specific variation (for both sensitivity and future projections) was high, such that there was little evidence for any species signals in body condition responses to climate. Visually, population sensitivities within one species varied more than species sensitivities (Fig 4). The variance component models supported this, as the ratio of among-species variation to total variation was low for sensitivity (on average 0.3% across all climate variables, ranging between 0-1.6%) and future projections (0.0%; Table S4 in Appendix 4). This suggests that among-population variation was much higher than among-species variation. Such low species variance components mean that the correlation between the climate sensitivity (or future projections) of populations of the same species was no higher than the correlation between populations of different species. Indeed, population sensitivities often differed in their sign, meaning that populations of the same species often showed opposite responses (Fig 4).

Species and site traits

While species traits did not explain variation in species' sensitivities and future projections, some variation was explained by site-level traits. Variation among species in their climate sensitivity or future projection was not explained by the species traits average body size, migration strategy, preferred habitat type or lifespan (see Tables S4 & S5 in Appendix 4 for model selection tables), nor by our proxy for unknown species traits, phylogenetic distance between species (Fig 6). Additionally, species that were more closely related did not tend to be affected by the same climate variables (Fig S3 in Appendix 4).

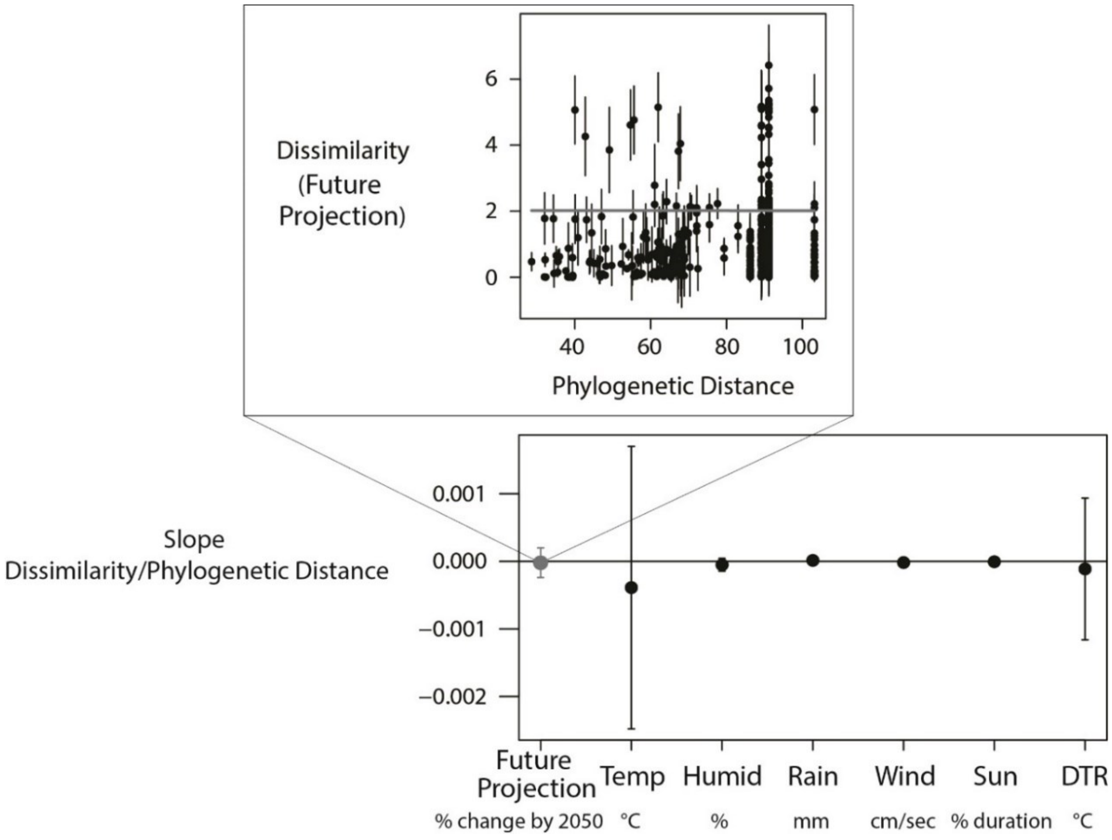

Figure 6 The effect of phylogenetic relatedness on the dissimilarity in future projections and sensitivity of avian body condition. The top figure illustrates what the slopes in the lower figure (the y-axis) represent. In the top figure, we specifically show the relationship between dissimilarity and phylogenetic distance for future projections (grey line), where the slope of 0 reflects that each species had the same projections. A positive slope would indicate that more closely related species have more

similar responses of body condition to climate. The bottom figure summarises the slopes obtained from the linear regressions (slope±SE) of phylogenetic relatedness on the dissimilarity in climate sensitivity to each of the six specific climate variables and to future projections (where the grey dot relates to the grey slope in the top figure).

The site specific trait, habitat type (wet or dry), explained variation in sensitivities to temperature and rainfall among sites (Fig 7). Warmer temperatures in dry habitats resulted in far stronger decreases in body condition compared to populations in wet habitats (which make up 66% of sites; Fig 7). Populations in dry habitats showed comparatively larger increases in body condition per mm of rainfall compared to those in wet habitats (although this model was only slightly better than the null model; Table S7 in Appendix 4). Habitat type did not explain variation in future projections, nor did our proxy for habitat quality, population density, explain variation in future projections or sensitivity across sites for any climate variables except humidity.

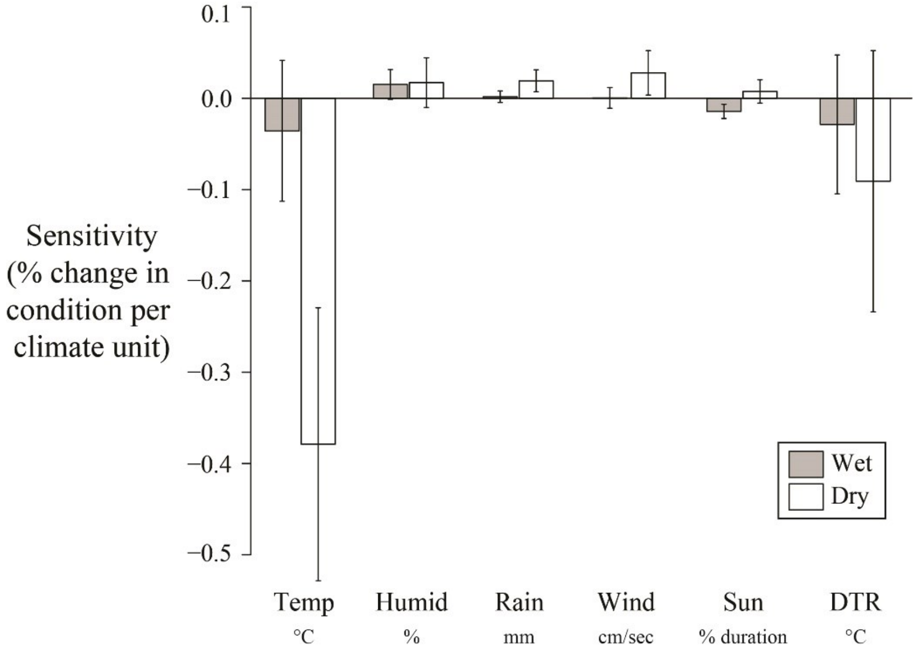

Figure 7 The relationships between site habitat characteristics and sensitivities (±SE) for each climate variable. The shaded bars indicate wet habitats and the clear bars represent dry habitats. Note that the units for each climate variable are not comparable as the units differ.

In only a few species, spatial proximity of sites were able to predict dissimilarity in climate sensitivity, with 13% (14 out of 104 species and climate combinations) of species having more similar sensitivities in populations that were closer together (Fig 8; Table S8 in Appendix 4). However, future projections were more similar in populations that were closer together for 24% (7 out of 29) of species (Fig 8).

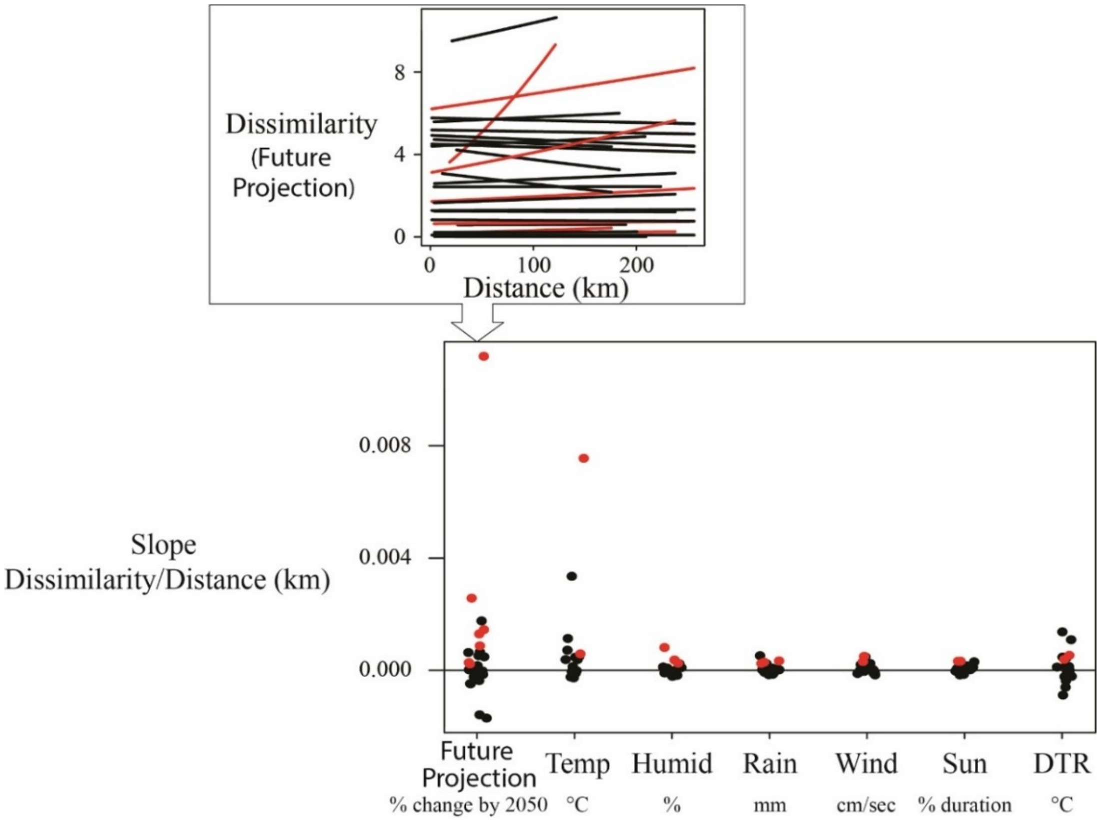

Figure 8 The distribution across species of relationships between distance (km) and dissimilarity in sites sensitivities and future projections. The top figure illustrates how the slopes were estimated in the lower figure (the y-axis). In the top figure, we specifically show the relationship between dissimilarity and distance (km) for future projections, where each line represents a different species. A slope of 0 would mean that projections did not differ with distance, while a positive slope would indicate that closer sites were more similar. The red slopes indicate when a slope was positive and their 95% CI did not cross zero. The bottom figure summarises the slope estimates for each species for future projections and climate sensitivity for each of the six specific climate variables. There were 7 species that showed a significant increase for future projections, 3 species were sensitive to rain, and 2 were sensitive to all other climate variables.

Discussion

In this study, we aimed to determine how avian body condition responds to changes in climate and how consistent these responses are across, and within, species. The size-adjusted body condition of Dutch birds was sensitive to multiple climate variables, with each of the six climate variables affecting about half of the species, predominantly in a non-linear way. Warmer temperatures were associated with decreased body condition, and higher humidity with increased body condition. However, responses to other climate variables varied widely in direction and size among both species and populations. In the future, body condition was projected to decline in the majority of species, primarily due to temperature effects. We found that sensitivities and future projections among populations of the same species were just as variable as responses across species, suggesting that there was no species signal in climate responses of avian body condition. As a predicted consequence, species traits were unable to explain variation in responses across species, while the local population traits habitat type and geographic distance could explain some of the large amount of among-site variation in climate sensitivity.

Species signal

By comparing intra-specific variation in body condition sensitivity across 80 populations to inter-specific variation among 39 species, we were able to quantify what 'a lot' of intraspecific variation might be. We showed that populations of a given species were almost no more alike than populations of different species in their climate responses, suggesting that species signals in body condition responses likely do not exist here. As such, looking for responses to climate change at a species-specific resolution could be too coarse. Instead, more focus should be on explaining variation in responses within-species. In contrast to our result, Rubolini et al. [5] and Thackeray et al. [7] found that phenological responses over time varied much more across-species than within-species. Yet a study on plant growth response to climate by Malyshev et al. [6], as well as other studies unrelated to climate, show that intraspecific variation can exceed interspecific variation (dispersal ability of butterflies, [8]; range of traits of freshwater fish, [11]). An important question therefore seems to be, why is there a species signal in some response types, such as phenology, but not in others? Only with more research into when such species signals occur for a range of different types of climate responses will we be better able to generate and test potential explanations.

Species and site traits

Understanding more about how climate change responses vary across populations and species and which species and populations are most at risk is vital. This knowledge will not only help to identify the underlying mechanisms, but is also important for improving the accuracy of our predictions [6], such as those from climate change vulnerability assessments [25,69]. A weak species signal suggests that species-specific traits will be of little use in explaining responses to climate [5]. As such, species traits (including our proxy for unknown traits, phylogenetic distance) did not explain variation in body condition sensitivities to climate or future projections. The current focus in the literature on identifying species life history traits that can explain climatic responses [e.g. 1–3], is potentially misplaced if the amount of intra-specific variation has not been quantified (as is the situation most of the time) and the average species response is unrepresentative of most individual population responses [5].

The fact that responses varied among sites indicates that local external factors are important (e.g. micro-refugia, habitat quality, resource availability), or that populations themselves may differ in their responses (due to genetic, behavioural or plastic differences). For instance, there was no temperature effect on body condition in wet habitats, suggesting that the overall effect of temperature seems to have been driven by dry habitats. Wet habitats might lessen the direct effects of hot weather through hydration or the opportunity for bathing in available standing water, as populations in dry habitats showed much stronger declines in body condition in hot temperatures than those in wet habitats [70,71]. Alternatively, the effects could work indirectly through food availability. Food abundance fluctuates more strongly in woodland and scrub habitats with warmer temperatures (i.e. dry habitats), as they tend to be less stable than marshes (i.e. wet habitats) [72]. Aubry et al. [28] also found habitat type to be an important predictor of body condition sensitivity to temperature, suggesting that it may more generally have an important role in modulating body condition responses to climate.

Substantial intra-specific variation in responses to environmental change could have important ecological effects [10]. If declining body condition has negative consequences for survival and population growth, for example, then in line with the portfolio effect, variation in body condition responses among populations could counteract the overall effects at higher levels. Indeed, species distribution models show much less severe projections when they take intraspecific variation into account [22]. Somero [73] suggested that populations could be locally adapted, with different genetically determined thermal optima and tolerance limits [see also 74]. If such population variation is heritable this could provide a potential buffer against species extinction [23]. Consequently, the degree of intraspecific consistency has important implications for predicting future projections of species to climate change [5].

Is temperature the main climatic driver?

In line with previous studies [28–30,34,41], we have shown that warmer temperatures generally resulted in decreased body condition. Temperature was found to be affecting body condition during spring, suggesting that cold winters are not important for body condition during the breeding season for these species living in the temperate climate of the Netherlands. Additionally, we have shown that higher humidity generally resulted in higher body condition. However, as this has not been investigated previously, other studies are needed to establish whether this is a general pattern in birds.

The majority of the literature—on climate change ecology generally, and on body size in particular—only investigates the effects of temperature, yet we found that all six climate variables were important. However, with the exception of temperature and humidity, there were no clear trends across species and the time periods that were associated with the strongest changes in body condition differed substantially (with the exception of temperature and wind speed). Therefore, despite the fact that many species are sensitive to changes in these climate variables, their responses differ substantially. Even populations of the same species differ substantially. It is possible that these associations are not real. However, given how conservative our method to avoid false-positives was and the fact that so many species show associations we do not believe this is likely. Rather, it is possible that only once we have a better understanding of the underlying mechanisms will we be able to tease apart these different responses. In the same way that populations in dry habitats showed different responses to temperature, other unknown local factors could be further influencing these patterns.

Despite all six climate variables being found to be important climatic drivers of body condition, from a future projections perspective to climate change, temperature was found to be the key variable. By combining the sensitivity estimates of species and populations with exposure (i.e. add the change in mass per climate unit with the projected change in climate) we were able to project for the first time how avian body condition might change in the near future. Most species were projected to decrease their body condition by 2050, driven mainly by temperature effects. All other climate variables were less important in determining species' future projections either because they were less sensitive to these climate variables, or because these variables are projected to change less strongly than temperature. Overall, the current focus in the literature on temperature may actually not be as problematic as first thought, despite the fact that body condition may be sensitive to other climate variables.

Statistical issues

We performed the first comparative study on body condition responses that investigated multiple climate variables and allowed different time periods to impact different species in linear or non-linear ways. This high level of detail introduces a level of complexity that restricts options for integrative analyses and also makes interpretation more difficult. However, it also includes biological realism that other studies might be missing. For instance, we found that the majority of responses to climate variables were non-linear, and different species were found to be impacted by different combinations of climate variables. The fact that body condition was affected by different climate variables and that different species exhibited different response curvatures meant that the analysis comparing the within- versus among-species variation was not able to be carried out in one single combined analysis based on the individual observations. Instead, we first estimated the climate sensitivity of each population for each species separately and subsequently analysed the climate sensitivity of all populations and species in a subsequent model. Such multi-step procedures (see Fig 1) are not ideal as they introduce issues with propagation of uncertainty (e.g. due to sampling variance among populations), which we tried to alleviate by weighting climate sensitivities by their standard errors and checking for dependencies of their variance on sample size.

Although we took several steps to avoid false positives in our climate window selection, it is possible that some windows could still be identified as the best model by chance. Such false windows could disrupt the detection and explanation of among-species variation. This is inevitable in any study that compares multiple models and species, as all analyses that test a high number of models will face this problem. However, many studies do not even consider the possibility that there is no climate signal, nor do they account for multiple testing of the many potential windows tried [44].

We investigated the local climatic conditions for all migratory and non-migratory species, which could potentially mean that windows were selected during times which migratory species may not be present. In such cases, local conditions could be correlated with their overwintering habitats, for instance if local weather reflects wide-spread conditions due to large-scale oceanic climate indices such as the North Atlantic Oscillation Index [75]. If this is not the case, it is more likely that species sensitivities are occurring via climate effects on habitat quality in the breeding areas. However, the migration strategy of the different species did not explain any differences in sensitivities, suggesting that perhaps the underlying mechanisms acting on body condition do not differ drastically among migratory and non-migratory species.

Conclusions

The fact that body condition sensitivities to climate varied so substantially among populations of the same species draws attention to the need for researchers to investigate variation within species, and not just to assume that a species-level response will be representative. Given that there are now two studies showing weak species signals in body condition, mass or growth ([6] and this study) and two studies showing strong species signals for phenological changes with climate [5,7], other comparative analyses are needed to better understand how frequently species signals are occurring and how this may vary among traits. This is particularly needed for other key traits such as physiology or offspring sex ratio, or vital rates such as survival and reproduction. The absence of a species signal in the climate sensitivity of vital rates determining population growth, for instance, would be problematic for conservation prioritisation. Climate change vulnerability assessments based solely on species traits would be inadequate, while intraspecific traits such as habitat type might be more useful. Accurate predictor variables need to be identified if we are to improve conservation management planning, especially given that almost all species were projected to decrease in body condition by 2050.

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Appendix 3 - Methods

Data

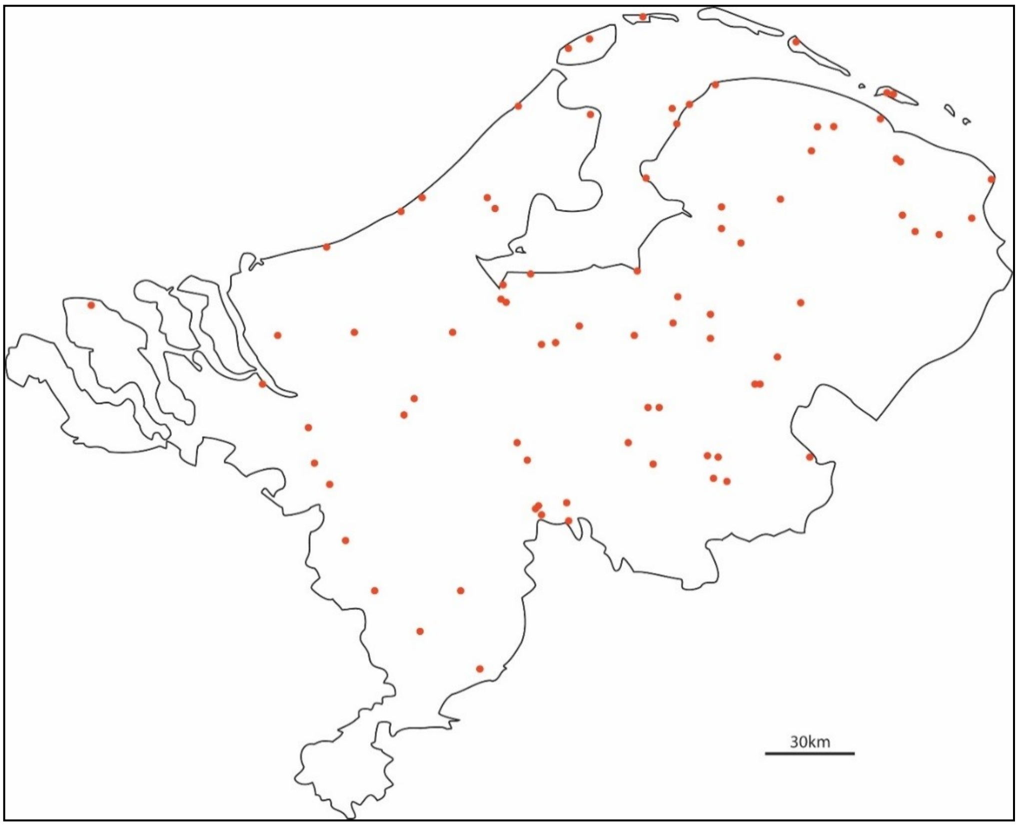

Figure S1 Map of the Netherlands with all study sites (indicated by the red dots).

Data selection

For data selection we removed observations in which (i) measurements seemed highly likely to be mistakes, (ii) the bird had died, and (iii) crucial parameters were not recorded (i.e. missing body mass, wing length, date of capture, or age-class). Before conducting any of our analyses, we first removed any extreme values that we deemed as highly likely to be mistakes in the data (e.g. typos; it was not uncommon to find values orders of magnitude out from the main distribution). We used a two-step process to remove any suspicious data points in a standardised way. Firstly, for each species, we calculated where the inner 68.27% of the data lay from the median (approximately 1 standard deviation; i.e. 34.13% of the data on either side of the median) and then extrapolated in both directions to 3 standard deviations (99.7%). Any data points that were outside of this 99.7% region were considered extreme values and were removed. This method of identifying extreme values is preferable to using the mean and standard deviation, since it is unaffected by the extreme values or skews in the distribution. Secondly, we conducted a regression with body mass as the response variable and wing length as the explanatory variable. Any residuals that were outside of 3 standard deviations (calculated in the same way as above) were removed. This step identified any potential mistakes that would not have been recognised independently, for instance, a bird with small wing length that is very heavy or large wing length that is extremely light. Although it is possible that we could have potentially removed real values, we decided that it was more important to be certain that those values that we do use in our analysis were real. Several species did not have any data collected in the year 2002.

Table S1 Species removed due to low sample sizes. These species' sample sizes were too small for the model to converge in the R package *climwin.*

Common Name	# Individuals	Years
Barn swallow	638	20
Coal tit	120	14
Common redpoll	53	7
Eurasian penduline tit	105	15
Great reed warbler	65	19
Meadow pipit	151	17
Sand martin	16	8
Western yellow wagtail	35	9

Climatic data

Table S2. CES site and weather station coordinates and the distances between the two.

CES Site	Lat (CES)	Long (CES)	Weather Station	Lat (Stn)	Long (Stn)	Distance (km)
C01	52.61	5.90	273	52.70	5.89	10.1
C02	52.45	5.82	269	52.46	5.53	20.3
C03	52.34	4.52	240	52.30	4.77	17.7
C04	52.54	6.47	278	52.44	6.26	18
C05	53.21	5.44	270	53.23	5.76	21.2
C06	53.11	4.79	235	52.92	4.79	20.3
C07	53.20	6.80	280	53.13	6.59	16.8
C08	52.33	5.16	265	52.13	5.27	23.7
C09	52.91	5.83	273	52.70	5.89	23.9
C10	51.85	5.12	356	51.86	5.15	1.9
C11	52.61	5.64	269	52.46	5.53	18.2
C12	51.57	4.90	350	51.57	4.93	2.1
C13	53.04	5.40	267	52.90	5.38	15.8
C14	52.54	4.83	249	52.64	4.98	15.6
C15	53.26	4.95	251	53.39	5.35	30.9
C16	51.69	4.47	344	51.96	4.44	29.8
C17	52.23	6.61	283	52.07	6.65	17.3

C18	52.28	6.52	283	52.07	6.65	24.8
C19	52.29	6.09	278	52.44	6.26	20.5
C20	52.63	6.08	273	52.70	5.89	15.5
C21	52.42	5.23	269	52.46	5.53	20.4
C22	52.53	6.46	278	52.44	6.26	16.6
C23	51.83	5.93	375	51.66	5.71	24.5
C24	52.85	5.44	267	52.90	5.38	6.2
C25	51.84	5.96	275	52.06	5.89	25.1
C26	52.44	6.88	290	52.27	6.90	18.5
C27	51.34	5.79	377	51.20	5.76	16.1
C28	52.42	4.56	240	52.30	4.77	19.7
C29	51.44	5.24	370	51.45	5.41	12.4
C30	51.84	4.39	344	51.96	4.44	13.4
C31	52.14	4.33	210	52.17	4.42	6.8
C32	52.31	5.21	265	52.13	5.27	20.5
C33	53.33	6.42	277	53.41	6.20	16.9
C34	53.07	5.33	267	52.90	5.38	19.4
C35	52.86	6.00	273	52.70	5.89	19.1
C36	52.31	6.13	278	52.44	6.26	16.9
C37	51.57	3.57	310	51.44	3.60	14.2
C38	52.27	6.47	278	52.44	6.26	23.7
C39	53.04	4.74	235	52.92	4.79	13.2
C40	51.65	4.77	350	51.57	4.93	14.7
C41	53.33	6.43	277	53.41	6.20	17.8
C42	52.81	6.42	279	52.75	6.58	12.6
C43	52.91	5.03	235	52.92	4.79	16.3
C44	52.86	5.88	273	52.70	5.89	17.5
C45	53.31	6.05	277	53.41	6.20	14.7
C46	53.46	5.66	251	53.39	5.35	21.8
C47	53.21	6.03	270	53.23	5.76	18.8
C48	51.90	5.12	356	51.86	5.15	4.9
C49	52.54	5.95	273	52.70	5.89	18.7
C50	52.57	6.15	278	52.44	6.26	16.9
C51	51.35	6.13	391	51.50	6.20	17.4
C52	51.36	5.49	370	51.45	5.41	11.2
C53	52.14	5.09	260	52.10	5.18	7.6
C54	53.20	6.59	280	53.13	6.59	8
C55	52.27	5.48	265	52.13	5.27	20.9
C56	51.97	4.69	348	51.97	4.93	16.4
C57	53.44	6.87	286	53.20	7.15	32.6
C58	53.41	6.22	277	53.41	6.20	1.9
C59	52.22	6.55	283	52.07	6.65	17.5
C60	51.51	5.84	375	51.66	5.71	18.8
C61	52.33	5.16	265	52.13	5.27	23.7
C62	53.48	6.16	277	53.41	6.20	8.3
C63	51.91	6.03	275	52.06	5.89	20

C64	51.87	6.08	275	52.06	5.89	25
C65	51.96	5.74	275	52.06	5.89	15.4
C66	52.52	4.91	249	52.64	4.98	14.8
C67	52.53	6.15	278	52.44	6.26	12.7
C69	52.42	5.23	269	52.46	5.53	20.3
C70	52.29	5.53	269	52.46	5.53	18.3
C71	53.28	6.00	270	53.23	5.76	17.4
C72	51.82	5.94	375	51.66	5.71	24.2
C73	53.17	6.70	280	53.13	6.59	9
C74	52.37	5.58	269	52.46	5.53	10.4
C75	52.81	4.69	235	52.92	4.79	14.3
C76	53.04	6.04	270	53.23	5.76	28.6
C77	53.31	6.89	286	53.20	7.15	21.5
C78	52.57	6.14	278	52.44	6.26	16.8
C79	52.16	6.26	275	52.06	5.89	27.6
C81	51.55	5.03	350	51.57	4.93	7
C82	53.48	6.18	277	53.41	6.20	8.4
C83	52.63	6.47	279	52.75	6.58	14.7
C84	53.44	6.87	286	53.20	7.15	32.6
C85	52.31	5.20	265	52.13	5.27	20.6
C86	52.17	6.10	275	52.06	5.89	18.9
C87	51.98	5.66	275	52.06	5.89	18.2
C88	53.10	5.39	267	52.90	5.38	22.7

A small number of the daily measurements at some weather stations were missing; such potential windows were excluded in the climate window analysis.

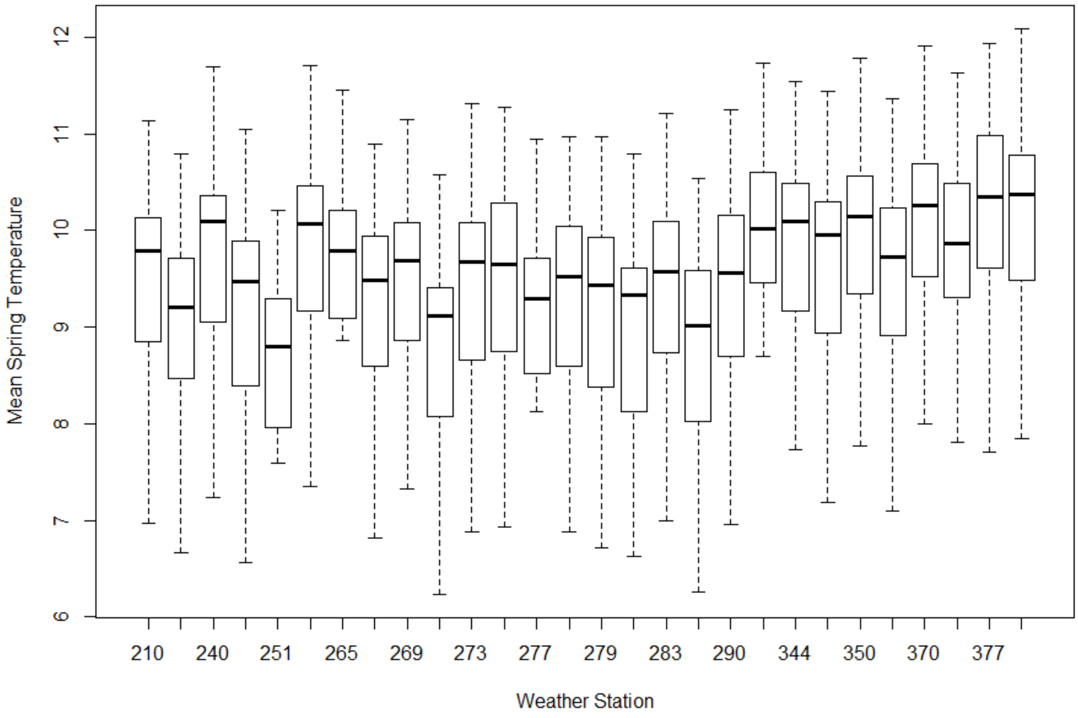

Figure S2 Variation in mean spring temperature among the different weather stations. Here, we show annual mean spring temperatures for each weather station over the course of the study period. This shows that temporal variation within sites is larger than the spatial variation among sites.

Species and site trait data

Adult life-expectancy was calculated as $\frac{1}{1-mean\ annual\ survival}$ for the span of the study. Each habitat category (Urban, Woodland, Wet, Open) was coded as a separate dummy variable (0 or 1) because each species could potentially be found in multiple habitat types. Habitats were assigned to each species based on Mullarney et al. (2000), however we condensed the number of potential habitat types in the following way:

- Urban: parks, gardens, farmland, human habitation and orchards
- Woodland: woods, scrubby areas, open woodland, mixed woods, coniferous forest, bushy areas, open forest, deciduous woods and upland birch forest
- Wet: reedbeds, lowland lakes, swampland, rivers and lakes, coastal heaths and wet ground
- Open: heaths and commons

Statistical analyses

Climate windows and signals

The R package climwin (Bailey & van de Pol 2015) was used to find the time period during which the mean of each of the six climatic variables explained the most variation in body condition for each species. Because we were most interested in identifying the periods over which these climatic variables affected body condition, we were looking for fixed windows (i.e. all individuals were assumed to be affected by climate over the same time period) rather than variable windows (time windows that are relative to the timing of expression or measurement of a trait for each individual) (van de Pol et al., 2016). The climwin analysis calculates the mean of the daily climate estimates for each site per year over the specific period being tested (e.g. mean of all days in May) and conducts a linear regression with this mean climate as the predictor variable and body condition as the response variable. The AIC model fit value is used to compare each regression model to a null model without climate (thereby providing an indication of how much better the model with those mean climate estimates is to one without climate at all). This is repeated until all possible combinations of consecutive days have been tested.

We first determined a baseline model structure without climate effects. The baseline model takes into account the age of individuals (juvenile or adult; where juveniles are first years and adults are older than 1 year), a quadratic effect of weighing time (minutes since midnight) and a quadratic effect of the time in the season (number of days since 1st April). Individual ID was included as a random effect to account for non-independence of those birds that were captured multiple times. Unfortunately, we could not include both Site ID and Individual ID as a random effect because most species did not have large enough sample sizes to deal with such a complex model. Individual ID was chosen to remain in the model (rather than Site ID) because it explained more variation. The baseline model was the same for all species with the exception that sex (male, female or unknown) was only included for those species that could be accurately sexed in the field.

Table S3 The 12 models analysed for each species using the *climwin* function.

	Model
1	Body condition ~ mean temperature + baseline
2	Body condition ~ mean rainfall + baseline
3	Body condition ~ mean wind speed + baseline
4	Body condition ~ mean humidity + baseline
5	Body condition ~ mean % sunshine + baseline
6	Body condition ~ mean DTR + baseline
7	Body condition ~ mean temperature^2 + baseline
8	Body condition ~ mean rainfall^2 + baseline
9	Body condition ~ mean wind speed^2 + baseline
10	Body condition ~ mean humidity^2 + baseline
11	Body condition ~ mean % sunshine^2 + baseline
12	Body condition ~ mean DTR^2 + baseline

Reducing False Positives

When testing so many models, the chances of spurious results are high (van de Pol et al., 2016). We took two steps to reduce the chances of getting false positives (type I errors). Firstly, we excluded short windows that we deemed unlikely to be biologically plausible. Windows that were shorter than 5 days were excluded, and windows less than 15 days for if they were further than 60 days before the sampling season starts (on the 12th April; i.e. long-term windows). Such short windows are biologically less plausible and are often incorrectly selected as best windows by chance (van de Pol et al., 2016).

Secondly, we performed a formal randomisation analysis to determine if climate windows were likely to be false positives. If the randomisation analysis suggested that the best fitted model was likely a true positive, this window was added into the baseline model and the *climwin* analysis was rerun to check whether any second climate signal window was present after accounting for the best window. If it suggested that the best model was likely only due to chance, that species was not considered to show a climate signal, meaning that body condition was not considered to be affected by that climate variable. The randomisation analysis determined a highly conservative cut-off AICc value (see below), above which time windows were considered to be false positives. To quantify the likelihood of obtaining strong model support by chance we randomised the data and analysed the distribution of 'best' AICc values. Rather than carrying out multiple randomisations for each species, due to constraints with computational time, we carried out three randomisations on a subset of 15 species (Table S4).

Table S4 Subset of species selected and their sample sizes (total number of individuals and total number of years captured) used in the randomisation analysis.

	Common Name	# Individuals	Years
1	Common blackbird	5817	20
2	Common chaffinch	1511	19
3	Common chiffchaff	15089	20
4	Common grasshopper warbler	1182	20
5	Common Kingfisher	177	13
6	Common linnet	969	19
7	Eurasian jay	232	18
8	Eurasian nuthatch	127	17
9	European crested tit	380	19
10	European goldfinch	431	16
11	European pied flycatcher	358	19
12	Great tit	10720	20
13	Lesser whitethroat	1594	20
14	Marsh tit	299	18
15	Marsh warbler	5197	21

The same *climwin* analyses were carried out three times on the randomised data for each climate variable and for linear and quadratic responses (i.e. 6 climate variables x 2 responses types x 3 replications = 36 randomised analyses per species). The AICc values from the best model were recorded from each randomisation. These values were then used to determine what the AICc cut-off would be, whether this cut-off value should be different for each climate variable, for linear or quadratic responses and for different species (with different sample sizes).

Should the AICc cut-off value differ between climate variables?

Using the best model AICc values from the randomised analyses, we found a small difference between the best model AICc values among climate variables (Fig S3a). A linear model with climate variables as the explanatory variable and ‘best model AICc’ as the predictor variable was 6.3 AICc units better than the null model (intercept only model). However, the mean best-model AICc only ranged from -7.5 to -5.3 AICc units across the different climate variables, suggesting that although the randomised AICc values did differ among climate variables, this difference was small.

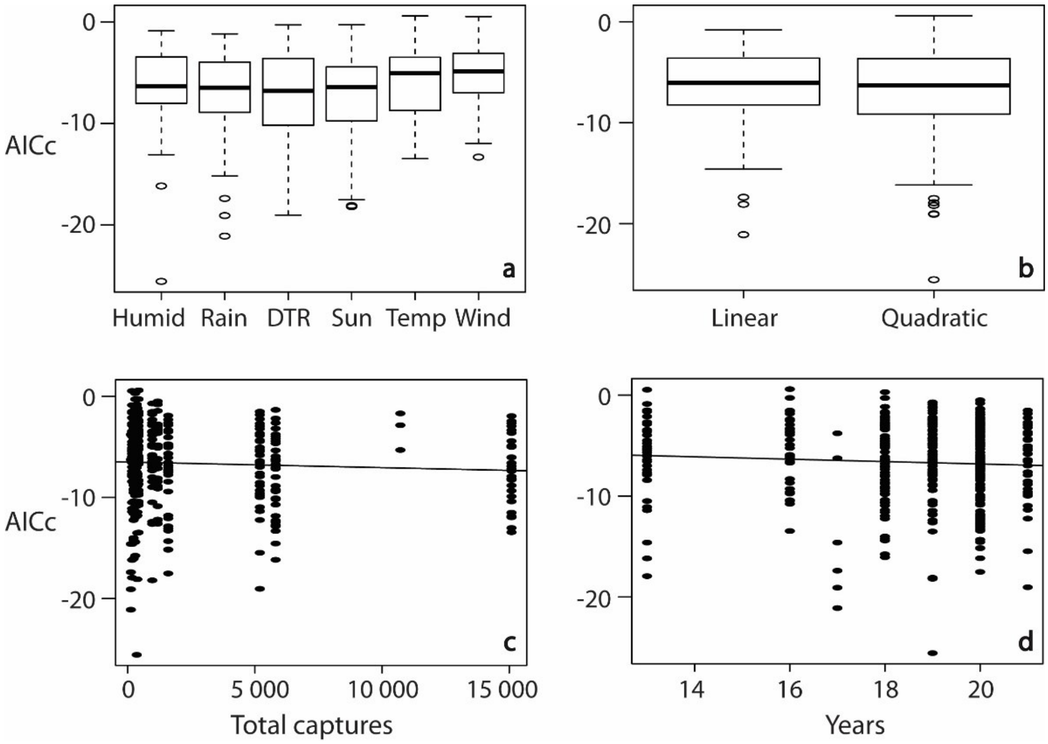

Figure S3 Best model delta AICc values from the randomisation analysis. Here, we show an overview of how the best-model AICc values from randomised climwin analyses vary with (a) climatic variables, (b) linear or quadratic responses to climate variables, (c) differing numbers of total captures of individuals, and (d) differing numbers of years with observations.

2. Should the AICc cut-off value differ between linear and quadratic responses in body condition?

We found that there was no difference between the randomised best model AICc values among linear or quadratic response types (Fig S3b). A linear model with curvature (linear or quadratic as categorical variables) as the explanatory variable and ‘best model AICc’ as the predictor variable was within 2 AICc units of the null model (intercept only model).

3. Should the AICc cut-off value differ among species with different sample sizes?

Overall sample size (total number of individuals caught; Fig S3c) and the number of years (Fig S3d) had no effect on the randomised best-model AICc values. Both models were within 2 AICc units of the null model.

As we found little evidence suggesting that the best-model AICc values from the random data differed, we decided to use a single cut-off value for all climate variables, linear and quadratic responses, and species (even over a range of years and sample sizes). The majority of the randomised best model AICc values fell between 0 and -10, with a mean AICc value of -6.6 (Fig S4). In order to keep our cut-off value conservative, we chose to assign a value of -14.5. This value was 2 standard deviations lower than the mean (standard deviation = 3.9). This conservative cut-off value also reduces any potential for differences in false positive rates among climate variables. If AICc values from the real analyses were higher than the cut-off value they were not considered a real window. This decision will mean that we will be rejecting some ‘real’ climate windows, but we felt that it was more important to be certain that those windows that we do accept as being correct are as likely as possible to be real (true positives).

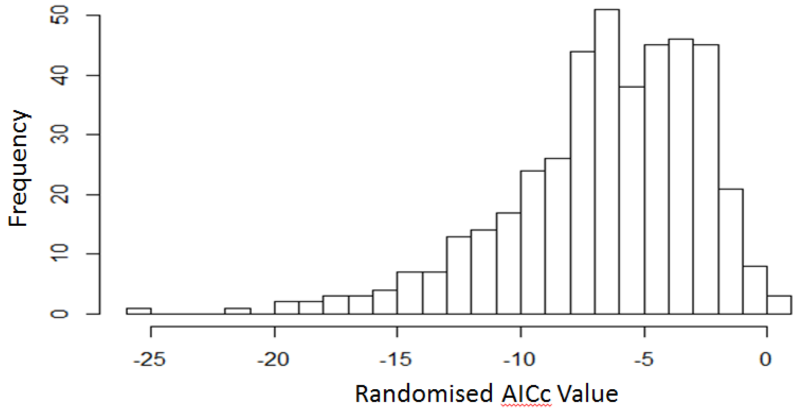

Figure S4 Frequency of the best model AICc values from the randomised data across all species and climate variables.

When the best window’s AICc value was below the cut-off value, then the best model was added into the baseline model and the *climwin* analysis was run a second time to check whether any additional windows were present after accounting for the best window. If a second window was found, but the critical time period overlapped with the first window, then we discarded the second window and focused on the first window only. To determine whether the body condition response was linear or non-linear, the model with the best AICc value was selected. However, if the best AICc value was within 2 AICc units of one another then we selected the linear response.

Model Selection and Averaging

Model selection and averaging was used to determine which climate variables were important and to calculate parameter estimates after accounting for the other climate variables. We adopted an Information-Theoretic approach to quantify and rank the models based on the different climate variables (Burnham and Anderson, 2002). Climate variables were considered hitchhikers and were subsequently removed from the model set if they met two requirements,

(1) the addition of the climatic variable did not improve the model by > 2 AICc units (i.e. it does not occur in the best model but does occur in a model that is within 2 AICc units of the very best model) (Arnold, 2010), and (2) if their relative importance was less than 0.5 (w+) (K. Burnham and Anderson, 2002). We used the function 'importance' from the package AICcmodavg.

Climate variables were rarely correlated, but when this did occur, collinear climate variables were always kept in the same models when testing the different combinations of variables (i.e. both always included or excluded from the same models)(Freckleton, 2010). This allows the effects of the two climate variables, which are essentially indistinguishable, to be measured together and contrasted with the other models. If one variable was to be removed from the model, we would run the risk of systematically over or under-estimating the remaining variable depending on the sign of the correlation between the predictors (Freckleton, 2010). For example if rainfall and temperature were negatively correlated (hot conditions associated with low rainfall) and low rainfall increased body condition while high temperatures decreased body condition, then removing, say rainfall, would result in an under-estimated slope value of the effect of temperature on body condition (Freckleton, 2010).

Once the final climatic variables had been identified we calculated model-averaged slope estimates for each of the sites (or populations). By combining all of the important climate variables into the final model, we can account for their effects when calculating body condition responses. Model averaging uses the average of the parameter estimates from each candidate model, weighted by its Akaike weight (Freckleton, 2010). The reference categories used for the categorical variables were adult (as opposed to juvenile) and (if the species could be sexed) female (as opposed to male) (see Age and Sex Difference section below). Climate variables were all mean centred. Standardised model-averaged slope estimates were also calculated by dividing the mean centred climate variables by their standard deviation. To calculate the model-averaged slope estimates for each site, an interaction term between the site and the climate variable was included. This analysis was run for every site and climate variable separately to make sure that the number of parameters in the model remained low enough that the model could converge. In this way, sensitivity estimates along with their standard errors for all relevant climate variables were calculated for every site.

Age and Sex Differences

We investigated whether responses to each of the climate variables differed between adults and juveniles, and males and females. Only 40 of the 181 species by climate variable combinations were found to have an interaction term between age and climate that improved the original model (when looking at the model-averaged slope estimates, not sensitivity values), and 13 of the 83 species by climate variable combinations were found to have an interaction term between sex and climate. This suggests that the majority of responses to climate are similar among sex and age groups. We also calculated the sensitivity estimates (rather than the slopes) of the adults and juveniles, and males and females (by including the interaction term between age or sex and climate). We compared these sensitivity estimates to the original sensitivity estimates (without the interaction) to see how well correlated they were. Adult sensitivities (from the interaction) were extremely strongly correlated to the original sensitivity values, suggesting that there was no overall difference between those values estimated with an interaction term and those without (Fig S5a). We also found moderate correlation between the adult and juvenile sensitivities (Fig S5b). This suggested that adults and juveniles have very similar responses (i.e. interactions were sometimes significant, but their effect size was weak). The sensitivity estimates of females also closely correlated to the original sensitivities (Fig S5c). The correlation between male and female sensitivities was very strong (Fig S5d), suggesting that males and females have very similar sensitivities to climate.

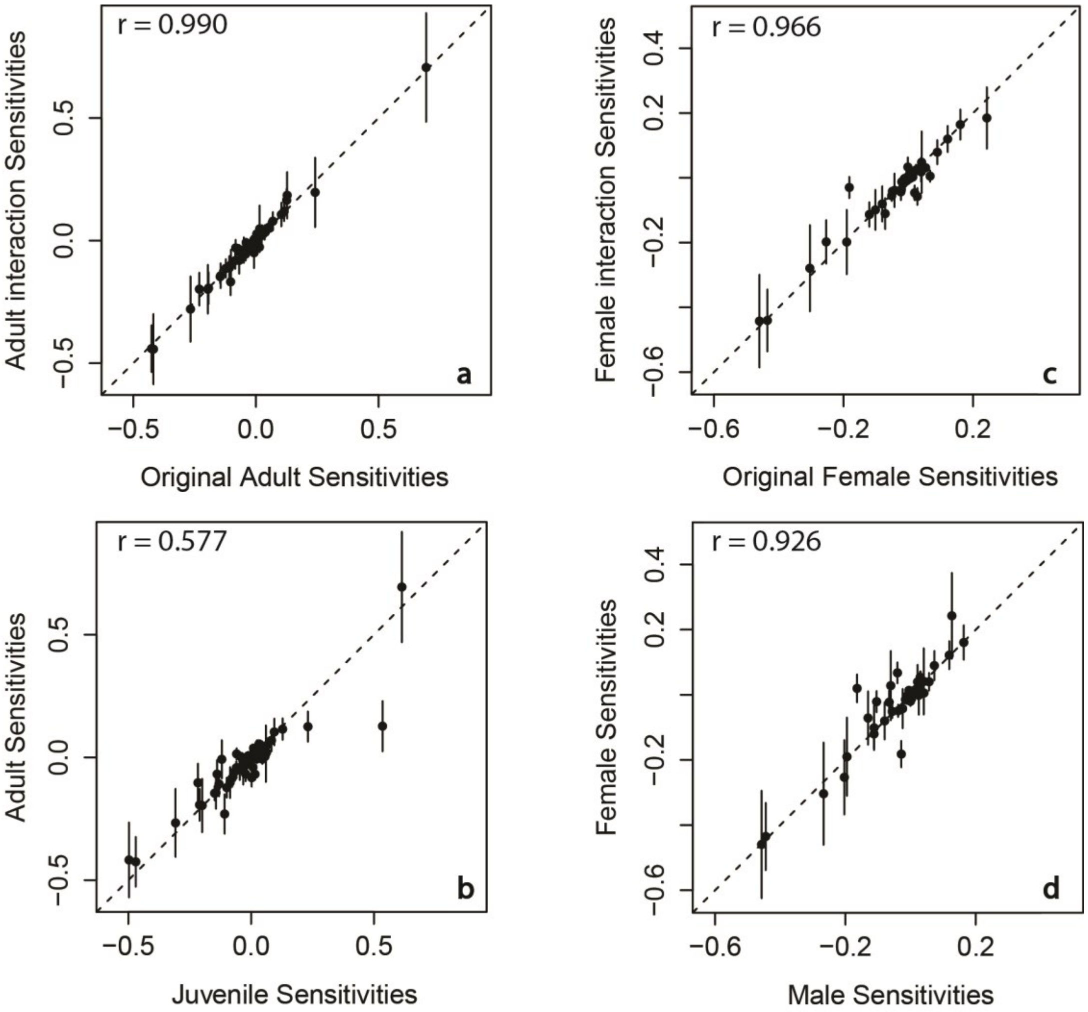

Figure S5 Correlation in sensitivities between groups. Shows the correlations between (a) the original sensitivities (i.e. sensitivities without an interaction between age and climate) and adult interaction sensitivities (i.e. sensitivity values for adults with an interaction between age and climate), (b) between juvenile interaction sensitivities and adult interaction sensitivities (i.e. sensitivity values for juvenile and adults, respectively, with an interaction between age and climate), (c) the original and female sensitivities and (d) female and male sensitivities.

Climate Sensitivities

Our measure of sensitivity was the tangent at the mean climate (i.e. the first derivative of the climate regression function or the local slope estimate at the mean value of the climate variable of interest; Fig. S5).

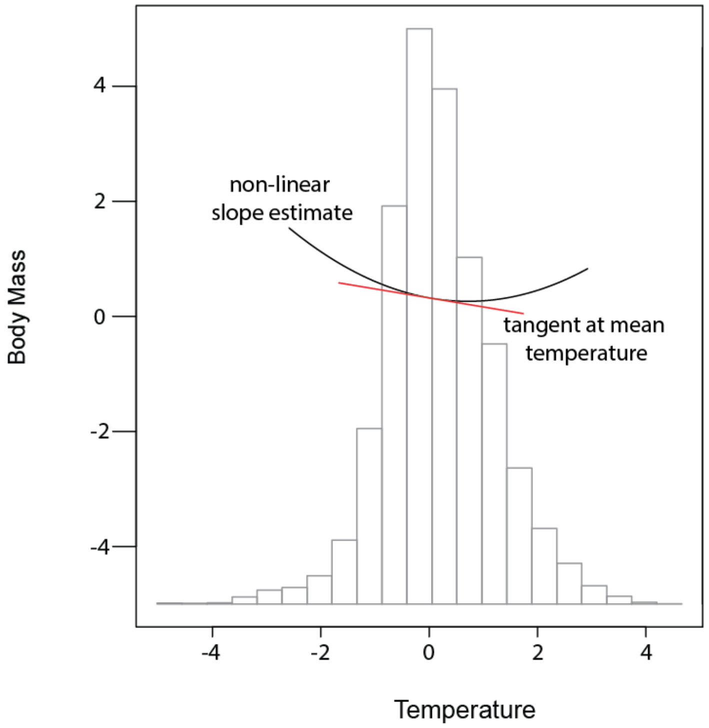

Figure S6 Illustration of how the sensitivity estimate is calculated for a non-linear response between body mass and temperature. The black slope shows the non-linear relationship for a species, and the red linear slope shows the sensitivity estimate, i.e. the tangent at the mean. The histogram shows the distribution of mean annual temperature values (i.e. the range of temperatures experienced over the study period) mean centred such that 0 is the mean temperature.

Climate Vulnerabilities

We calculated seasonal projections (Winter (December-February), Spring (March-May), Summer (June-August) and Autumn (September-November)) based on Royal Netherlands Meteorological Institute's predictions. There currently are no predictions for how the levels of sunshine are expected to change in the future under climate change scenarios.

Species and site traits

We generated matrices of phylogenetic distances between species (distances are directly proportional to time [millions of years ago]) for each tree so that our results were independent of the tree used (Fig S7). Dissimilarity in climate sensitivity was calculated as the absolute difference in the climate response estimates between two species. We calculated pairwise dissimilarities and their standard errors by generating 1,000 data points centred on the sensitivity value with a distribution equal to its standard error (i.e. bootstrapping). We then calculated the differences between all 1,000 data points, with the final dissimilarity value between two sites calculated as the mean, and the standard error derived from the standard deviation of the differences.

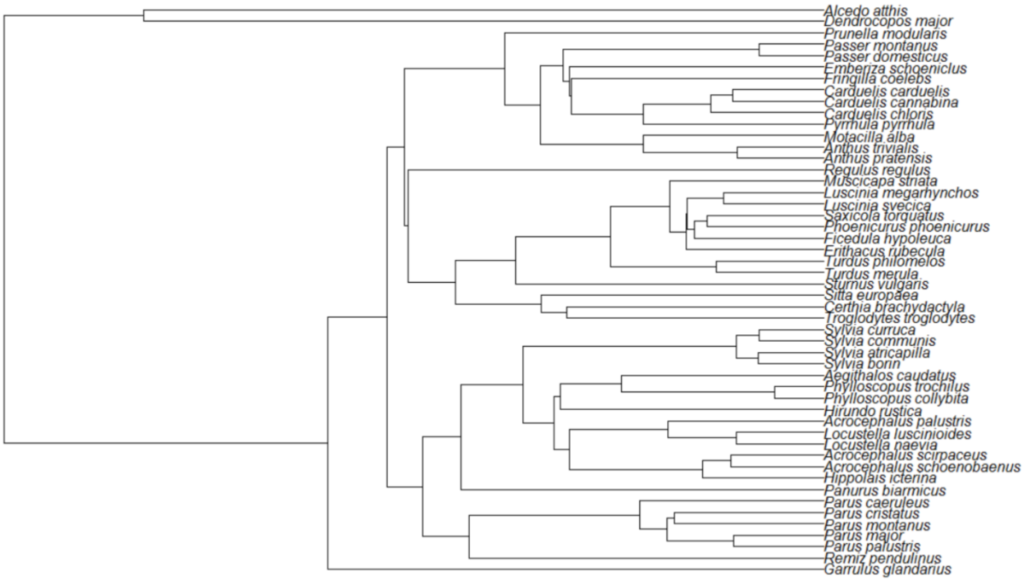

Figure S7 Phylogenetic tree (from one of the 1000 trees) showing relatedness among species.

For the analysis, the pairwise dissimilarities in sensitivity estimates among each of the species were squared to improve adherence to the assumption of a normal distribution and to stop the estimates from being negative numbers (the values of dissimilarity cannot fall below 0). We used the 'lmer()' function from the R-package 'lme4' (Bates *et al.*, 2015). Both species identities in each pairwise dissimilarity value were included as a random effect in the model to account for the non-independence among values (i.e. as species 1 is compared to species 2 and 3 etc. these values are non-independent).

For the second analysis investigating whether more closely related species are impacted by the same climate variables, we carried out logistic regression using the 'glmer' function from the R package 'lme4'. Dissimilarity in climate signal was scored by comparing whether two species were both affected (or both unaffected) by the same climate variable (same=0, different=1).

The analysis for spatial distances was carried out similarly to the phylogenetic distances. The two site identities of the pairwise comparison were included as random effects and the dissimilarities were squared to improve adherence to the assumption of normality. We used the 'lmer()' function from the R-package 'lme4' (Bates *et al.*, 2015).

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Appendix 4 - Results

Climate windows and signals

No particular climate variable was clearly more important overall: 19 out of 46 species were affected by temperature, 26 by rainfall, 21 by sunshine, 24 by humidity, 25 by wind and 24 by DTR (Table S1).

Table S1 Importance values, calculated as the sum of ‘Akaike weights’ over all models, for each climate variable in the final model for each species. Variables are represented by NA if they did not have any windows below the cut-off value or were subsequently removed as they appeared to be hitchhiker values. The sexed column shows which species were able to be accurately sexed, and therefore which species had sex differences included in the models. Temp is temperature, DTR is the climate variable daily temperature range.

	Common name	**Species name**	**Temp**	**Rain**	**Sun**	**Humid**	**Wind**	**DTR**	**Sex**
1	Bearded reedling	*Panurus biarmicus*	**0.55**	**0.57**	NA	**1.00**	**0.92**	**0.92**	yes
2	Bluethroat	*Luscinia svecica*	NA	**1.00**	**0.92**	**0.64**	**0.98**	**1.00**	yes
3	Common blackbird	*Turdus merula*	**0.87**	NA	**0.57**	**0.61**	**1.00**	**1.00**	yes
4	Common chaffinch	*Fringilla coelebs*	**0.68**	**0.99**	NA	**0.65**	NA	NA	yes
5	Common chiffchaff	*Phylloscopus collybita*	**0.56**	**1.00**	**0.73**	**0.91**	**1.00**	**1.00**	no
6	Common grasshopper warbler	*Locustella naevia*	NA	NA	**0.98**	NA	**0.96**	**0.84**	no
7	Common linnet	*Carduelis cannabina*	**0.56**	**1.00**	NA	NA	**1.00**	**0.46**	yes
8	Common redstart	*Phoenicurus phoenicurus*	**0.81**	NA	**0.84**	**0.77**	NA	NA	yes
9	Common reed bunting	*Emberiza schoeniclus*	**1.00**	**0.97**	**0.98**	**1.00**	**1.00**	**0.51**	yes
10	Common starling	*Sturnus vulgaris*	**0.94**	**0.99**	**1.00**	**0.93**	**0.92**	NA	yes
11	Common whitethroat	*Sylvia communis*	NA	**0.81**	**0.97**	**0.99**	NA	0.75	yes
12	Dunnock	*Prunella modularis*	**0.85**	**0.94**	NA	**0.63**	**0.91**	NA	no
13	Eurasian blackcap	*Sylvia atricapilla*	**1.00**	**0.92**	NA	**0.89**	**0.89**	NA	yes
14	Eurasian blue tit	*Cyanistes caeruleus formerly Parus caeruleus*	NA	**0.99**	**0.89**	**0.78**	**1.00**	**1.00**	no
15	Eurasian bullfinch	*Pyrrhula pyrrhula*	**1.00**	NA	NA	**0.99**	NA	**0.63**	yes
16	Eurasian jay	*Garrulus glandarius*	NA	**0.98**	NA	**0.95**	**0.90**	NA	no
17	Eurasian reed warbler	*Acrocephalus scirpaceus*	**1.00**	**0.99**	**1.00**	**1.00**	NA	**1.00**	no

18	Eurasian tree sparrow	*Passer montanus*	**0.58**	NA	NA	NA	**0.53**	**0.90**	no
19	Eurasian wren	*Troglodytes troglodytes*	**0.53**	**0.99**	**0.84**	NA	**0.77**	**1.00**	no
20	European crested tit	*Lophophanes cristatus, previously Parus cristatus*	NA	**0.84**	NA	**0.87**	**0.99**	**0.92**	no
21	European goldfinch	*Carduelis carduelis*	NA	**1.00**	NA	**0.99**	NA	NA	yes
22	European greenfinch	*Carduelis chloris*	NA	**0.72**	NA	**0.94**	NA	**0.97**	yes
23	European pied flycatcher	*Ficedula hypoleuca*	NA	NA	NA	NA	**0.80**	**0.99**	yes
24	European robin	*Erithacus rubecula*	**0.99**	**0.57**	**0.89**	NA	**1.00**	NA	no
25	European stonechat	*Saxicola torquata rubicola*	NA	NA	**0.51**	**0.79**	**0.71**	**0.82**	yes
26	Garden warbler	*Sylvia borin*	NA	NA	NA	NA	NA	**1.00**	no
27	Great tit	*Parus major*	NA	**1.00**	**0.89**	**0.69**	**1.00**	**0.57**	yes
28	House sparrow	*Passer domesticus*	0.89	NA	NA	NA	**0.92**	**0.96**	yes
29	Icterine warbler	*Hippolais icterina*	NA	NA	NA	**1.00**	NA	NA	no
30	Long-tailed tit	*Aegithalos caudatus*	**0.99**	**0.93**	**0.58**	NA	**1.00**	NA	no
31	Marsh tit	*Poecile palustris*	NA	NA	**1.00**	NA	NA	NA	no
32	Marsh warbler	*Acrocephalus palustris*	NA	NA	**0.98**	**0.97**	**0.99**	NA	no
33	Sedge warbler	*Acrocephalus schoenobaenus*	NA	**1.00**	**1.00**	NA	**0.89**	**1.00**	no
34	Short-toed treecreeper	*Certhia brachydactyla*	0.98	**1.00**	**0.74**	**0.55**	NA	NA	no
35	Song thrush	*Turdus philomelos*	NA	**0.98**	**0.78**	NA	NA	**0.99**	no
36	Spotted flycatcher	*Muscicapa striata*	NA	**1.00**	NA	NA	NA	NA	no
37	Tree pipit	*Anthus trivialis*	NA	**0.97**	NA	NA	**0.77**	NA	no
38	Willow tit	*Parus montanus*	NA	NA	NA	NA	NA	**1.00**	no
39	Willow warbler	*Phylloscopus trochilus*	**1.00**	**1.00**	**0.64**	**0.78**	**1.00**	**1.00**	no
40	Common nightingale	*Luscinia megarhynchos*	NA	NA	NA	NA	NA	NA	no
41	Eurasian nuthatch	*Sitta europaea*	NA	NA	NA	NA	NA	NA	yes
42	Goldcrest	*Regulus regulus*	NA	NA	NA	NA	NA	NA	yes
43	Great spotted woodpecker	*Dendrocopos major*	NA	NA	NA	NA	NA	NA	yes
44	Lesser whitethroat	*Sylvia curruca*	NA	NA	NA	NA	NA	NA	yes

45	Savi's warbler	*Locustella luscinioides*	NA	NA	NA	NA	NA	NA	no
46	White wagtail	*Motacilla alba*	NA	NA	NA	NA	NA	NA	yes

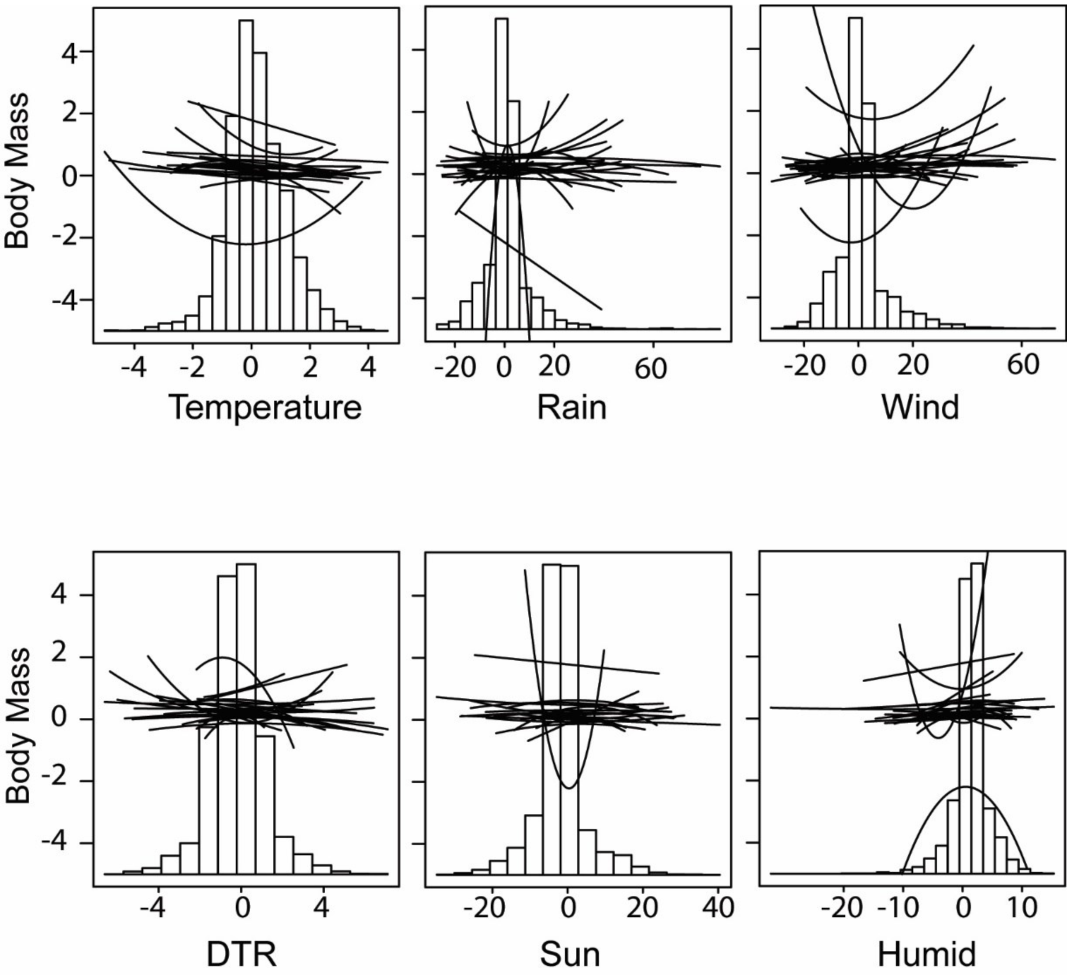


Figure S1 Model averaged slope estimates for the climate impacts on body mass. Each line shows the relationship between climate and body mass for a different species. The histogram shows the distribution of mean annual climate values (i.e. the range of climate experienced over the study period).

Table S2 Climate windows for all species. Blank spaces indicate where those climate variables had no effect on body condition. From and till indicate the earliest and latest dates of the windows, respectively. Italicised dates indicate secondary windows. Temp is temperature and CTR is daily temperature range. The I.D. refers to the Species I.D. in Fig 3.

		Temp		**Rain**		**Sun**		**Humid**		**DTR**		**Wind**	
ID	**Species**	**from**	**till**	**from**	**till**	**from**	**till**	**from**	**till**	**from**	**till**	**from**	**till**
1	Bearded reedling	1-Sep	17-Oct	23-Jun	1-Jul			20-Nov	13-Feb	6-Aug	11-Aug	2-Apr	8-Apr
2	Bluethroat			2-May	7-May	6-Nov	14-Dec	15-Jan	30-Jan	19-May	24-May	2-Apr	7-Apr
3	Common blackbird	29-May	12-Jul			24-Jun	18-Jul	27-Jun	17-Jul	2-Jan	30-Jan	20-Nov	24-Dec
4	Common chaffinch	29-May	23-Jul	20-Apr	30-Apr			27-Jun	9-Aug				
5	Common chiffchaff	25-Jul	6-Aug	3-Jun	8-Jun	12-May	17-May	12-Mar	10-Aug	5-Jul *4-Feb*	2-Aug *17-Feb*	8-Feb	18-Feb
6	Common grasshopper warbler					30-May	9-Jun			7-Apr	7-Jul	21-Sep	11-Oct
7	Common linnet	29-May	9-Jul	13-Dec	28-Dec					23-Mar	29-Apr	18-Feb	27-Feb
8	Common redstart	13-Jun	1-Jul			14-Feb	22-Apr	9-Jul	14-Jul				
9	Common reed bunting	29-May	15-Jun	20-Apr	25-Apr	27-Dec	20-Jan	30-Oct	26-Apr	12-Sep	5-Jul	26-Aug	21-Nov
10	Common starling	5-Mar	12-Mar	4-Dec	27-Dec	14-Jan	14-Mar	4-Mar	9-Mar			24-Nov	5-Feb
11	Common whitethroat			10-Feb	17-Feb	2-Feb	22-Feb	9-May	30-Jun	5-Jan	25-Jan		
12	Dunnock	28-May	2-Jul	11-Sep	14-Oct			6-Apr	22-May			9-Feb	25-Feb
13	Eurasian blackcap	12-May	9-Jul	24-Jun	2-Jul			25-Jun	2-Jul			4-Apr	9-Apr
14	Eurasian blue tit			24-Nov	25-Jun	7-Jul	19-Jul	19-Jun *24-Dec*	3-Aug *21-Jan*	10-Jan	26-Jan	12-Jun *22-Jan*	20-Jun *20-Feb*
15	Eurasian bullfinch	8-Jun	29-Jun					20-Jan	4-Feb	4-Dec	19-Dec		
16	Eurasian jay			14-Mar	3-Jul			11-Sep	28-Sep			2-Mar	7-Mar
17	Eurasian reed warbler	14-May	23-May	8-Nov	1-Dec	3-Apr	25-May	18-Jan	13-Feb	21-Jan *16-May*	6-Feb *21-May*		
18	Eurasian tree sparrow	22-Sep	18-May							1-Feb	19-Feb	21-Feb	27-Feb
19	Eurasian wren	28-May	8-Jul	9-Sep *16-Feb*	6-Oct *23-Feb*	2-Feb	1-Mar			11-Apr	21-Apr	11-Feb	22-Feb
20	European crested tit			8-Feb	17-Feb			29-Aug	17-Sep	21-Nov	21-Dec	11-Mar	2-May
21	European goldfinch			30-Apr	12-May			18-Dec	2-Jan				
22	European greenfinch			17-Sep	28-Nov			22-Aug	24-Jul	12-Feb	17-Feb		
23	European pied flycatcher									30-May	16-Jun	8-Mar	27-Mar
24	European robin	28-May	8-Jul	26-Aug	30-Sep	28-Jan	25-Feb					27-Jan *28-Mar*	7-Mar

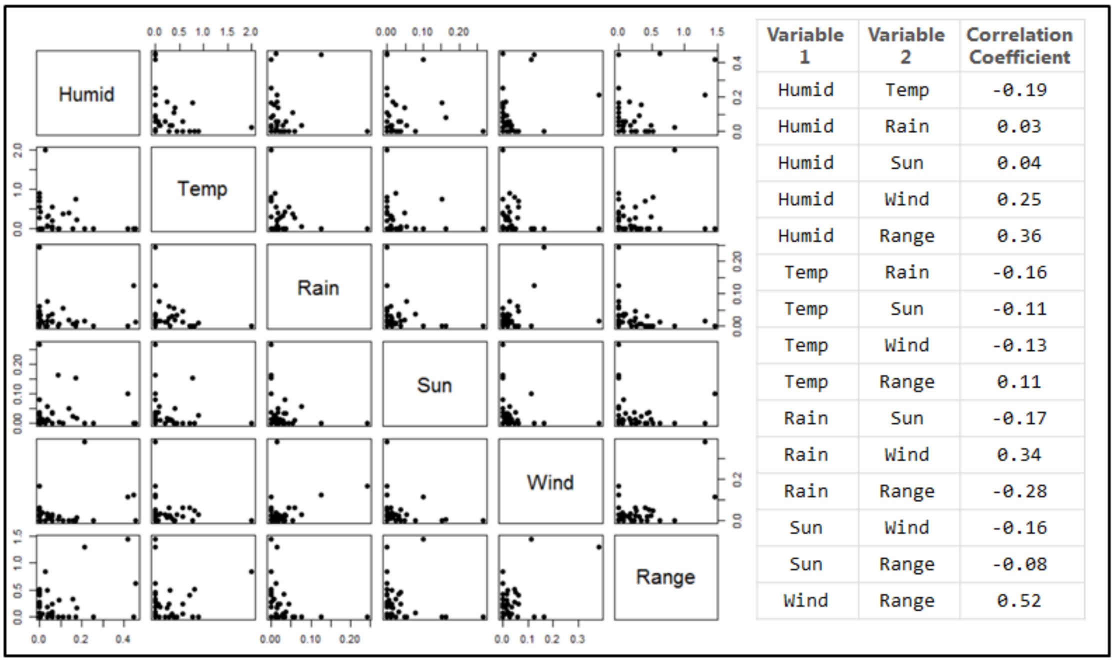
													2-Apr
25	European stonechat					18-Nov	12-Dec	6-Oct	13-Nov	24-Dec	9-Feb	2-Sep	28-Sep
26	Garden warbler									8-Feb	17-Feb		
27	Great tit			7-Dec	17-Apr	5-Jun	17-Jun	27-Feb	7-Mar	6-Jun	17-Jun	16-Feb	21-Feb
28	House sparrow	14-May *12-Mar*	4-Jun *26-Mar*							22-May	31-May	11-Feb	23-Feb
29	Icterine warbler							15-Apr	15-Aug				
30	Long-tailed tit	9-Jun	22-Jun	2-Feb *7-Aug*	25-Feb *13-Aug*	7-Jul	14-Jul					3-Apr	11-Apr
31	Marsh tit					10-May	15-Aug						
32	Marsh warbler					17-Aug	19-Jul	20-Jun	19-Jul			5-May	10-May
33	Sedge warbler			27-Aug	18-Oct	16-Aug	7-Mar			21-Nov	8-Dec	18-May	23-May
34	Short-toed treecreeper	27-Apr	17-May	20-May	6-Jun	25-Jul	31-Jul	24-Jul	12-Aug				
35	Song thrush			15-Nov	26-Jan	19-Oct	8-Dec			2-Mar	7-Mar		
36	Spotted flycatcher			7-Dec	23-Dec								
37	Tree pipit			28-Aug	15-Sep							3-Feb	24-Feb
38	Willow tit									18-Nov	18-Feb		
39	Willow warbler	10-Jun	27-Jun	28-Aug *11-Nov*	12-Sep *11-Dec*	25-Jan	11-Mar	17-Mar	22-Mar	19-May	25-May	27-Aug *20-May*	11-Sep *25-May*

Climate Sensitivities

Table S3 The sensitivity estimates (as % change in total body mass per climate unit) for each species and climate variable. The % column gives the sensitivity, the SE column shows the standard error, and the Lin column describes whether the relationship between mass and each climate variable was linear (L), quadratic (Q), or no relationship was found (NA).

	Temperature			**Humid**			**Rain**			**Wind**			**DTR**			**Sunshine**		
Common name	%	SE	Lin	%	SE	Lin	%	SE	Lin	%	SE	Lin	%	SE	Lin	%	SE	Lin
Bearded reedling	0.559	0.266	Q	-0.057	0.103	Q	-0.013	0.008	L	-0.019	0.022	Q	0.056	0.069	Q	NA	NA	NA
Blue-throat	NA	NA	NA	-0.057	0.032	L	-0.038	0.008	Q	-0.019	0.011	Q	-0.105	0.044	Q	-0.031	0.023	Q
Common blackbird	-0.308	0.147	L	0.038	0.031	L	NA	NA	NA	-0.020	0.010	Q	-0.488	0.158	Q	-0.013	0.011	L
Common chaffinch	-0.372	0.254	L	0.110	0.078	L	0.055	0.020	Q	NA	NA	NA	NA	NA	NA	NA	NA	NA
Common chiffchaff	-0.087	0.056	L	0.035	0.012	Q	0.014	0.004	Q	0.033	0.008	Q	-0.180	0.047	Q	0.009	0.007	Q
Common grasshopper warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.049	0.035	Q	-0.452	0.207	Q	-0.037	0.016	Q
Common Linnet	-0.559	0.350	L	NA	NA	NA	0.044	0.021	Q	0.061	0.025	Q	-0.245	0.147	L	NA	NA	NA
Common redstart	-0.764	0.332	L	0.171	0.077	L	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.151	0.056	Q
Common reed bunting	-0.234	0.060	Q	0.174	0.046	L	-0.013	0.013	Q	0.013	0.021	Q	-0.167	0.186	Q	0.015	0.013	Q
Common starLg	0.067	0.134	Q	0.035	0.053	Q	-0.077	0.023	L	0.026	0.027	Q	NA	NA	NA	-0.054	0.073	Q
Common whitethroat	NA	NA	NA	0.155	0.049	Q	0.007	0.011	Q	NA	NA	NA	-0.334	0.166	L	-0.024	0.013	Q
Dunnock	-0.437	0.182	L	0.003	0.042	Q	0.034	0.014	Q	0.026	0.010	L	NA	NA	NA	NA	NA	NA
Eurasian blackcap	-0.206	0.108	Q	0.057	0.017	L	0.013	0.005	Q	0.027	0.007	Q	NA	NA	NA	NA	NA	NA
Eurasian blue tit	NA	NA	NA	0.092	0.030	Q	-0.005	0.021	Q	-0.015	0.011	Q	-0.316	0.095	Q	-0.004	0.007	Q
Eurasian bullfinch	-1.996	0.435	Q	0.024	0.080	Q	NA	NA	NA	NA	NA	NA	0.838	0.432	Q	NA	NA	NA
Eurasian jay	NA	NA	NA	0.449	0.141	Q	0.125	0.090	Q	-0.123	0.041	Q	NA	NA	NA	NA	NA	NA
Eurasian reed warbler	0.053	0.029	Q	-0.059	0.014	L	-0.016	0.005	Q	NA	NA	NA	0.239	0.050	Q	-0.037	0.008	Q
Eurasian tree sparrow	-0.818	0.267	Q	NA	NA	NA	NA	NA	NA	-0.047	0.026	Q	0.518	0.237	Q	NA	NA	NA

Eurasian wren	-0.284	0.206	L	NA	NA	NA	0.023	0.009	Q	0.020	0.009	L	-0.250	0.058	Q	0.013	0.011	Q
European crested tit	NA	NA	NA	0.212	0.110	Q	-0.015	0.019	Q	-0.381	0.085	Q	-1.302	0.464	L	NA	NA	NA
European goldfinch	NA	NA	NA	0.001	0.104	Q	-0.020	0.019	Q	NA	NA	NA	NA	NA	NA	NA	NA	NA
European greenfinch	NA	NA	NA	0.455	0.155	L	-0.012	0.036	Q	NA	NA	NA	0.624	0.178	L	NA	NA	NA
European pied flycatcher	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.045	0.047	Q	0.273	0.245	Q	NA	NA	NA
European robin	-0.901	0.171	L	NA	NA	NA	0.010	0.013	Q	0.025	0.013	Q	NA	NA	NA	0.025	0.012	Q
European stonechat	NA	NA	NA	-0.420	0.193	L	NA	NA	NA	0.114	0.055	Q	-1.447	0.728	L	0.099	0.066	Q
Garden warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.189	0.073	Q	NA	NA	NA
Great tit	NA	NA	NA	-0.014	0.018	Q	-0.011	0.014	Q	0.036	0.006	Q	0.053	0.040	Q	-0.013	0.009	Q
House sparrow	-0.709	0.242	Q	NA	NA	NA	NA	NA	NA	0.062	0.020	L	-0.406	0.136	L	NA	NA	NA
Icterine warbler	NA	NA	NA	0.256	0.085	Q	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Long-tailed tit	-0.280	0.170	Q	NA	NA	NA	0.060	0.024	Q	0.059	0.026	Q	NA	NA	NA	-0.010	0.016	Q
Marsh tit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.265	0.068	Q
Marsh warbler	NA	NA	NA	0.084	0.026	L	NA	NA	NA	0.001	0.009	Q	NA	NA	NA	-0.162	0.041	L
Sedge warbler	NA	NA	NA	NA	NA	NA	0.031	0.007	Q	-0.016	0.006	L	0.423	0.081	L	0.033	0.031	Q
Short-toed treecreeper	-0.398	0.154	Q	0.140	0.102	L	-0.017	0.028	Q	NA	NA	NA	NA	NA	NA	-0.048	0.027	L
Song thrush	NA	NA	NA	NA	NA	NA	-0.035	0.029	Q	NA	NA	NA	-0.072	0.091	Q	0.079	0.037	L
Spotted flycatcher	NA	NA	NA	NA	NA	NA	0.029	0.040	Q	NA	NA	NA	NA	NA	NA	NA	NA	NA
Tree pipit	NA	NA	NA	NA	NA	NA	0.242	0.050	Q	0.164	0.053	L	NA	NA	NA	NA	NA	NA
Willow tit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.430	0.401	Q	NA	NA	NA
Willow warbler	-0.342	0.065	Q	-0.038	0.018	L	0.030	0.005	Q	0.008	0.006	Q	-0.068	0.026	Q	0.011	0.012	Q



Variable 1	Variable 2	Correlation Coefficient
Humid	Temp	-0.19
Humid	Rain	0.03
Humid	Sun	0.04
Humid	Wind	0.25
Humid	Range	0.36
Temp	Rain	-0.16
Temp	Sun	-0.11
Temp	Wind	-0.13
Temp	Range	0.11
Rain	Sun	-0.17
Rain	Wind	0.34
Rain	Range	-0.28
Sun	Wind	-0.16
Sun	Range	-0.08
Wind	Range	0.52

Figure S2 Correlations between species sensitivities to climate variables. Temp is temperature and range is daily temperature range.

Species Signal

Table S4 The amount of variance explained by the random factor species ($\boldsymbol{u}$), the within-species variance ($\boldsymbol{v}$) (including sampling variance), and the % among-species variation. The % among-species variation is calculated as $^{u}/_{(u+v)}$. DTR is daily temperature range.

Climate Variables	u	V	% among-species variation
Temperature	0.03025	1.840	1.6
Wind	0.00046	0.286	0.2
Sun	0.00007	0.204	0.03
Rain	0.00001	0.210	0.005
Humid	0.00000	0.415	0.000
DTR	0.00000	2.289	0.000
Vulnerability	0.00000	2.722	0.000

Table S5 Model selection table for all combinations of species characteristics explaining variation in climate sensitivities. Shows the best to worst models for each of the six climate variables (ranked by AICc). Each model included either all or none of the habitat characteristics (including open, urban, wet and woodland habitats). The column Int. shows the intercept value, df the degrees of freedom and logLik the log-likelihood value. DTR is the daily temperature range.

Climate variable	**Int.**	**Body Mass**	**Migra-tion**	**Life-span**	**Open**	**Urban**	**Wet**	**Wood-land**	**R^2**	**df**	**logLik**	**AICc**
Humid	0.040	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	16.436	-28.301
Humid	-0.122	NA	NA	0.096	NA	NA	NA	NA	0.080	3.000	17.437	-27.675
Humid	0.015	0.001	NA	NA	NA	NA	NA	NA	0.078	3.000	17.414	-27.628
Humid	0.072	NA	-0.028	NA	NA	NA	NA	NA	0.060	3.000	17.173	-27.146
Humid	-0.106	0.001	NA	0.075	NA	NA	NA	NA	0.124	4.000	18.019	-25.934
Humid	-0.076	NA	-0.023	0.084	NA	NA	NA	NA	0.119	4.000	17.959	-25.812
Humid	0.042	0.001	-0.018	NA	NA	NA	NA	NA	0.100	4.000	17.701	-25.296
Humid	0.058	NA	NA	NA	-0.115	0.031	-0.078	-0.005	0.263	6.000	20.098	-23.255
Humid	-0.077	0.001	-0.016	0.072	NA	NA	NA	NA	0.141	5.000	18.260	-23.187
Humid	-0.106	NA	NA	0.104	-0.113	0.023	-0.100	-0.009	0.352	7.000	21.642	-22.284
Humid	0.056	0.001	NA	NA	-0.116	0.018	-0.084	-0.011	0.286	7.000	20.472	-19.944
Humid	0.087	NA	-0.013	NA	-0.122	0.018	-0.086	-0.014	0.271	7.000	20.236	-19.472
Humid	-0.096	0.000	NA	0.097	-0.113	0.017	-0.101	-0.011	0.357	8.000	21.728	-17.856
Humid	-0.090	NA	-0.005	0.101	-0.115	0.018	-0.102	-0.013	0.353	8.000	21.668	-17.735
Humid	0.075	0.001	-0.008	NA	-0.120	0.010	-0.089	-0.016	0.289	8.000	20.531	-15.462
Humid	-0.085	0.000	-0.004	0.096	-0.115	0.014	-0.103	-0.014	0.357	9.000	21.740	-12.622
Temp	-0.247	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	-9.851	24.452
Temp	-0.388	NA	0.136	NA	NA	NA	NA	NA	0.124	3.000	-8.598	24.796
Temp	0.188	NA	NA	-0.262	NA	NA	NA	NA	0.040	3.000	-9.465	26.529
Temp	-0.241	0.000	NA	NA	NA	NA	NA	NA	0.000	3.000	-9.848	27.296
Temp	-0.069	NA	0.126	-0.186	NA	NA	NA	NA	0.143	4.000	-8.385	27.627
Temp	-0.441	0.002	0.150	NA	NA	NA	NA	NA	0.135	4.000	-8.477	27.811
Temp	0.285	-0.002	NA	-0.302	NA	NA	NA	NA	0.047	4.000	-9.390	29.636
Temp	-0.153	0.001	0.136	-0.154	NA	NA	NA	NA	0.146	5.000	-8.354	31.324
Temp	-0.443	NA	NA	NA	0.079	-0.184	0.425	0.173	0.267	6.000	-6.897	32.794
Temp	0.474	NA	NA	-0.533	-0.003	-0.193	0.457	0.114	0.410	7.000	-4.834	33.850
Temp	-0.607	NA	0.107	NA	0.055	-0.116	0.453	0.221	0.330	7.000	-6.045	36.272
Temp	-0.523	0.005	NA	NA	0.132	-0.328	0.437	0.188	0.326	7.000	-6.106	36.393
Temp	0.264	NA	0.068	-0.471	-0.009	-0.149	0.471	0.151	0.433	8.000	-4.452	39.305
Temp	0.327	0.003	NA	-0.471	0.033	-0.265	0.460	0.128	0.424	8.000	-4.615	39.631
Temp	-0.721	0.006	0.122	NA	0.112	-0.271	0.470	0.245	0.406	8.000	-4.908	40.216

Temp	0.002	0.004	0.086	-0.369	0.041	-0.239	0.478	0.181	0.458	9.000	-4.024	46.048
DTR	-0.047	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	-9.162	22.895
DTR	-0.097	NA	0.046	NA	NA	NA	NA	NA	0.022	3.000	-8.892	24.985
DTR	-0.011	-0.002	NA	NA	NA	NA	NA	NA	0.013	3.000	-9.008	25.215
DTR	-0.119	NA	NA	0.043	NA	NA	NA	NA	0.001	3.000	-9.152	25.503
DTR	-0.068	-0.001	0.038	NA	NA	NA	NA	NA	0.026	4.000	-8.850	27.806
DTR	-0.118	NA	0.045	0.013	NA	NA	NA	NA	0.022	4.000	-8.891	27.888
DTR	-0.124	-0.002	NA	0.070	NA	NA	NA	NA	0.015	4.000	-8.981	28.068
DTR	-0.121	-0.001	0.036	0.034	NA	NA	NA	NA	0.026	5.000	-8.844	31.022
DTR	-0.196	NA	NA	NA	0.079	0.178	0.228	-0.010	0.094	6.000	-7.981	32.903
DTR	-0.167	-0.004	NA	NA	0.087	0.252	0.249	0.004	0.135	7.000	-7.423	35.846
DTR	-0.220	NA	0.073	NA	-0.041	0.209	0.155	-0.058	0.131	7.000	-7.472	35.944
DTR	0.047	NA	NA	-0.178	0.115	0.218	0.280	0.018	0.105	7.000	-7.834	36.668
DTR	0.180	NA	0.093	-0.299	-0.013	0.284	0.223	-0.023	0.160	8.000	-7.073	39.745
DTR	-0.191	-0.003	0.058	NA	-0.009	0.262	0.187	-0.036	0.157	8.000	-7.117	39.833
DTR	0.095	-0.004	NA	-0.192	0.126	0.296	0.305	0.034	0.148	8.000	-7.244	40.088
DTR	0.195	-0.003	0.077	-0.289	0.017	0.333	0.252	-0.003	0.183	9.000	-6.733	44.323
Sun	-0.007	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	31.992	-59.318
Sun	0.071	NA	NA	-0.047	NA	NA	NA	NA	0.041	3.000	32.429	-57.446
Sun	-0.005	NA	-0.003	NA	NA	NA	NA	NA	0.003	3.000	32.024	-56.636
Sun	-0.009	0.000	NA	NA	NA	NA	NA	NA	0.002	3.000	32.014	-56.616
Sun	0.082	NA	-0.005	-0.051	NA	NA	NA	NA	0.049	4.000	32.522	-54.544
Sun	0.069	0.000	NA	-0.048	NA	NA	NA	NA	0.044	4.000	32.460	-54.420
Sun	-0.007	0.000	-0.002	NA	NA	NA	NA	NA	0.004	4.000	32.033	-53.565
Sun	0.080	0.000	-0.004	-0.051	NA	NA	NA	NA	0.050	5.000	32.529	-51.058
Sun	-0.043	NA	NA	NA	0.067	-0.020	0.019	0.048	0.133	6.000	33.490	-48.980
Sun	0.029	NA	NA	-0.049	0.076	-0.017	0.031	0.054	0.173	7.000	33.981	-45.347
Sun	-0.043	0.000	NA	NA	0.064	-0.027	0.015	0.045	0.149	7.000	33.690	-44.765
Sun	-0.036	NA	-0.006	NA	0.071	-0.023	0.021	0.047	0.143	7.000	33.611	-44.606
Sun	0.058	NA	-0.010	-0.061	0.085	-0.021	0.038	0.053	0.200	8.000	34.330	-40.661
Sun	0.030	0.000	NA	-0.050	0.074	-0.024	0.027	0.051	0.190	8.000	34.207	-40.414
Sun	-0.038	0.000	-0.004	NA	0.067	-0.028	0.017	0.044	0.155	8.000	33.760	-39.521
Sun	0.055	0.000	-0.008	-0.060	0.082	-0.026	0.034	0.051	0.210	9.000	34.466	-34.569
Wind	0.011	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	37.841	-71.137
Wind	0.021	-0.001	NA	NA	NA	NA	NA	NA	0.074	3.000	38.797	-70.452
Wind	0.057	NA	NA	-0.028	NA	NA	NA	NA	0.035	3.000	38.291	-69.438
Wind	0.008	NA	0.002	NA	NA	NA	NA	NA	0.002	3.000	37.871	-68.599
Wind	0.041	0.000	NA	-0.013	NA	NA	NA	NA	0.079	4.000	38.874	-67.748

Wind	0.024	-0.001	-0.002	NA	NA	NA	NA	NA	0.075	4.000	38.820	-67.640
Wind	0.055	NA	0.002	-0.028	NA	NA	NA	NA	0.036	4.000	38.305	-66.609
Wind	0.042	0.000	-0.002	-0.012	NA	NA	NA	NA	0.081	5.000	38.892	-64.625
Wind	0.021	NA	NA	NA	0.003	-0.002	-0.022	-0.007	0.032	6.000	38.243	-59.819
Wind	0.025	-0.001	NA	NA	0.001	0.009	-0.019	-0.002	0.120	7.000	39.442	-58.297
Wind	0.062	NA	NA	-0.027	0.003	0.001	-0.019	-0.006	0.063	7.000	38.649	-56.711
Wind	0.013	NA	0.005	NA	0.003	0.001	-0.021	-0.004	0.037	7.000	38.317	-56.046
Wind	0.039	-0.001	NA	-0.009	0.001	0.009	-0.018	-0.003	0.123	8.000	39.485	-53.971
Wind	0.021	-0.001	0.002	NA	0.001	0.010	-0.019	-0.001	0.122	8.000	39.461	-53.921
Wind	0.054	NA	0.004	-0.027	0.003	0.004	-0.019	-0.003	0.068	8.000	38.719	-52.438
Wind	0.035	-0.001	0.002	-0.010	0.001	0.011	-0.018	-0.001	0.125	9.000	39.506	-49.012
Rain	0.008	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	46.508	-88.495
Rain	-0.031	NA	NA	0.024	NA	NA	NA	NA	0.029	3.000	46.895	-86.698
Rain	0.012	0.000	NA	NA	NA	NA	NA	NA	0.009	3.000	46.628	-86.165
Rain	0.005	NA	0.003	NA	NA	NA	NA	NA	0.005	3.000	46.579	-86.067
Rain	-0.031	0.000	NA	0.027	NA	NA	NA	NA	0.046	4.000	47.123	-84.342
Rain	-0.037	NA	0.004	0.025	NA	NA	NA	NA	0.038	4.000	47.012	-84.120
Rain	0.009	0.000	0.002	NA	NA	NA	NA	NA	0.012	4.000	46.662	-83.420
Rain	-0.036	0.000	0.003	0.028	NA	NA	NA	NA	0.050	5.000	47.180	-81.361
Rain	0.037	NA	NA	NA	0.001	-0.006	-0.038	-0.023	0.137	6.000	48.429	-80.438
Rain	-0.022	NA	NA	0.041	0.001	-0.009	-0.047	-0.028	0.218	7.000	49.708	-79.194
Rain	0.034	NA	0.003	NA	0.000	-0.005	-0.039	-0.023	0.142	7.000	48.497	-76.772
Rain	0.039	0.000	NA	NA	0.001	-0.004	-0.038	-0.023	0.141	7.000	48.477	-76.731
Rain	-0.023	0.000	NA	0.043	0.000	-0.006	-0.046	-0.028	0.228	8.000	49.867	-75.264
Rain	-0.029	NA	0.004	0.042	-0.001	-0.007	-0.048	-0.028	0.227	8.000	49.853	-75.236
Rain	0.035	0.000	0.003	NA	0.000	-0.003	-0.038	-0.023	0.144	8.000	48.531	-72.591
Rain	-0.029	0.000	0.003	0.044	-0.001	-0.005	-0.047	-0.028	0.234	9.000	49.979	-70.709

Species and site traits

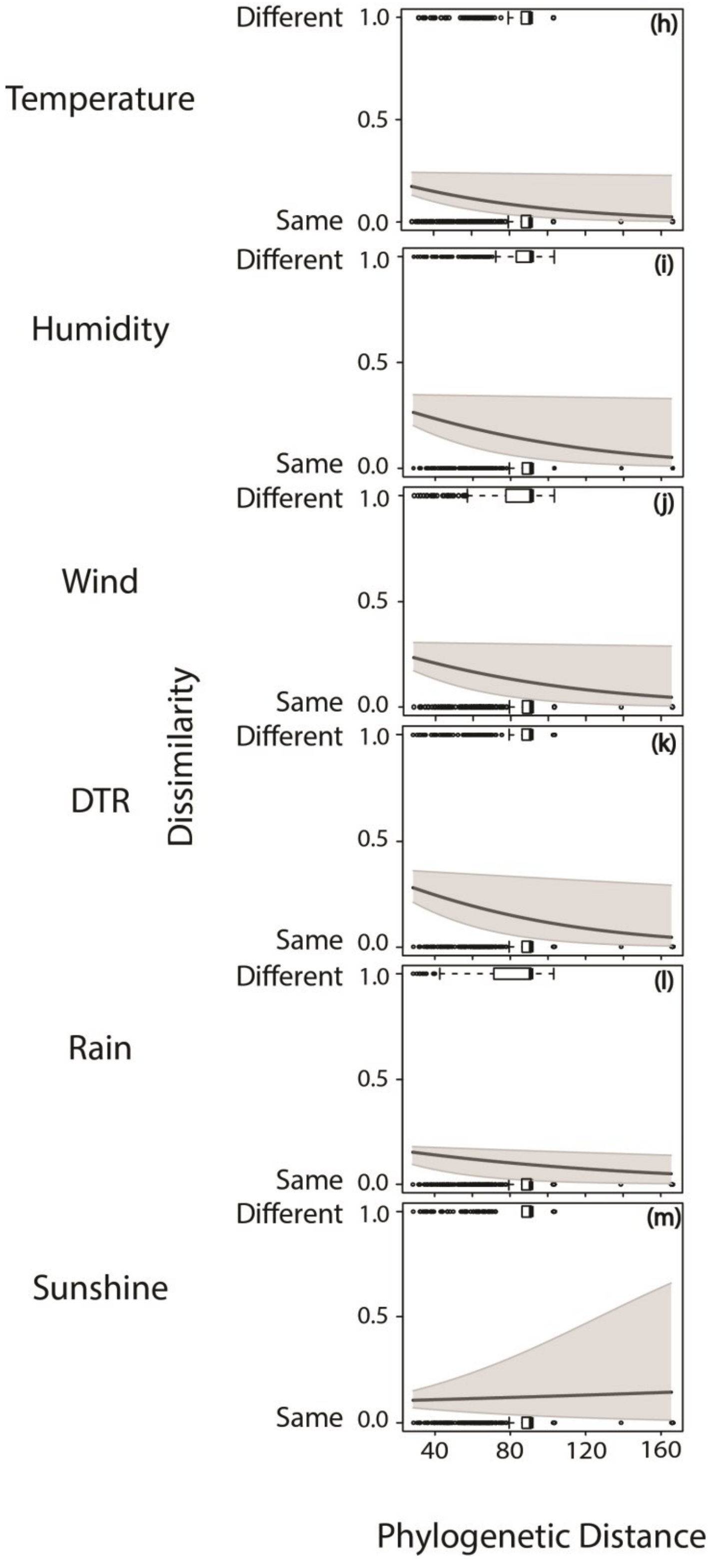


Figure S3 The effect of phylogenetic relatedness on whether species are affected by the same climate variables. Displays the pairwise phylogenetic distance in relation to whether species are impacted by the same climate variables (i.e. whether both species are or are not affected by that climate variable, or if one species is affected by that climate variable, but the other is not) with 95% confidence intervals. The boxplots show the distribution of the underlying data.

Table S6 Model selection table for all combinations of species characteristics explaining variation in climate vulnerabilities. Shows the best to worst models for each of the six climate variables (ranked by AICc). Each model included either all or none of the habitat characteristics (including open, urban, wet and woodland habitats).The column Int. shows the intercept value, df the degrees of freedom and logLik the log-likelihood value. DTR is the daily temperature range.

Int.	**Body Mass**	**Migration**	**Survival**	**Open**	**Urban**	**Wet**	**Wood land**	**R^2**	**df**	**logLik**	**AICc**
-0.017	NA	NA	NA	NA	NA	NA	NA	0.000	2.000	-22.121	48.584
-0.056	NA	0.026	NA	NA	NA	NA	NA	0.012	3.000	-21.894	50.495
-0.013	0.000	NA	NA	NA	NA	NA	NA	0.001	3.000	-22.100	50.907
-0.009	NA	NA	-0.004	NA	NA	NA	NA	0.000	3.000	-22.118	50.943
-0.088	NA	0.029	0.014	NA	NA	NA	NA	0.013	4.000	-21.872	52.957
-0.067	0.000	0.030	NA	NA	NA	NA	NA	0.013	4.000	-21.877	52.967
-0.054	-0.001	NA	0.027	NA	NA	NA	NA	0.002	4.000	-22.078	53.369
-0.086	0.000	0.029	0.013	NA	NA	NA	NA	0.013	5.000	-21.872	55.619
0.014	NA	NA	NA	-0.460	-0.022	-0.030	-0.012	0.031	6.000	-21.524	57.758
-0.060	NA	0.029	NA	-0.434	-0.006	-0.019	0.012	0.042	7.000	-21.303	60.340
0.014	0.000	NA	NA	-0.459	-0.020	-0.029	-0.008	0.032	7.000	-21.507	60.748
0.014	NA	NA	0.000	-0.460	-0.022	-0.030	-0.012	0.031	7.000	-21.524	60.781
-0.069	0.000	0.033	NA	-0.432	-0.006	-0.019	0.012	0.043	8.000	-21.292	63.551
-0.076	NA	0.031	0.010	-0.435	-0.008	-0.021	0.010	0.043	8.000	-21.294	63.553
-0.041	-0.001	NA	0.041	-0.467	-0.027	-0.035	-0.017	0.034	8.000	-21.462	63.890
-0.071	0.000	0.032	0.002	-0.433	-0.007	-0.019	0.012	0.043	9.000	-21.292	67.013

Table S7 The delta AICc values for the two population-level predictor variables (habitat and density) tested for each climate variable. Here, the null model does not contain any predictors but does include the random effect of species (*Sensitivity ~ 1 + (1|species)*), the habitat model includes the explanatory variable habitat (wet or dry) and includes a random slope term across all species (*Sensitivity ~ Habitat + (1|species) + (0 + Habitat|species)*), null habitat model is the same as the habitat model but does not include a random slopes term (*Sensitivity ~ Habitat + (1|species)*) and the density model includes the explanatory variable with a random intercept term(*Sensitivity ~ Density + (1|species)*). A delta AICc value of 0 indicated that it was the best model.

	Model delta AICc Values			
Climatic Variable	**Null**	**Habitat**	**Null Habitat**	**Density**
Humid	6.9	10.6	8.5	0
Rain	0.5	2.0	0	2.5
Temperature	3.8	1.7	0	3.7
Sunshine	0	3.8	1.7	1.5
Wind	0	1.7	0.1	2.1
DTR	0	3.7	1.6	0.4
Vulnerability	0	4.0	1.9	2.0

In populations with higher densities (i.e. better habitats), birds experienced stronger declines in body mass per percent change in humidity compared with those in lower densities (slope of -1.03 change in sensitivity per birds/net metre/day; Fig S4).

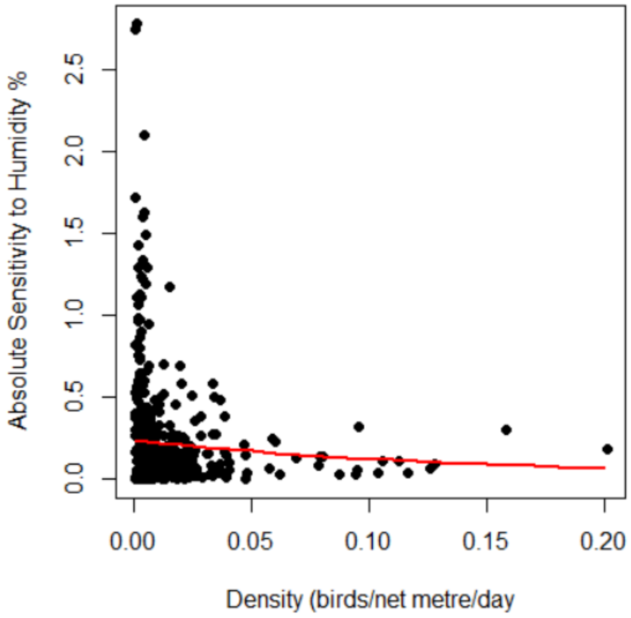


Figure S4 The relationship between body mass sensitivity to humidity (as a percent of total boy mass) and habitat density (slope = -1.03).

Nine species were found to have more similar sensitivities at sites that were closer together (Table S8). As we did not take into account the effects of multiple testing, some of these species would likely be significant due to chance. However, five species (the common chaffinch, garden warbler, short-toed treecreeper, sedge warbler and willow warbler) all had multiple positive relationships for different climate variables (or the only climate variable they were sensitive to), suggesting that these similarities are not due to chance. Overall vulnerabilities were more similar in populations that were closer together for 24% (7 out of 29) of species (Table S8).

Table S8 Species with significant relationships between distance (km) and dissimilarity in sites sensitivities and vulnerabilities. Species that have population sensitivities which are more similar at closer distances for each climatic variable are marked with an X. The grey cells indicate that the species was not affected by those climate variables (i.e. they did not have a climate window for that climatic variable).

Species	**Humid**	**Temperature**	**DTR**	**Rain**	**Wind**	**Sun**	**Vulnerability**
Willow warbler			X	X			X
Common chaffinch	X		▨	X	▨	▨	
Common chiffchaff		X					X
Bearded reedling		X				▨	X
Garden warbler	▨	▨	X	▨	▨	▨	X
Short-toed treecreeper	X		▨		▨	X	
Sedge warbler	▨	▨		X	X		
Eurasian tree sparrow	▨			▨	X	▨	
European robin	▨		▨			X	
Eurasian blackcap			▨			▨	X
Bluethroat		▨					X
Common grasshopper warbler	▨	▨		▨			X

Chapter 3

Reduced body condition due to global warming has little demographic or population consequences in European birds

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Abstract

Climate change has been found to have strong effects on traits such as phenology, morphology and physiology. However, most studies typically assume that climate-induced trait changes will have consequences for population dynamics. This question has only more recently begun to be explicitly tested and it is now becoming clear that this is not always the case. Body condition is one trait that has been proposed as one of the universal responses to climate change. Body condition reflects energy storage and may thus directly affect how much can be invested in reproduction and survival. However, the causal pathway by which decreased body condition impacts species' vital rates, and in turn population dynamics, has rarely been directly empirically quantified. Therefore, we currently have little understanding of what the consequences of changes in body condition are for variables more relevant for conservation, such as population size. Using structural equation modelling, we investigate how temperature-induced changes in body condition affect reproductive success and survival, and the subsequent impact on population growth rates of 19 common bird species across 80 Dutch sites over a 21-year period. We show that warmer temperatures were associated with decreased body condition and increased reproductive success and population growth rates. However, our path analysis revealed that body condition was not associated with reproductive success or survival and that the effect of temperature on the population growth rates of species was instead due to underlying changes in reproduction and other unidentified traits. We found substantial inter-specific, but little intra-specific variation, in the temperature dependency of population growth rates. About half of the species are expected to increase under global warming, but this variation was not associated with any species characteristic. Our results suggest that body condition responses to global warming are common but have no apparent consequences on demography and population dynamics. Therefore, this common assumption made throughout the literature was not met. However, given that warming temperatures have strong effects on reproductive success and population growth rates, it is vital that the traits and demographic rates that are driving these impacts are identified. Understanding the pathways via which temperature impacts population dynamics will be absolutely crucial for our ability to predict climate change effects in the future and therefore, improve conservation efforts.

Introduction

The vast majority of ecological climate change research has focused on the direct effects of climate on trait responses, such as phenology, morphology and physiology. These studies typically assume that climate-induced trait changes will have consequences for survival, reproduction and population dynamics, yet this idea has only more recently begun to be explicitly tested (Wilson & Arcese, 2003). It is now becoming clear that, although changes in physiology or phenology have been found to have significant demographic or population impacts in some species (Wilson & Arcese, 2003; Benton *et al.*, 2006; Wright *et al.*, 2009; Ozgul *et al.*, 2010; Plard *et al.*, 2014; Gardner *et al.*, 2016; Youngflesh *et al.*, 2017), this does not always occur (Reed *et al.*, 2013; Dunn & Møller, 2014; Stopher *et al.*, 2014). Additionally, trait changes can affect particular types of demographic or population variables, while other types remain unaffected (Wilson & Arcese, 2003; Reed *et al.*, 2013; McLean *et al.*, 2016). A general understanding of how frequently and in what situations and species trait responses have cascading consequences for populations, and the strength of these impacts, is lacking (Miller-Rushing *et al.*, 2010). As such, we have little ability to predict the outcomes of trait changes, and are unable to identify the particular species that are at most risk of population declines due to climate change (Fewster *et al.*, 2000). Such information is particularly crucial for effective conservation management in light of a rapidly warming world (McDermott & DeGroote, 2016).

The different types of responses to changes in climate can be categorised into hierarchical levels, from trait-level responses (phenology or physiology) to demographic- (survival or reproduction) and population- level responses (population size, growth rate or time to extinction) (Nichols & Hines, 2002; Jongejans *et al.*, 2010; Miller-Rushing *et al.*, 2010; McLean *et al.*, 2016; van Benthem *et al.*, 2017). Under this framework, changes in climate impact the most basal trait level, which in turn can affect demographic rates, and subsequently impact population dynamics. In order for changes in climate to result in an observable population-level response, the effects of climate must flow up through the hierarchical levels (McLean *et al.*, 2016). As climate change is expected to act as a major cause of species extinctions in the near future (Thomas *et al.*, 2004), it is equally important to understand both when trait changes have an effect on population dynamics, and when they do not (van Benthem *et al.*, 2017). By decomposing population responses into relationships among different underlying pathways, we can better understand the mechanisms that drive population decline (Nichols & Hines, 2002; Ådahl *et al.*, 2006; McLean *et al.*, 2016).

Despite the majority of research assuming that climate-induced changes in traits have strong impacts on population dynamics, there are four feasible mechanisms by which this may not occur (McLean *et al.*, 2016). There would be no change in population dynamics if: (1) the change in trait has little or no impact on any demographic rates, or (2) the change in trait does affect demographic rates but this has little or no impact on population dynamics, or (3) multiple pathways counteract one another and weaken any net population level effects (e.g. decreased survival is compensated for by increases reproduction), and finally (4) multiple climate variables have counteracting effects that weaken population level effects. These mechanisms have only been explicitly tested in a hand full of single species or theoretical studie (Wilson & Arcese, 2003; Ådahl *et al.*, 2006; Ozgul *et al.*, 2010), and large-scale comparative studies such as this are very rare (only McLean *et al.*, 2016). This is in part because it can be difficult to integrate traditional modelling techniques to test for cascading effects, but also because very few studies have trait, demographic and population level data available on a large number of species.

Understanding the degree of inter- and intra-specific variation can be important for predicting how likely species or populations are to encounter a climate-induced trait change that impacts their population dynamics. High inter-specific variation can indicate that certain species with particular characteristics might be more at risk than others. For example, changes in phenology are expected to have more severe consequences for specialist species compared to generalists, which are less constrained by the availability of particular resources (Gilman *et al.*, 2010; Miller-Rushing *et al.*, 2010). Alternatively, if responses to trait changes differ substantially in different populations of the same species (i.e. high intra-specific variation in trait consequences), then species characteristics will not predict responses well. Rather, local characteristics such as habitat type will likely be more effective at predicting which populations are most at risk of changes in population sizes (Stevens *et al.*, 2010; McLean *et al.*, 2018). Broadly speaking, it is important to understand and incorporate both inter- and intra-specific variation when making predictions about global change impacts (Moran *et al.*, 2015), as this informs us how well we can generalize both across population and species.

Body size, mass or condition is a type of trait level response which, although being recognised as one of the major responses to climate across the globe (Gardner *et al.*, 2011), is much less studied compared to phenological traits. Since body condition, mass or size reflect energy reserves, and thus directly affect how much can be invested in reproduction and survival, demographic responses can be expected (Gardner *et al.*, 2011; Labocha & Hayes, 2012). For example, decreased body condition reduces survival (Bergan & Smith, 1993; Møller & Szép, 2002; Harding *et al.*, 2011; Krams *et al.*, 2013; Paquette *et al.*, 2014; Gardner *et al.*, 2016) and reproduction (Naef-Daenzer *et al.*, 2001; Aubry *et al.*, 2013; Paquette *et al.*, 2014). Furthermore, body mass and size have been shown to be important early warning signals of population decline (Clements *et al.*, 2018), suggesting that these traits are also affecting population dynamics. However, studies that specifically investigate the full pathway of whether climate-induced changes in body condition, mass or size affects demographic rates and whether this in turn results in population consequences have been limited to a couple of single species studies (Ozgul *et al.*, 2010; van Benthem *et al.*, 2017). Consequently, broader comparative studies are needed for improving understanding on this topic and to determine the generality of patterns across populations and species.

Previous studies have generally found that hotter temperatures have been associated with decreased body condition in both juvenile and adult bird species (Garant *et al.*, 2004; Van Buskirk *et al.*, 2010; du Plessis *et al.*, 2012; Aubry *et al.*, 2013; Gardner *et al.*, 2016; McLean *et al.*, 2018). However, very little is known about the consequences of climate-induced changes in body condition. Although it is often found that decreased body mass results in reduced survival and reproduction, perhaps as a consequence of foraging conditions (Harding *et al.*, 2011; Aubry *et al.*, 2013; Paquette *et al.*, 2014; Gardner *et al.*, 2016), conversely, decreased body condition could potentially be beneficial. For instance, being heavier can increase energy expenditure (Covas *et al.*, 2002; Quillfeldt *et al.*, 2006), raise predation risk (through the need to feed more and also increased fat content; Covas *et al.*, 2002; Rogers, 2015), and impact flight performance (Senar *et al.*, 2002). Thus, lower body condition could be advantageous and actually lead to higher survival and reproduction.

Here, we investigate the consequences of temperature-induced changes in body condition (mass corrected for size; i.e. amount of fat and protein reserves; Labocha & Hayes, 2012) on demography and population dynamics of 19 common small passerines using 21 years of field data collected from 80 sites across the Netherlands. We have previously shown that warming typically leads to reduced body condition in these species (McLean *et al.*, 2018). Now, we directly quantify the effects that temperature-induced changes in body condition have on annual survival and reproductive success, and indirectly via their subsequent effects on the population growth rate, using structural equation modelling, a network-based technique that models cascading effects. We then determine inter- and intra-specific patterns, and how much intra- and inter-specific variation occurs at each level of the hierarchy to ask whether species or local, site-specific characteristics would be expected to better explain variation in population responses. Finally, we attempt to identify any life history and ecological characteristics that can explain responses to temperature among species and sites.

Methods

Biological data for common Dutch bird species

Body mass, survival and reproduction data were collected as part of the Dutch Constant Effort Site (CES) program, which covers 80 sites across the Netherlands, spanning 21 years (1994-2014; see Appendix 5 Fig. S1 for map). The CES-project follows a standardised protocol (Robinson *et al.*, 2009) where birds are captured using mist nets from the 12th April until the 14th August every year. Most sites were sampled 12 times per year (ranging from 9-12 times). Captured birds are ringed and morphometric measurements taken, including body mass (grams) and wing length (maximum chord measurement; Svensson (1992)). The sex and age-class (juvenile or adult) are also noted, typically based on the plumage of the bird. Birds are considered adults after their first year in all species. We conducted our analyses on 19 (out of 46) passerine species that were previously found to have temperature effects on body condition (McLean *et al.*, 2018). For each species there were data from 33 sites on average (range 7-50) and 18 years (range 9-20) with a total sample size of 3,106 site and year estimates across all species (Appendix 5 Table S1).

Annual population growth rates were calculated using abundance count data from the Dutch Breeding Bird Monitoring Program (BMP) which has been running since 1984. It is based on territory mapping in fixed study plots (Van Turnhout *et al.*, 2010). Although the recapture data from the CES scheme used to derive the demographic data also includes information about abundance, the population estimates would not be independent of the demographic estimates and therefore we prefer to use these independent estimates from an alternative data source. Van der Jeugd *et al.* (2007) have previously found close overlap in population measures for the BMP and CES programs for several species.

Climatic data

Daily temperature records over the study period were taken from 37 weather stations across the Netherlands (Royal Netherlands Meteorological Institute). Each CES-location was matched with the closest weather station (mean distance 17 km, range 1.9-32.6 km; see Appendix 5 Table S2). In a previous paper (McLean *et al.*, 2018), we performed climate window analyses for each species to find the time period during which mean temperature explained the most variation in body condition (R package *climwin*; Bailey & van de Pol 2015). This time period was found to be from early May to mid-July (spring-early summer) for the majority of species (Appendix 5 Table S3). Because we are interested in how climate-induced changes in body condition affects demographic and population rates, rather than explaining which parameters contribute to climate-induced changes in population rates, we use the same spring temperature periods that were found to affect body condition to explain variation in reproductive success, survival and population growth rates (i.e. we do not change the time period based on when temperature best explains these higher level responses).

Calculation of Response Variables

Body Condition

Body condition was calculated by correcting body mass for wing length (a measure of structural size), but also accounting for the confounding effects of age (adult or juvenile), sex (if identifiable for that species), time of day and date of capture (both non-linear) and the random intercept individual ID (to account for any non-independence due to recaptures of individuals) (see Appendix 5 for details on standard error calculation). Consequently, our measure of body condition is more of a measure of body fat (Balbontín *et al.*, 2012; Labocha & Hayes, 2012; Gardner *et al.*, 2016), or whether an individual's weight is above or below average given their size and demographic characteristics. When investigating the effects of climate on body size or condition, wing length is generally thought to be the best single linear predictor of structural size for passerines (Gosler *et al.*, 1998; Gardner *et al.*, 2009). Although wing length has been found to be affected by climate (for example, Collins *et al.*, 2017), we found no change in wing length over the length of the study, suggesting that our measure of body condition was not affected by any changes in wing length. The body mass residuals were centred such that a body condition of 0 means that an individual's mass is exactly average given its demographic characteristics. To make changes in condition comparable across species we then converted body condition residuals to a percentage of the species' mean weight. As all other response variables apart from body condition have annual estimates for each site, we calculated the mean and the standard error of the body condition residuals for each site and year per species to match the format of other variables. We present results for adult females because we previously found no difference among males and females (McLean *et al.*, 2018).

Survival

Adult survival estimates were calculated using capture-mark-recapture analysis implemented using Program MARK (White & Burnham, 1999) with the RMark interface (Laake & Rexstad, 2010). Apparent adult survival was estimated for each year and site (with standard errors). The analysis took into account age (juveniles and adults), included a residency parameter (accounts for transient individuals that have zero probability of being in the population on sampling occasions subsequent to their initial capture by accounting for differences in survival as a function of time since marking; Saracco *et al.*, 2010; Cooch & White, 2015) and an encounter probability parameter for both adults and juveniles (as not all individuals are guaranteed to be captured when sampling; White & G.C., 2015; Johnston *et al.*, 2016). Annual adult survival estimates per site were not always estimable due to low sample sizes (see Appendix 5 Table S1 for details).

Reproductive success

The proportion of juveniles (and the binomial standard error) caught at each site per year was used as a relative measure of breeding productivity (Du Feu & McMeeking, 1991; Peach *et al.*, 1996; Nur *et al.*, 2000). This measure can be thought of as an index of per capita reproduction.

Population growth rate

We first calculated the weighted mean abundance for each CES site by averaging the 5 closest BMP sites within 15km that had the same habitat type (or if there were less than 5 sites within 15km, the 5 closest sites within 30km). Mean abundance values were weighted by the inverse of the spatial distance (closer sites had a higher influence on the mean abundance value). We then calculated the population growth rate (r) at a given site (s) and year (t) from the change in abundance (n) between years :

$$\mathrm{r}_{\mathrm{s,t}} = \log\left(\frac{n_{s,t+1} + c}{n_{s,t} + c}\right)$$

The constant *c* reflects a small term that was included in the formula in order to account for situations when no territories were found at a site in a given year, and was set to the mean number of territories at that site across all years multiplied by 0.01. The standard error of r_t was also calculated (see Appendix 5 for details).

Statistical Analyses

Structural Equation Models

Structural equation modelling is a regression-based approach to evaluating causal linkages among variables in a single multivariate network. It is ideal for our analysis as variables can function as both predictors and responses within a single model, and therefore is useful in identifying indirect effects. We constructed a single structural equation model (SEM) using the R-package *piecewiseSEM* (Lefcheck, 2016). Piecewise SEMs translate a path diagram (i.e., box-and-arrow diagram indicating directed linkages) into a set of linear equations that are evaluated independently (Lefcheck, 2016). As such, they are able to include response variables that are not normally distributed, as well as random effects that account for non-independence in the data.

Following from McLean et al. (2016), our SEM has two focal (or indirect) pathways which flow up from temperature to body condition and on to either reproductive success or survival, then onto the population growth rate (see Appendix 6, Fig S4i for full path diagram). Temperature has a direct pathway to all four response variables, which allows us to evaluate whether any temperature related changes are due to changes in the focal, or instead, some other unknown trait response.

We included all species in one model so that we could determine the overall relationships and compare intra- versus inter-specific variability. The model was implemented with the following equations for each response variable (See Appendix 5 for R code):

1. **Population growth rate** ~ Reproduction + Survival + Temperature + (1:Reproduction |Species/Site) + (1:Survival |Species/Site) + (1:Temperature |Species/Site)
2. **Survival** ~ Body Condition + Temperature + (1:Body Condition |Species/Site) + (1:Temperature |Species/Site)
3. **Reproduction** ~ Body Condition + Temperature + (1:Body Condition |Species/Site) + (1:Temperature |Species/Site)
4. **Body Condition** ~ Temperature + (1:Temperature | Species/Site)

Each of the four equations included random intercept and slope terms with a hierarchical structure of sites nested within species to address both non-independence of observations made on different sites of the same species. The response variables body condition and survival were both weighted by the inverse of their standard errors such that estimates with larger standard errors contributed less, upweighting samples with higher precision. Likewise, population growth and the proportion of juveniles (reproductive success) were weighted by sample size, as estimates based on fewer individuals are more uncertain. The sample size for population growth was calculated as the difference between consecutive years. We can be confident that a change in abundance from 30 and 0 in two consecutive years would be a real and strong change, whereas a change in growth rate would be less certain if it only varied by a few individuals (e.g. 3 and 0) as some individuals could have been missed during sampling. Equations 1 and 4 both have Gaussian distributions, while equations 2 and 3 have binomial error distributions and logit link functions. Specific species or site estimates were extracted from the random slopes from the mixed SEM.

The total change in population from a small change in temperature is the product of each of the underlying relationships between climate, trait and demography (McLean *et al.*, 2018).

$$\frac{dPop}{dTemp} = \frac{dMass}{dTemp} * \frac{\partial Repro}{\partial \mathrm{Mass}} * \frac{\partial \mathrm{Pop}}{\partial \mathrm{Repro}} \qquad \textit{eq. 1}$$

$$+ \frac{\partial Repro}{\partial \mathrm{Temp}} * \frac{\partial \mathrm{Pop}}{\partial \mathrm{Repro}}$$

$$+ \frac{\partial \mathrm{Pop}}{\partial \mathrm{Temp}}$$

Where, we use ‘∂’ and ‘d’ to distinguish partial and full regression coefficients, respectively. The top line of equation 1 gives the indirect effect via the focal pathway (i.e. via body condition and reproduction), while the second line shows the indirect effect via reproduction alone, and the third line the direct effects via other unknown traits or demographic rates. Similarly, the total effect of temperature on reproductive success is calculated as:

$$\frac{\mathrm{dRepro}}{\mathrm{dTemp}} = \left(\frac{\mathrm{dCond}}{\mathrm{dTemp}} * \frac{\partial \mathrm{Repro}}{\partial \mathrm{Cond}}\right) \qquad \textit{eq. 2}$$

$$+ \frac{\partial \mathrm{Repro}}{\partial \mathrm{Temp}}$$

Here, the top line of equation 2 gives the indirect effect of temperature via body condition, while the second line gives the direct effect unrelated to condition.

Because piecewise SEMs do not solve equations simultaneously, we needed to account for any potential uncertainty across levels. Instead of taking each data point to be a single point estimate (e.g. mean body condition), we used a bootstrapping technique and ran the SEM 4000 times (each time with the data points being chosen randomly from a normal distribution centred at the mean value with variance equal to the standard error of the point estimate). In this way, points that are more accurate have a smaller standard error and therefore the values will remain roughly the same in each of the runs, while a value with large error will move over a larger distribution for subsequent runs. To summarize the results from the 4000 SEM results, we took the median as the overall partial regression estimate and the 0.025% and 0.975% quantiles as the 95% confidence intervals. The same procedure was carried out to determine model fit statistics, R^2 values and estimates of the variance of the random effects 'site' and 'species'. Additionally, because the slope estimates with reproductive success as the response variable were on the logit scale (i.e. nonlinear), we calculated a linear approximation on the absolute (back-transformed) scale to be able to calculate the combined pathways. To do this, we calculated the tangent at each site's or species' mean x-value (i.e. the linear slope around temperature or body mass mean-0.0001 and +0.0001).

Intra- and inter-specific analysis

We used the amount of intra- versus inter-specific variation in relationships as a measure to determine whether there was relatively higher intra-specific variation (Blanck & Lamouroux, 2006; Rubolini *et al.*, 2007; Stevens *et al.*, 2010). We compared the ratio of the among-species variance (u; variance component for the random effect 'species' in the above models) to the independent variation at the level of site (the sum of the species and within-species variance, an estimate of the variance of the random effect 'site') for each pathway (see Appendix 5 for details). A value closer to one would indicate there would be relatively more among-species variation compared to within-species variation, suggesting that intra-specific responses are fairly consistent. We would expect this value to be closer to zero if there is a lot of within-species variance relative to among-species variance. This ratio can also be interpreted as the intra-class correlation coefficient (i.e. the similarity between the climate responses of populations of the same species; Snijders, 2011; Nakagawa *et al.*, 2017).

We also investigate all pathways at the site scale in order to determine whether intra-specific variation could potentially mask or buffer species responses. Understanding how intra-specific variation effects the overall species responses (for instance, by potentially counteracting or averaging out a species response if some populations have positive responses while others have negative) can elucidate important trends that otherwise might be unidentified. Site estimates were extracted as the random slopes from the mixed SEM.

Results

Species scale effects

Based on initial exploration, we found that there was no effect of body condition on survival (β= -0.007 [95%CI: -0.042, 0.025]), and in turn, survival did not affect the population growth rate (β= 0.173 [-0.148, 0.524]) (full model results are presented in Appendix 6). Although temperature did have a positive association with survival (β= 0.038 [0.006, 0.074]), we decided to exclude survival from the final SEM (Fig. 1). When survival was removed in the final SEM, all other path estimates remained the same as in the original model, suggesting that survival did not play a substantial role in explaining relationships among variables in this system. The removal of the survival pathway from the model had the added benefit of strongly increasing the sample size (from 625 to 3106 site-years and 14 to 19 species; many survival estimates were not estimable in the capture-mark-recapture model) and thereby statistical power for other pathways.

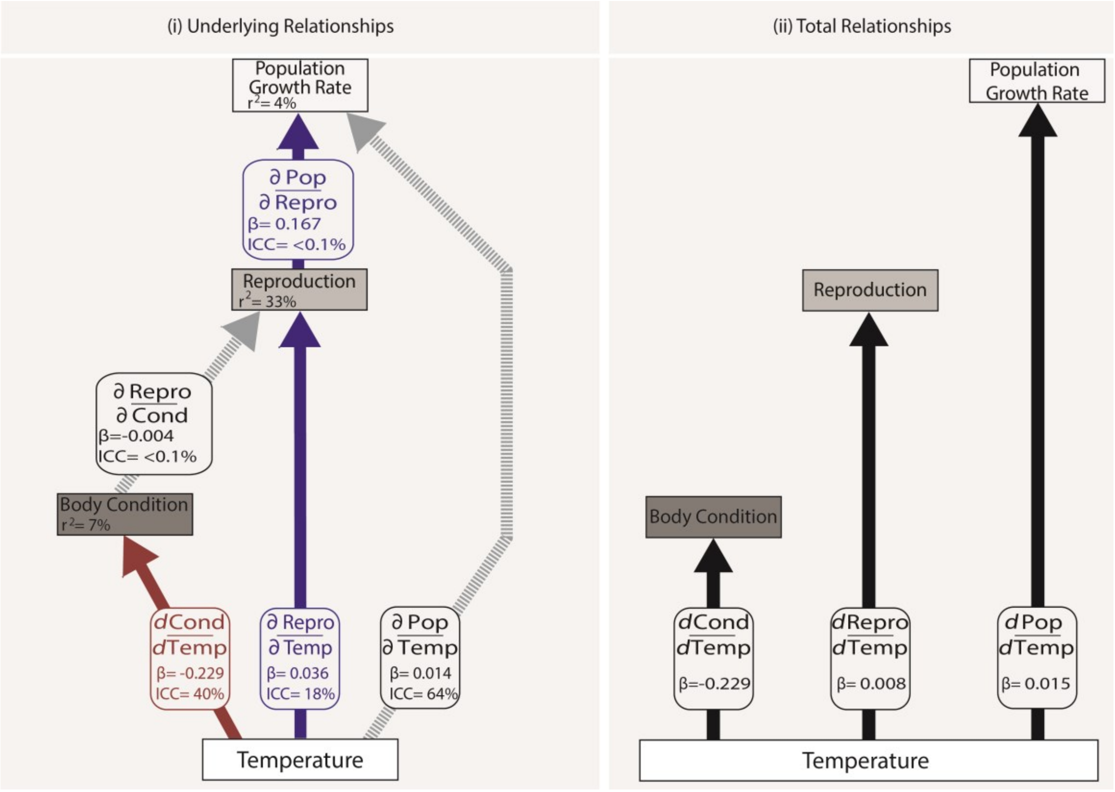

Figure 1 Decomposition of pathways in the structural equation model by which temperature-driven changes in body condition affect reproductive success and population growth rate in 19 bird species (n=3,106). Panel (i) 'Underlying Relationships' displays the graphical model used in the structural equation analysis carried out on all species. The model includes the indirect effects of temperature on population growth rate via body condition and reproduction (the focal pathway), as well as the direct

effects of temperature on reproductive success ($\frac{\boldsymbol{\partial}\textbf{Repro}}{\boldsymbol{\partial}\textbf{Temp}}$) and on population growth rate ($\frac{\boldsymbol{\partial}\textbf{Pop}}{\boldsymbol{\partial}\textbf{Temp}}$). The red and blue solid arrows indicate significant negative and positive relationships (determined by whether the 95% confidence intervals cross zero), respectively, while the grey broken arrows indicate that there was no significant trend. The r^2 values for each variable show the mean amount of variation explained by all pathways. ICC gives the ratio of the among-species variance or the intra-class correlation coefficient for each pathway. Panel (ii) 'Total Relationships' shows the total effect of temperature on body condition, reproduction and population growth rate, based on the combined direct and indirect effects. Note: Here, we show the β estimates on the logit scale for those individual pathways where reproduction is the response variable, but use the linearised β estimates to calculate the total pathways. The linearized estimates for the pathways on the absolute scale are $\frac{\partial \text{Repro}}{\partial \text{Temp}} = 0.008$ and $\frac{\partial \text{Repro}}{\partial \text{Cond}} = -0.001$.

In the final (reduced) SEM, an increase of 1°C in mean temperature was associated with a decrease of 0.23% (95%CI: -0.252,-0.207) of total body condition, averaged across all species and sites (Fig. 1). There was not, however, a statistically significant effect of body condition on reproductive success (β= -0.004 [-0.017,0.008] productivity per % body condition on the logit scale). However, there was an important direct effect of temperature on reproduction, such that warmer temperatures increased reproductive success (β= 0.036 [0.022,0.049] productivity per °C on the logit scale). These results suggest that the effects of temperature on reproductive success are not acting via the effects on body condition, but that another pathway mediated by an unmeasured trait(s) is important. Increased reproduction was associated with increased population growth rates (β= 0.167 [0.084, 0.255]), but growth rate had no direct association with temperature on average (β= 0.014 [-0.005, 0.032] productivity per °C). Overall, these results suggest that warmer temperatures indirectly enhance population growth by increasing reproduction, but this effect is not mediated by changes in body condition. We tested the model fit of the SEM by the test of directional separation (Lefcheck, 2016) and found that the model represents the data well and no important paths are missing (P=0.28, Fisher C=2.55, df=2).

The total effect of temperature on the population growth rate (i.e. all pathways combined) showed that population growth rates increased on average by 0.015 per °C across all species. However, the response of population growth rate to temperature differed among species, such that roughly half of the species increased population growth rates with warmer temperatures, while the other half decreased or showed no change (Fig. 2).

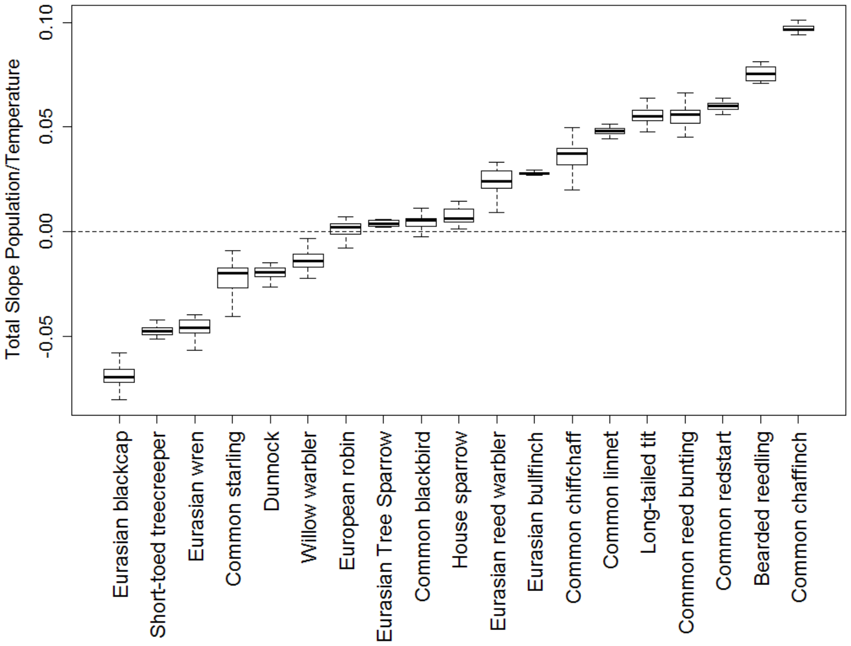

Figure 2 Species and site trends for the total effects of temperature on population growth rate (where the observed slope is $\frac{\mathbf{dPop}}{\mathbf{dTemp}} = \left(\frac{\mathbf{dMass}}{\mathbf{dTemp}} * \frac{\mathbf{\partial Repro}}{\mathbf{\partial Mass}} * \frac{\mathbf{\partial Pop}}{\mathbf{\partial Repro}}\right) + \left(\frac{\mathbf{\partial Repro}}{\mathbf{\partial Temp}} * \frac{\mathbf{\partial Pop}}{\mathbf{\partial Repro}}\right) + \frac{\mathbf{\partial Pop}}{\mathbf{\partial Temp}}$)).

Intra- and inter-specific variation in path estimates

We compared intra- to inter-specific variation in responses across 80 sites and 19 species in order to provide a baseline for quantifying what ‘a high level’ of intra-specific variation might be. We found high among species variation for the direct effects of temperature on body condition (ICC = 40% [95% CI: 37%-44%]; Fig. 3a) and on reproductive success (ICC = 18% [95% CI: 14%-23%]), suggesting that intra-specific responses to these pathways were fairly similar. The effects of changes in body condition on reproductive success, and reproductive success on the population growth rate, were highly variable among sites, such that within-species variation was substantially higher than the among-species variation (both ICC <0.01%; Fig. 3b & 3c).

There was little variation in responses among sites within species, for both the direct and total pathways from temperature to population growth rate, suggesting that there is a clear species signal in population responses to temperature (Fig. 2). For the direct pathway, 13 species showed clear increases in population growth rate and 10 clear decreases with very little variation among sites (ICC = 64% but precision of this intra-class correlation coefficient was low 95%CI: 0.001, 0.999]; see Appendix 6 Fig. S2). On average across all species, there was no direct effect of temperature on population growth rate, but individual species showed strong relationships, with half have negative or positive effects, essentially cancelling out any overall effect.

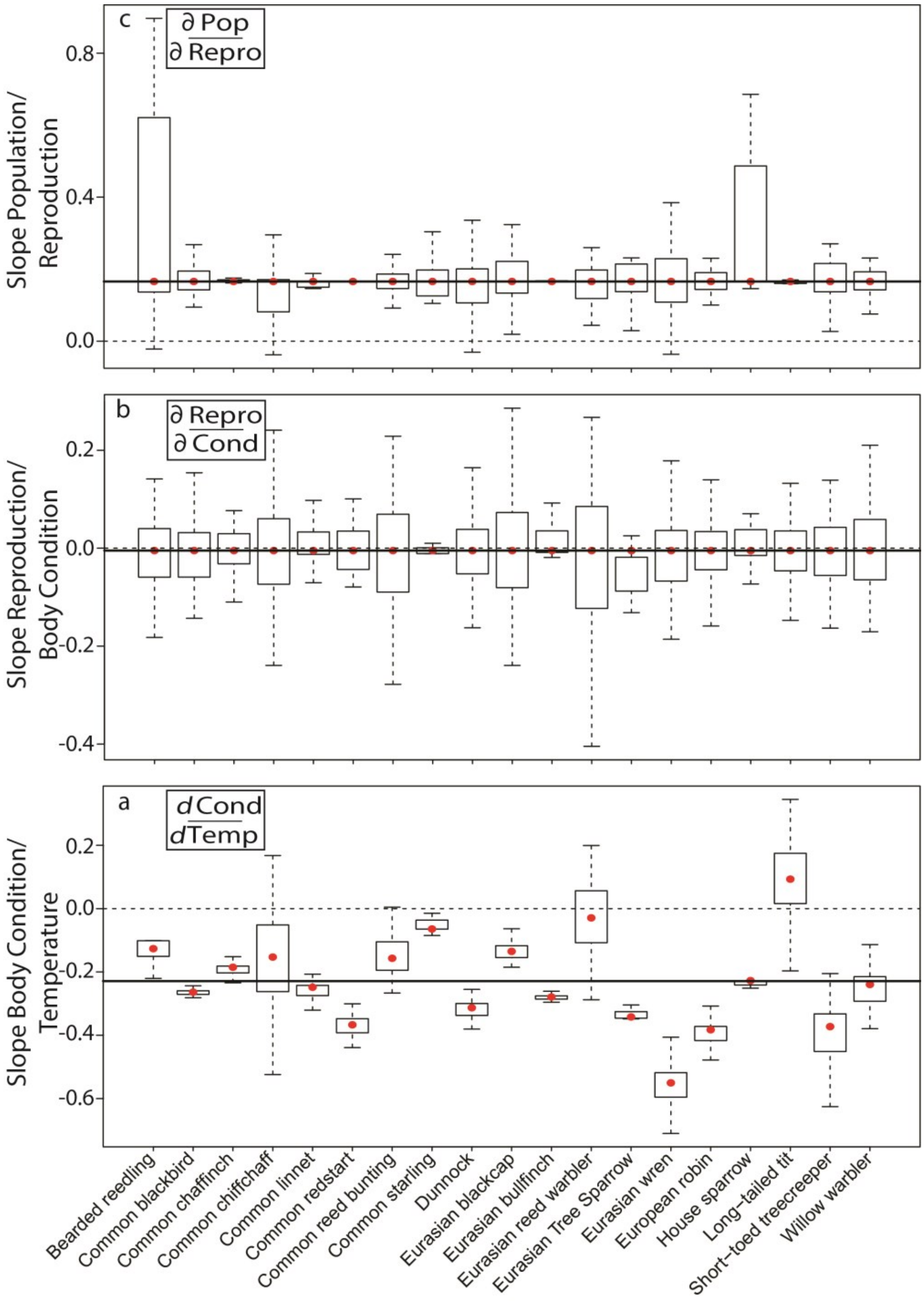

Figure 3 Intra- and inter-specific variation in the focal path estimates, where (a) shows the slope estimates for body condition responses to temperature, (b) shows the slope estimates for reproductive success responses to body condition, and (c) shows the slope estimates for population growth estimates to reproductive success. The boxplots show the distribution (minus any extreme values) of estimates across the sites. The red points show the species estimate, and the black solid line shows the overall slope estimate derived from the SEM. The dotted horizontal line shows where the slope is zero. All species and site estimates were extracted from the SEM as random slope coefficients. As such, because there was such little variation among species for (b) and (c) the slope estimates only vary by tiny amounts.

Site scale effects

We next investigated pathways at the site scale. The sign and direction of the body condition to reproduction relationship varied widely, yet averaged out to be approximately zero (Fig. 3b & Fig. 4b). There was also substantial intra-specific variation in population growth rate responses to reproductive success, however these were on average positive associations (Fig. 3c & Fig. 4c). In contrast, responses of body condition to temperature among sites were more consistently negative (Fig. 4a).

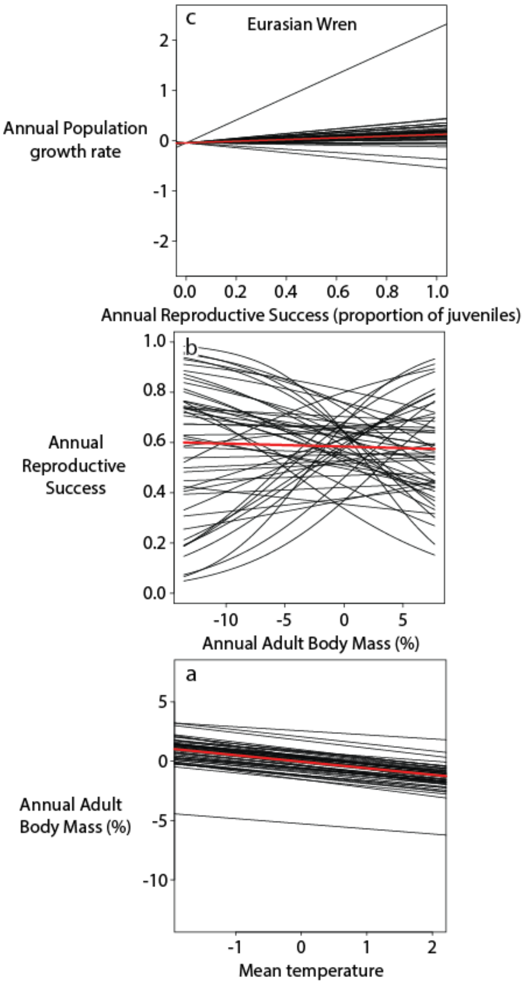

Figure 4 Species and site slope responses for the example species Eurasian Wren. Each black slope shows the path estimate for a different site, while the red slope shows the overall species estimate. (a) shows the responses of body condition to temperature, (b) reproductive success to body condition, and (c) population growth rate to reproductive success. The slopes are the random intercept and slope terms from the final SEM.

There was no relationship between the slope of body condition on reproduction with the total change in population with temperature (Slope= -0.07 ± 0.07, r^2= 0.00; Fig. 5a), such that sites which showed stronger changes in reproduction from body condition fluctuations did not have stronger changes in population growth rate from temperature. This suggests that the effects of temperature on population growth rates are independent of body condition (even though body condition is strongly affected by temperature). Instead, the total effects of temperature on the population growth rate were almost perfectly predicted by the non-focal pathway (i.e. the direct effect of temperature on population, and the indirect effect via reproduction only; Slope= 1.003, r^2= 0.99; Fig. 5b). This suggests that the effects of temperature on population growth rates are working via reproductive success and the direct pathway, which is mediated by an unmeasured trait (or traits).

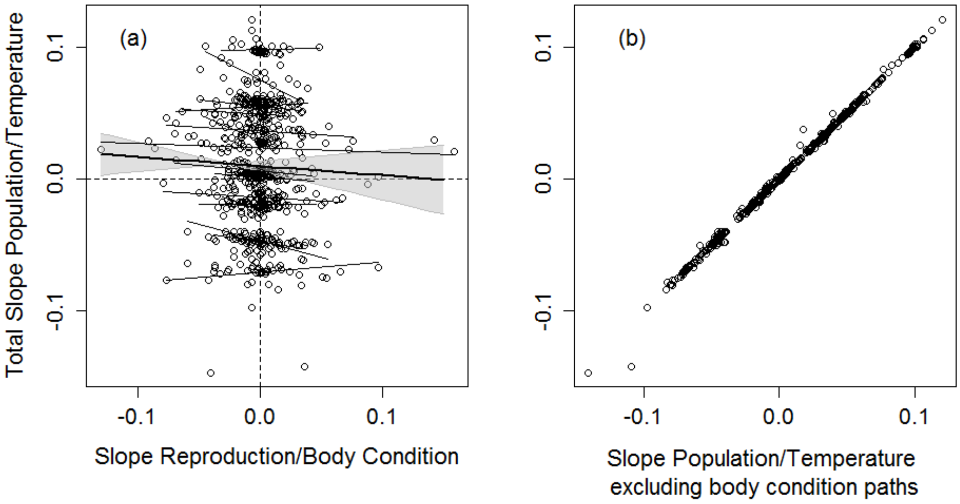

Figure 5 Relationships underlying the total effect of temperature on the population growth rate (i.e. $\frac{\mathbf{dPop}}{\mathbf{dTemp}}$). Shown are the relationships between the total effects of temperature on the population growth rate with (a) the body condition to reproduction pathway (the partial regression coefficient; $\frac{\mathbf{\partial RS}}{\mathbf{\partial Mass}}$), and (b) the temperature to population pathway with the body condition pathway excluded (i.e. the effect of temperature via the reproduction pathway and the direct pathway to population; $\left(\frac{\mathbf{\partial Repro}}{\mathbf{\partial Temp}} * \frac{\mathbf{\partial Pop}}{\mathbf{\partial Repro}}\right) + \frac{\mathbf{\partial Pop}}{\mathbf{\partial Temp}}$). The thick black slope in (a) is the overall relationship across all sites and species with 95% confidence intervals shaded in grey. Sites with stronger changes in reproduction from body mass do not show stronger changes in population growth rate with temperature. The thin black slopes show trends across sites for each species individually.

Explaining species and site differences

We adopted an exploratory approach and examined whether any species- or site-specific characteristics could explain variation in the total temperature to population growth pathway and the reproduction to population pathway. Two species characteristics (body mass and life-expectancy) and five site characteristics (average mean and minimum spring temperatures, habitat type, wet/dry site and predation pressure) were investigated. We also investigated the strength of density dependence, population density (a proxy for habitat quality), mean body condition and mean temperature from species-specific temperature windows for each species and site. We ran model selection to determine if any combinations of site- and species-specific characteristics were able to indicate any potential mechanisms (see Appendix 5 for details and Appendix 6 Table S1 for model selection table). No characteristics were able to explain the variation in either the total population growth on temperature pathway or the population on reproduction pathway (Appendix 6 Table S1 & S2).

Discussion

We have found that temperature-induced changes in adult body condition do not have further consequences on demography and population dynamics in 19 common passerines in the Netherlands. In general, warmer temperatures were associated with decreased body condition and increased reproductive success and population growth rates. At first glance these associations may suggest that climate induced change in body condition have population consequence. However, our path analysis approach revealed that body condition was not associated with reproductive success or survival and that the effect of temperature on the population growth rates of species was not due to body condition, but instead due partly to underlying changes in reproduction and other unidentified traits or demographic rates. We found strong species-signals in population growth rate responses to temperature, with roughly half of the 19 species increasing their population growth rates with warmer temperatures, and the other half either decreasing or showing no changes but were unable to identify species or site characteristics that could explain these trends.

Temperature-induced declines in body condition have no consequences

Our results suggest that body condition responses to global warming are common, but have no apparent consequences on demography and population dynamics. Declining body condition in adults was not associated with a change in reproductive success, and temperature-induced changes in population growth rates were independent of these effects. Consequently, the common assumption that climate-induced changes in body condition will have strong impacts on population dynamics has not been met. Specifically, the mechanism blocking such flow-on effects from occurring was that the change in trait did not affect demographic rates. This is one of only a few studies to have explicitly tested the mechanism by which trait changes may not have population consequences, and is the first looking at body condition in birds (but see Wilson & Arcese, 2003; Ozgul *et al.*, 2010; McLean *et al.*, 2016). Indeed, the decomposition approach used here is important for answering such questions as these patterns could have easily been misinterpreted using standard multiple regression techniques, as all response variables are correlated to temperature.

The fact that temperature-induced changes in body condition have no consequences on demographic and population dynamics, does provide some insights into the possible mechanisms underlying condition fluctuations. Firstly, it would suggest that decreasing body condition under warmer conditions is not an adaptation. If it was an adaptation to ‘keep up’ with the climate, you would expect to see negative consequences in those populations which had no change or increased body condition (Croll *et al.*, 1991; Chevin *et al.*, 2010). Similarly, if decreased body condition provided some advantage, for example, through lowered energy expenditure (Covas *et al.*, 2002; Quillfeldt *et al.*, 2006), reduced predation risks (Rogers, 2015) or improved flight performance (Senar *et al.*, 2002) a positive relationship between body condition and reproduction or population growth would be expected. Secondly, if decreased body condition was a direct negative effect from poorer foraging conditions in warmer weather, for example, then species or populations with the strongest declines would be expected to have negative consequences on reproduction or population dynamics (Harding *et al.*, 2011). None of these options appear to be the case. Perhaps, the changes in body condition are not yet strong enough and as the climate continues to become more extreme in the future, consequences will become evident.

Associations between body condition and reproductive success have been previously found in a range of taxa (Chastel *et al.*, 1995; Naef-Daenzer *et al.*, 2001; Masello & Quillfeldt, 2003; Quillfeldt *et al.*, 2006; Ozgul *et al.*, 2010; Aubry *et al.*, 2013; Paquette *et al.*, 2014), although most are are not explored in the context of climate. There could be a number of reasons why we might not have found a similar trend. We were unable to account for several factors in our model that could provide further insight into trends. For example, we could not distinguish between potential differences in male and female responses (which has previously been found to affect relationships in some cases (Chastel *et al.*, 1995; Møller & Szép, 2002; Paquette *et al.*, 2014; Gardner *et al.*, 2016)), or among birds of different ages (e.g. effects of senescence;

Rebke *et al.*, 2010). Additionally, our measure of reproductive success was fairly coarse. For instance, the effects of body condition on reproduction might actually change over the breeding season, a scale at which we were unable to focus on. Quillfeldt *et al.* (2006) found that only high adult body mass before egg laying was important for reproduction. After egg laying, adults tend to lose mass because they do not need to be buffered against unpredictable food supply (as food is usually plentiful at the time that chicks hatch).

Unknown pathways affecting reproduction and population growth

By using a structural equation modelling framework, we were able to decompose the contributions of different pathways and identify missing and major pathways. For instance, temperature-induced changes in body condition did not have any consequences for reproduction or survival, but there were important direct effects of temperature which were most likely mediated by an (unknown) trait other than body condition. We previously found the timing of egg laying to be strongly impacted by spring temperature (similar time periods to those used here based on body condition), and that it had a positive effect on reproductive success in common bird species in the United Kingdom (McLean *et al.*, 2016). Therefore, the effect of temperature on reproduction could be mediated by the timing of breeding or some other unknown trait correlated with temperature. Although part of the temperature-induced changes in population growth were due to reproductive success, the direct pathway was also important for individual species. This also suggests that these effects are mediated by some unknown traits (e.g.phenology) and demographic rates (e.g. juvenile survival). The decomposition of effects into direct and indirect pathways is critical for determining such patterns and would not have been possible to distinguish using traditional regression techniques. Moreover, the existence of multiple important pathways could be identified even though not all relevant traits were measured.

Consistent effects of temperature across populations

We found strong species signals (i.e. all sites tended to have similar responses) in responses to temperature at all hierarchical levels. This has two key implications: that certain species with particular characteristics might be more at risk from global warming than others, and that population- or location-specific features have no influence on these relationships. Low intra-specific variation suggests that local site-specific characteristics are unlikely to be good predictors, but that species-specific characteristics will be more important. However, we were unable to identify any species or site characteristics (e.g. size, life expectancy, migration strategy, habitat types) that explained population growth responses to temperature. Little intra-specific variation also suggests that neither site-specific features (e.g. presence of climate refuges, habitat type or quality, predation pressures) nor local adaptations and traits among populations influence the effect of temperature on responses. Intra-specific variation has been suggested to reduce the effects of climate change on species by buffering, or stabilising, the overall impact (termed portfolio effects; Abbott et al., 2017; Gamfeldt et al., 2005; Malyshev et al., 2016; Oney, Reineking, O'Neill, & Kreyling, 2013). Therefore, given the low intra-specific variation, there is little evidence that portfolio effects are important here.

Methodological issues with large scale hierarchical models

There are considerable challenges involved with 'matching up' so many response variables that are sampled and calculated in differing ways. Our measure of annual apparent survival included a residency parameter to account for transient individuals (i.e. those individuals that are not residents in the population but are passing through). This parameter was not taken into account for any of the other response variables, and could add noise to the data by increasing the number of adults in our reproductive success measure (transients are presumably adults). It could potentially be a problem if these individuals have a different body condition, or if their abundance changes in different years. Furthermore, survival estimates were unable to distinguish between mortality and emigration, whereas the population growth rate data from the BMP scheme does make this distinction. In order to make sure that our population growth estimates were independent of our survival and reproductive success estimates, we used abundance count data from BMP scheme and matched these sites as best as possible (based on distance and habitat type) to the Dutch CES locations. Some abundance estimates might not have been as representative of the CES sites as others (for instance if there is large population variation at very small spatial scales), therefore potentially weakening any potential relationships between population growth rate and any of the predictor variables. However, the fact that every trait-, demographic- and population-level response was found to be affected by at least one other variable, and in particular that there was a positive relationship between reproduction and population growth rate, does suggest that our measures are meaningful and that we have sufficient statistical power.

We investigated species and site level responses which meant that for the less common species sample sizes can become small, which can reduce the accuracy of their estimates. Extracting the random slope estimates for either species or sites can be difficult to interpret at times as the estimates based from smaller sample sizes will generally be 'shrunk' substantially towards the mean. Annual survival was not estimable for many sites and years due to the demanding nature of parameter estimation in capture-recapture analysis, meaning that our sample sizes were often too low. As such, the pathways for survival and rarer species should be interpreted with care. In general, we believe that our statistical power to detect effects was strong. The final SEM did include many parameters (k=26), yet we still had 113 observations per parameter, which is generally considered an appropriate number for accurate estimates even with a high number of random groups.

Implications

The majority of climate change research assumes that a change in a trait will have further consequences on demography and population dynamics. However, we did not find this pattern in 19 Dutch bird species over 21 years. Given that temperature was associated with reproduction and population growth, but body condition was not the underlying mechanism, it is vital that we identify the causal traits and demographic rates that are driving these changes. Once these unknown pathways are identified, we will not only have a better understanding of exactly how the effects of climate change flow up to impact population dynamics in species, but will also be better able to predict species responses in the future under climate change. Finally, because species showed strong species-specific responses in population dynamics to temperature that ranged from positive to negative, it is now vital to identify life-history characteristics that can predict those species which are more sensitive to warmer temperatures. This will potentially be of great value to biodiversity conservation because practitioners could use species characteristics to prioritize conservation efforts to those more at risk of declining population sizes, something of particular importance for species lacking in data.

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Appendix 5 - Methods

Data

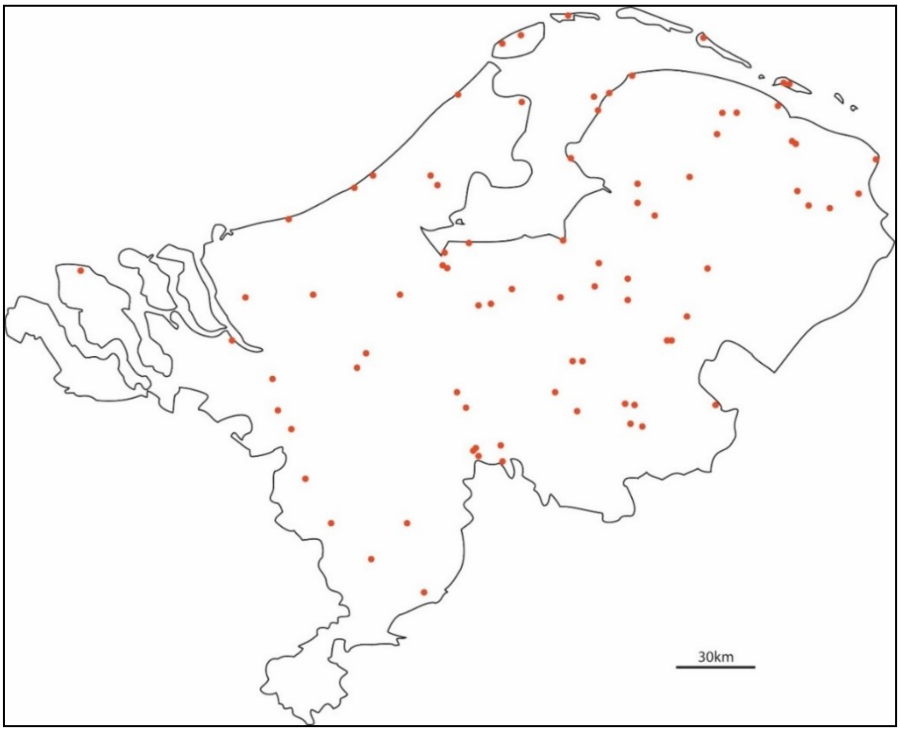

Figure S1. Map of the Netherlands with all study sites (indicated by the red dots).

Table S1 The percentage of sites and years in which annual adult survival was estimable. The sites and years columns show the sample sizes for each species included in the SEM model with survival excluded (i.e. the largest sample size). The last column shows the percentage of sites per year where adult survival could be successfully estimated. The low estimation rate is due to small sample sizes.

	Species	**Sites**	**Years**	**% of sites/years with survival estimated**
1	Bearded reedling	15	19	10
2	Common blackbird	48	19	34
3	Common chaffinch	41	17	10
4	Common chiffchaff	50	19	27
5	Common linnet	23	18	1
6	Common redstart	26	18	8
7	Common reed bunting	39	20	41
8	Common starling	21	17	0
9	Dunnock	47	18	20
10	Eurasian blackcap	48	19	16
11	Eurasian bullfinch	14	13	9
12	Eurasian reed warbler	41	20	85
13	Eurasian Tree Sparrow	11	14	13
14	Eurasian wren	50	20	18
15	European robin	44	19	2
16	House sparrow	7	9	4
17	Long-tailed tit	32	18	5
18	Short-toed treecreeper	31	18	1
19	Willow warbler	47	20	69

Table S2 CES site and weather station coordinates and the distances between the two.

CES Site	Lat (CES)	Long (CES)	Weather Station	Lat (Stn)	Long (Stn)	Distance (km)
C01	52.61	5.90	273	52.70	5.89	10.1
C02	52.45	5.82	269	52.46	5.53	20.3
C03	52.34	4.52	240	52.30	4.77	17.7
C04	52.54	6.47	278	52.44	6.26	18
C05	53.21	5.44	270	53.23	5.76	21.2
C06	53.11	4.79	235	52.92	4.79	20.3
C07	53.20	6.80	280	53.13	6.59	16.8
C08	52.33	5.16	265	52.13	5.27	23.7
C09	52.91	5.83	273	52.70	5.89	23.9
C10	51.85	5.12	356	51.86	5.15	1.9
C11	52.61	5.64	269	52.46	5.53	18.2
C12	51.57	4.90	350	51.57	4.93	2.1
C13	53.04	5.40	267	52.90	5.38	15.8
C14	52.54	4.83	249	52.64	4.98	15.6
C15	53.26	4.95	251	53.39	5.35	30.9
C16	51.69	4.47	344	51.96	4.44	29.8
C17	52.23	6.61	283	52.07	6.65	17.3
C18	52.28	6.52	283	52.07	6.65	24.8
C19	52.29	6.09	278	52.44	6.26	20.5
C20	52.63	6.08	273	52.70	5.89	15.5
C21	52.42	5.23	269	52.46	5.53	20.4
C22	52.53	6.46	278	52.44	6.26	16.6
C23	51.83	5.93	375	51.66	5.71	24.5
C24	52.85	5.44	267	52.90	5.38	6.2
C25	51.84	5.96	275	52.06	5.89	25.1
C26	52.44	6.88	290	52.27	6.90	18.5
C27	51.34	5.79	377	51.20	5.76	16.1
C28	52.42	4.56	240	52.30	4.77	19.7
C29	51.44	5.24	370	51.45	5.41	12.4
C30	51.84	4.39	344	51.96	4.44	13.4
C31	52.14	4.33	210	52.17	4.42	6.8
C32	52.31	5.21	265	52.13	5.27	20.5
C33	53.33	6.42	277	53.41	6.20	16.9
C34	53.07	5.33	267	52.90	5.38	19.4
C35	52.86	6.00	273	52.70	5.89	19.1
C36	52.31	6.13	278	52.44	6.26	16.9
C37	51.57	3.57	310	51.44	3.60	14.2
C38	52.27	6.47	278	52.44	6.26	23.7
C39	53.04	4.74	235	52.92	4.79	13.2
C40	51.65	4.77	350	51.57	4.93	14.7
C41	53.33	6.43	277	53.41	6.20	17.8
C42	52.81	6.42	279	52.75	6.58	12.6
C43	52.91	5.03	235	52.92	4.79	16.3

C44	52.86	5.88	273	52.70	5.89	17.5
C45	53.31	6.05	277	53.41	6.20	14.7
C46	53.46	5.66	251	53.39	5.35	21.8
C47	53.21	6.03	270	53.23	5.76	18.8
C48	51.90	5.12	356	51.86	5.15	4.9
C49	52.54	5.95	273	52.70	5.89	18.7
C50	52.57	6.15	278	52.44	6.26	16.9
C51	51.35	6.13	391	51.50	6.20	17.4
C52	51.36	5.49	370	51.45	5.41	11.2
C53	52.14	5.09	260	52.10	5.18	7.6
C54	53.20	6.59	280	53.13	6.59	8
C55	52.27	5.48	265	52.13	5.27	20.9
C56	51.97	4.69	348	51.97	4.93	16.4
C57	53.44	6.87	286	53.20	7.15	32.6
C58	53.41	6.22	277	53.41	6.20	1.9
C59	52.22	6.55	283	52.07	6.65	17.5
C60	51.51	5.84	375	51.66	5.71	18.8
C61	52.33	5.16	265	52.13	5.27	23.7
C62	53.48	6.16	277	53.41	6.20	8.3
C63	51.91	6.03	275	52.06	5.89	20
C64	51.87	6.08	275	52.06	5.89	25
C65	51.96	5.74	275	52.06	5.89	15.4
C66	52.52	4.91	249	52.64	4.98	14.8
C67	52.53	6.15	278	52.44	6.26	12.7
C69	52.42	5.23	269	52.46	5.53	20.3
C70	52.29	5.53	269	52.46	5.53	18.3
C71	53.28	6.00	270	53.23	5.76	17.4
C72	51.82	5.94	375	51.66	5.71	24.2
C73	53.17	6.70	280	53.13	6.59	9
C74	52.37	5.58	269	52.46	5.53	10.4
C75	52.81	4.69	235	52.92	4.79	14.3
C76	53.04	6.04	270	53.23	5.76	28.6
C77	53.31	6.89	286	53.20	7.15	21.5
C78	52.57	6.14	278	52.44	6.26	16.8
C79	52.16	6.26	275	52.06	5.89	27.6
C81	51.55	5.03	350	51.57	4.93	7
C82	53.48	6.18	277	53.41	6.20	8.4
C83	52.63	6.47	279	52.75	6.58	14.7
C84	53.44	6.87	286	53.20	7.15	32.6
C85	52.31	5.20	265	52.13	5.27	20.6
C86	52.17	6.10	275	52.06	5.89	18.9
C87	51.98	5.66	275	52.06	5.89	18.2
C88	53.10	5.39	267	52.90	5.38	22.7

Table S3 Climate windows for all species. Blank spaces indicate where those climate variables had no effect on body condition, and those species were excluded from the SEM analysis. Start and finish indicate the earliest and latest dates of the windows, respectively.

Species	Start	Finish
Bearded reedling	1-Sep	17-Oct
Bluethroat		
Common blackbird	29-May	12-Jul
Common chaffinch	29-May	23-Jul
Common chiffchaff	25-Jul	6-Aug
Common grasshopper warbler		
Common linnet	29-May	9-Jul
Common redstart	13-Jun	1-Jul
Common reed bunting	29-May	15-Jun
Common starling	5-Mar	12-Mar
Common whitethroat		
Dunnock	28-May	2-Jul
Eurasian blackcap	12-May	9-Jul
Eurasian blue tit		
Eurasian bullfinch	8-Jun	29-Jun
Eurasian jay		
Eurasian reed warbler	14-May	23-May
Eurasian tree sparrow	22-Sep	18-May
Eurasian wren	28-May	8-Jul
European crested tit		
European goldfinch		
European greenfinch		
European pied flycatcher		
European robin	28-May	8-Jul
European stonechat		
Garden warbler		
Great tit		
House sparrow	14-May	4-Jun
Icterine warbler		
Long-tailed tit	9-Jun	22-Jun
Marsh tit		
Marsh warbler		
Sedge warbler		
Short-toed treecreeper	27-Apr	17-May
Song thrush		
Spotted flycatcher		
Tree pipit		
Willow tit		
Willow warbler	10-Jun	27-Jun

Calculation of Estimates

Body Condition

Body condition residuals were taken from the model,

Body Condition ~ Wing length + Age class + Time + Time^2 + Season + Season^2 + Sex + (1|Individual ID))

where individual ID is included as a random intercept term, and time of day and day within the season are included as quadratic terms. The standard error was calculated as sqrt(variance/n). However, in the case where there was a sample size of 1, we assigned the standard error to be the maximum standard error value that was calculated. As these error values are only used to help with weighting in the structural equation model, we felt that as long as they were noted to have high errors, this would be adequate.

Population growth rate

We used the following function in R to calculate the standard error of the population growth rate.

Function to calculate standard error of population growth rate:

```
se_growthrate <- function(Ncurrent, Nnext, SmallTermAdded,
                          replicates) {
  Ncurrent_SmallTermAdded_bootstrap <-
      rpois(replicates, Ncurrent) + SmallTermAdded
  Nnext_SmallTermAdded_bootstrap <-
      rpois(replicates, Nnext) + SmallTermAdded
  growthrate <- log((Nnext + SmallTermAdded) /
       (Ncurrent + SmallTermAdded))
  growthrate_bootstrap <-
      log(Nnext_SmallTermAdded_bootstrap /
            Ncurrent_SmallTermAdded_bootstrap)
  # For a normal distribution this percentile would reflect
  # 1 standard deviation
  upper_se_growthrate_bootstrap <-
      quantile(growthrate_bootstrap, 0.841) - growthrate
  # For a normal distribution this percentile would reflect
  # 1 standard deviation
  lower_se_growthrate_bootstrap <-
      growthrate - quantile(growthrate_bootstrap, 0.159)
  se_growthrate_bootstrap <-
      mean(c(upper_se_growthrate_bootstrap,
            lower_se_growthrate_bootstrap))
  return (se_growthrate_bootstrap)
}
```

Here, Ncurrent is the mean abundance of the current year, Nnext is the mean abundance in the following year. The SmallTermAdded was included in the formula in order to account for situations when no territories were found at a site in a given year. The SmallTermAdded was set to the mean number of territories at that site across all years multiplied by a small constant (0.01). Weights were calculated as the absolute difference between the consecutive years (nt and nt+1). For instance, if nt = 30 and nt+1 = 0 between two consecutive years the population growth rate between these years would be weighted more heavily in the SEM than if nt = 3 and nt+1 = 0. This is because we can be more confident that the difference in abundance between 30 and 0 in two consecutive years is a real and strong change, whereas the sign of the change in growth rate is less certain if it only varies by a couple of individuals, as some individuals could have been missed, and therefore change the sign of r_t.

Intra- and inter-specific analysis

Using the amount of among species variance (u) and the within-species variance (v) for each pathway (random slopes) in our SEM model, we calculated the total amount of variation explained by species as:

$$\%\ among\ species\ variation = \frac{u}{u+v}$$

Details of the SEM Analysis

We used the following code in R to calculate the structural equation modelling analysis, where the model was calculated 4000 times using new bootstrapped data each time.

The r code used to calculate the structural equation model is as follows:

```
modelList = psem(
      ### Population
      lme(bootPop ~ bootRS + Tempcnt,
          random = list(Species = pdDiag(~ Tempcnt + bootRS),
                        Site = pdDiag(~ Tempcnt +bootRS)),
          na.action = na.exclude,
          weights = varFixed(~ 1/(sqrt(PopWt))),
          data = data),
      ### Survival
      glmer(Svl ~ BMpcnt + Tempcnt + (1|Species/Site) +
                  (0+BMpcnt|Species/Site) +
                  (0+Tempcnt|Species/Site),
            family = binomial(link = "logit"),
            weight = 1/SvlSE,
            data = total2),
      ### Reproduction
      glmer(bootRS ~ bootBMpcnt + Tempcnt + (1|Species/Site) +
                     (0 + bootBMpcnt|Species/Site) +
                     (0 + Tempcnt|Species/Site),
            family = binomial(link = "logit"),
            weight = N,
            data = data),
      ### Body mass
      lme(bootBMpcnt ~ Tempcnt,
          random = list(Species = pdDiag(~ Tempcnt),
                        Site = pdDiag(~ Tempcnt)),
          na.action = na.exclude,
          weights = varFixed(~ BMresSE),
          data = data)
)#End List
```

Explaining variation among sites

To investigate differences in pathways among species and sites, we ran multiple models testing all combinations of site and species characteristics to see whether they could explain variation in the slopes of total population growth on temperature, and population growth on reproduction. We used two species' characteristics, body condition and life-expectancy, which could act as proxies for ecologically similar species. Body size was calculated as the average body condition across all individuals across all years. Life-expectancy was calculated as 1/(1-annual survival rate) of the species over the entire period. Five site-specific characteristics were investigated; average spring temperature at each site (unrelated to species' temperature windows), average minimum spring temperature at each site, wet or dry habitat types (where wet habitats were composed of reed bed and wet scrub, and dry habitat types as dry scrub, garden and woodland), habitat type (reed bed, wet scrub, dry scrub, garden, woodland) and predation pressure (the density of sparrowhawks and other goshawks at each site averaged across all years).

We also investigated four characteristics that were site- and species-dependent: the strength of density dependence, population density (a proxy for habitat quality), mean body condition (for each species and site) and mean temperature from species-specific temperature windows. The three site- and species-dependent characteristics were simply added as fixed effects only. To test density-dependence, we calculated the strength of density-dependence by linear regression of the population growth rate (r_t) over the population size in year t. Population density was calculated as the number of individuals of the same species caught (per meter of net per day) for each site averaged across all years. Site mean temperature (based on each species-specific temperature window) was calculated by averaging mean temperatures at each site over all years.

The AICc from each of the models was compared to a null model that was a simple intercept only model, and a model with both fixed effects without the interaction term (the R package "*AICcmodavg*" was used). In addition to the previous characteristics, species and site were also included as factors in these models to investigate whether any characteristics explained variation in responses among sites or species.

Appendix 6 - Results

Normality of random intercept and slope terms for the SEM

All intercepts and slopes showed adequately normal distributions.

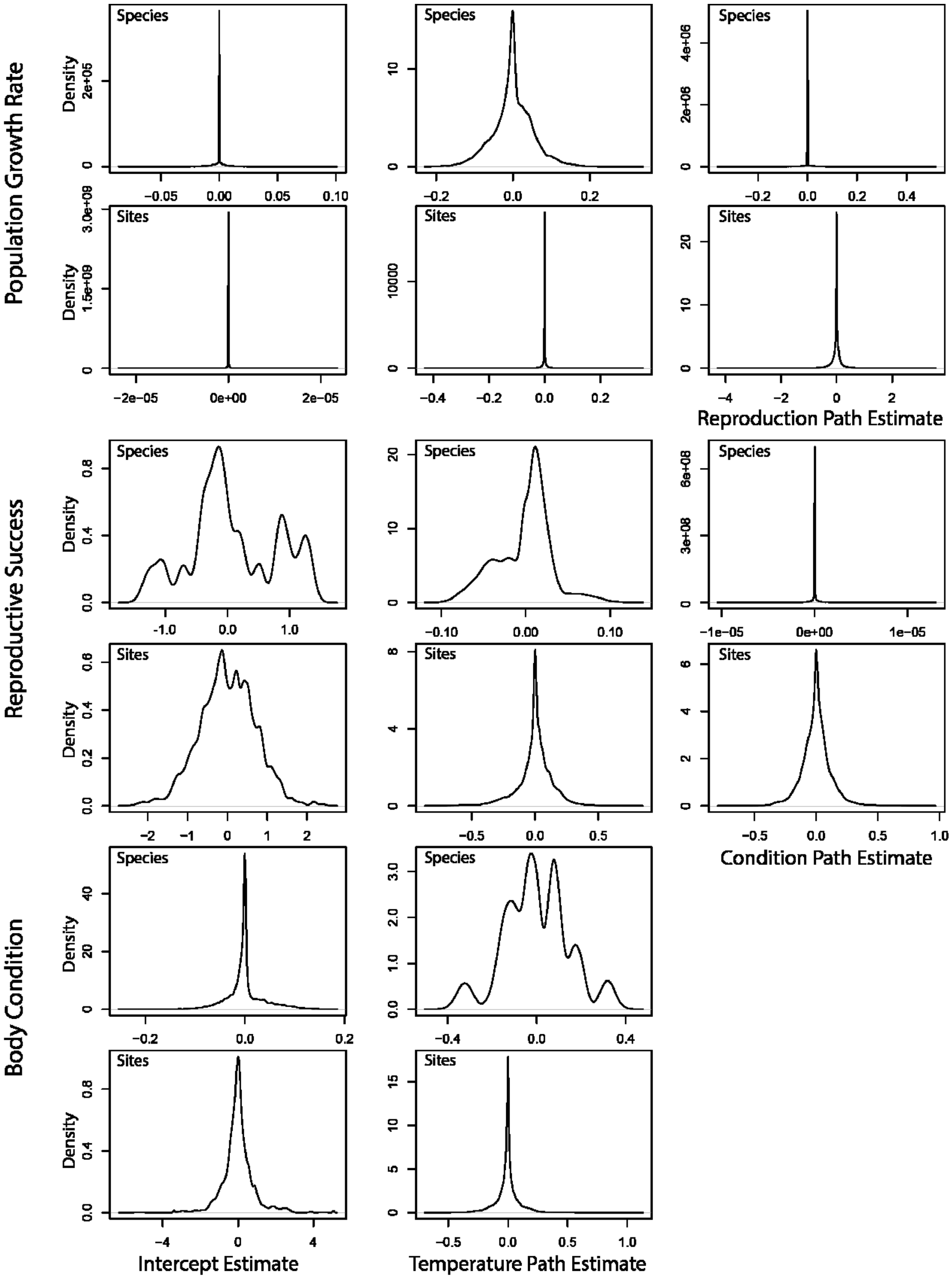

Figure S1 Distribution of random intercept and slope values for each of the three response variables (top two rows show the population growth rate, middle two rows show reproductive success and the bottom two rows show body condition). The first column shows the distribution of intercept values for each response variable. The middle column shows the distributions of path estimates (or partial slope estimates) for the explanatory variable temperature. The right column shows the distributions of path estimates for the explanatory variables reproduction (for the top two plots) and body condition (the lower two plots). The distributions of species' and site estimates are both shown and indicated by the text in the plots.

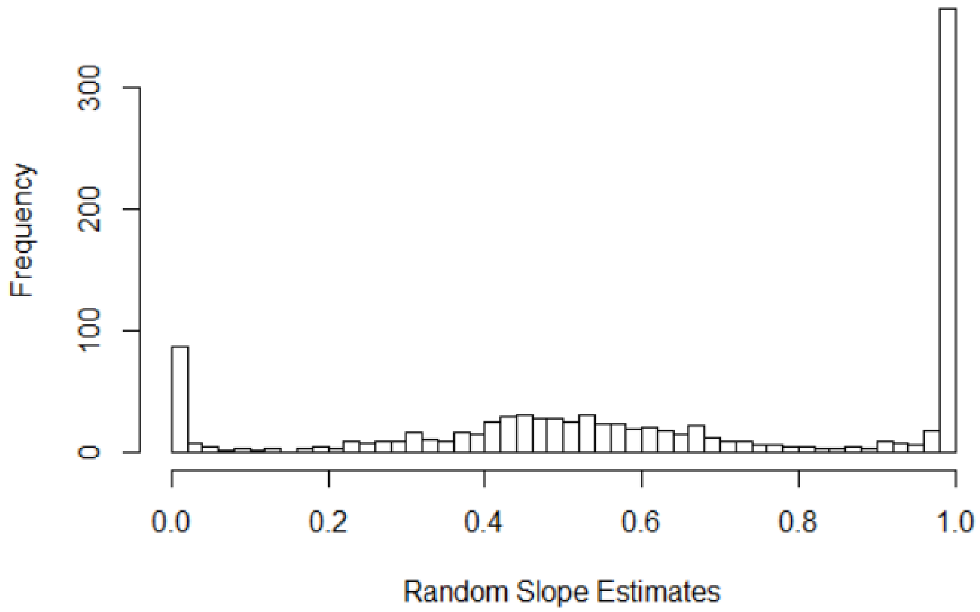

Figure S2 Distribution of the percent among-species variation for the temperature to population pathway across all 4000 bootstrapped models.

The random slopes for species when looking at the effect of temperatures on population growth rate was highly variable (Fig. S2). It appears that for different bootstrapped simulations the model found it hard to distinguish between among- and within-species variance.

Additional results from the SEM output

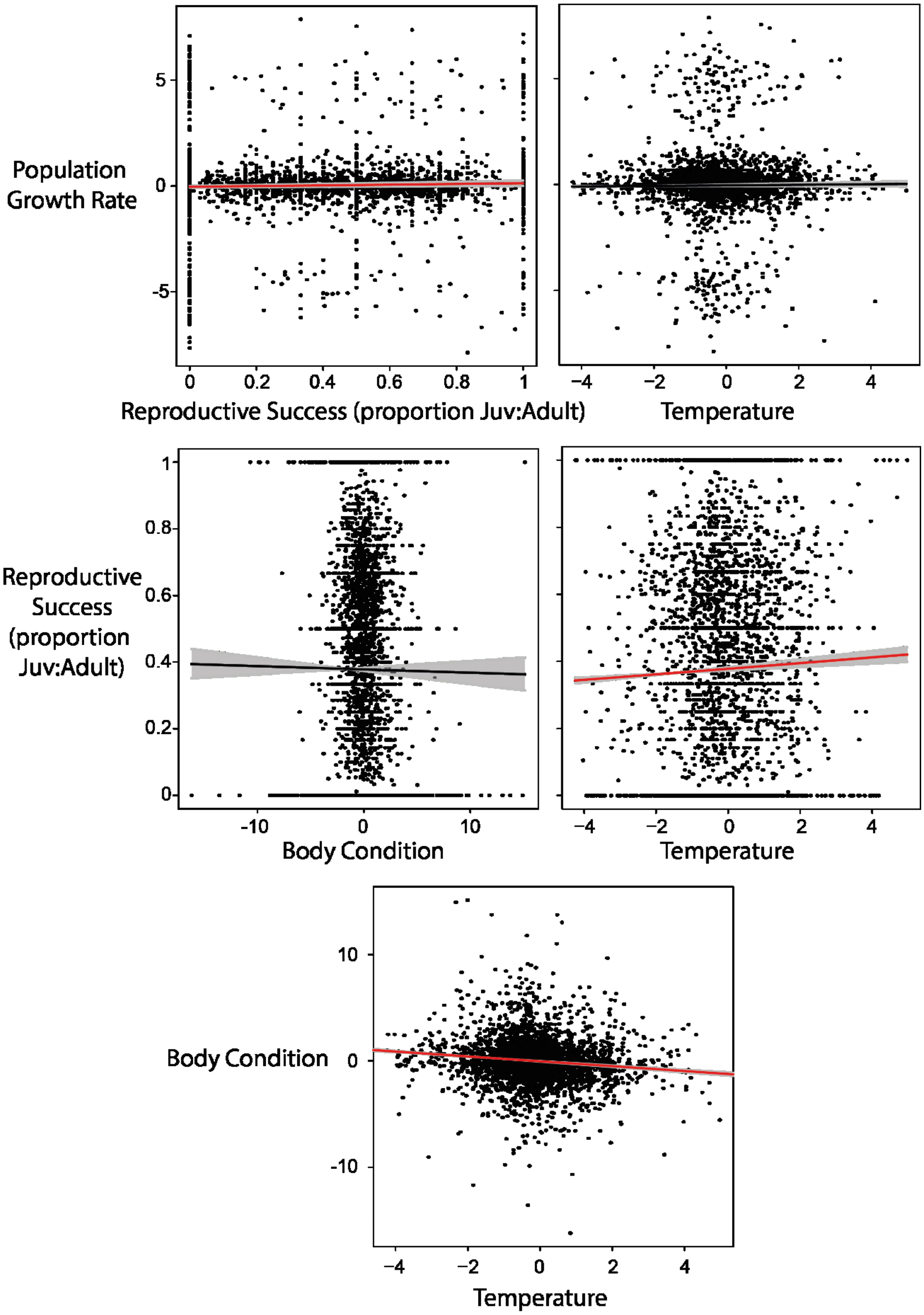

Figure S3 Graphical representation of the relationships for each pathway in the structural equation model with the underlying data. Each black point shows the estimate for all years and sites including all populations from all species. The slopes are red if the 95% confidence intervals do not cross zero. Note that each point is weighted based its accuracy.

Intra-specific Patterns

Table S1 AICc results for all combinations of models tested to explain variation in the total temperature to population growth pathway. Int is the intercept value, DD is strength of density dependence, life exp. Is life expectancy, +/- is whether the association between body condition and reproduction is positive or negative for that site/species, Site ave temp is the mean temperature at that site across all years while site temp var. is the variance. Size is average wing length of the species. Wgt is the weight of the model.

Int	DD	Habitat	Life exp.	Ave con	Migration	+/-	Site ave temp	Site temp var.	Size	R^2	df	Log-Lik	AICc	Delta	wgt
0.02	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.95	3	1802.26	-3598.49	0.00	0.92
-0.04	NA	NA	0.03	NA	NA	NA	NA	NA	NA	0.95	4	1800.35	-3592.64	5.85	0.05
0.02	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.95	4	1799.17	-3590.26	8.22	0.02
0.02	NA	NA	NA	NA	NA	+	NA	NA	NA	0.95	4	1798.44	-3588.82	9.67	0.01
0.02	0.00	NA	NA	NA	NA	NA	NA	NA	NA	0.95	4	1797.66	-3587.24	11.24	0.00
0.02	NA	NA	NA	0.00	NA	NA	NA	NA	NA	0.95	4	1797.58	-3587.09	11.40	0.00
0.03	NA	NA	NA	NA	+	NA	NA	NA	NA	0.95	5	1797.46	-3584.82	13.66	0.00
0.02	NA	NA	NA	NA	NA	NA	0.00	NA	NA	0.95	4	1796.35	-3584.64	13.85	0.00
-0.04	NA	NA	0.03	NA	NA	NA	NA	NA	NA	0.95	5	1797.26	-3584.41	14.08	0.00
0.02	NA	+	NA	NA	NA	NA	NA	NA	NA	0.95	4	1796.21	-3584.35	14.13	0.00
0.02	NA	NA	NA	NA	NA	NA	NA	NA	0.00	0.95	4	1795.77	-3583.47	15.02	0.00
-0.04	NA	NA	0.03	NA	NA	+	NA	NA	NA	0.95	5	1796.54	-3582.97	15.51	0.00
-0.04	0.00	NA	0.03	NA	NA	NA	NA	NA	NA	0.95	5	1795.84	-3581.57	16.92	0.00
-0.04	NA	NA	0.03	0.00	NA	NA	NA	NA	NA	0.95	5	1795.67	-3581.24	17.25	0.00
0.02	NA	NA	NA	NA	NA	+	NA	NA	NA	0.95	5	1795.33	-3580.55	17.94	0.00
0.02	NA	NA	NA	NA	NA	NA	NA	0.00	NA	0.95	4	1793.64	-3579.21	19.27	0.00
-0.03	NA	NA	0.03	NA	+	NA	NA	NA	NA	0.95	6	1795.61	-3579.08	19.40	0.00

0.02	0.00	NA	NA	NA	NA	NA	NA	NA	NA	0.95	5	1794.56	-3579.01	19.47	0.00
0.02	NA	NA	NA	0.00	NA	NA	NA	NA	NA	0.95	5	1794.48	-3578.85	19.64	0.00
-0.04	NA	NA	0.03	NA	NA	NA	0.00	NA	NA	0.95	5	1794.44	-3578.78	19.70	0.00
-0.04	NA	+	0.03	NA	NA	NA	NA	NA	NA	0.95	5	1794.30	-3578.50	19.99	0.00
-0.04	NA	NA	0.03	NA	NA	NA	NA	NA	0.00	0.95	5	1793.89	-3577.67	20.81	0.00
0.02	0.00	NA	NA	NA	NA	+	NA	NA	NA	0.95	5	1793.84	-3577.57	20.92	0.00
0.03	NA	NA	NA	NA	+	NA	NA	NA	NA	0.95	6	1794.37	-3576.59	21.90	0.00
0.02	NA	NA	NA	0.00	NA	+	NA	NA	NA	0.95	5	1793.29	-3576.48	22.01	0.00
0.02	NA	NA	NA	NA	NA	NA	0.00	NA	NA	0.95	5	1793.26	-3576.42	22.07	0.00
0.02	NA	+	NA	NA	NA	NA	NA	NA	NA	0.95	5	1793.11	-3576.12	22.37	0.00
0.02	0.00	NA	NA	0.00	NA	NA	NA	NA	NA	0.95	5	1792.97	-3575.84	22.65	0.00
0.02	NA	NA	NA	NA	NA	NA	NA	NA	0.00	0.95	5	1792.67	-3575.24	23.25	0.00
0.03	NA	NA	NA	NA	+	+	NA	NA	NA	0.95	6	1793.64	-3575.14	23.35	0.00
0.02	NA	NA	NA	NA	NA	+	0.00	NA	NA	0.95	5	1792.53	-3574.95	23.54	0.00
-0.04	NA	NA	0.03	NA	NA	+	NA	NA	NA	0.95	6	1793.42	-3574.69	23.79	0.00
0.02	NA	+	NA	NA	NA	+	NA	NA	NA	0.95	5	1792.37	-3574.64	23.84	0.00
0.03	0.00	NA	NA	NA	+	NA	NA	NA	NA	0.95	6	1792.99	-3573.83	24.66	0.00
0.02	NA	NA	NA	NA	NA	+	NA	NA	0.00	0.95	5	1791.95	-3573.79	24.69	0.00
0.03	NA	NA	NA	0.00	+	NA	NA	NA	NA	0.95	6	1792.78	-3573.41	25.08	0.00
0.02	0.00	NA	NA	NA	NA	NA	0.00	NA	NA	0.95	5	1791.75	-3573.39	25.10	0.00
-0.04	NA	NA	0.03	NA	NA	NA	NA	0.00	NA	0.95	5	1791.73	-3573.36	25.13	0.00
-0.04	0.00	NA	0.03	NA	NA	NA	NA	NA	NA	0.95	6	1792.74	-3573.33	25.16	0.00
0.01	NA	NA	NA	0.00	NA	NA	0.00	NA	NA	0.95	5	1791.70	-3573.29	25.20	0.00

0.02	0.00	+	NA	NA	NA	NA	NA	NA	NA	0.95	5	1791.60	-3573.10	25.38	0.00
0.02	NA	+	NA	0.00	NA	NA	NA	NA	NA	0.95	5	1791.55	-3573.00	25.48	0.00
-0.04	NA	NA	0.03	0.00	NA	NA	NA	NA	NA	0.95	6	1792.57	-3572.99	25.50	0.00
0.02	0.00	NA	NA	NA	NA	NA	NA	NA	0.00	0.95	5	1791.20	-3572.30	26.19	0.00
0.02	NA	NA	NA	0.00	NA	NA	NA	NA	0.00	0.95	5	1791.08	-3572.06	26.42	0.00
-0.04	0.00	NA	0.04	NA	NA	+	NA	NA	NA	0.95	6	1792.02	-3571.89	26.59	0.00
0.02	NA	NA	NA	NA	NA	NA	NA	0.00	NA	0.95	5	1790.54	-3570.98	27.50	0.00
0.03	NA	NA	NA	NA	+	NA	0.00	NA	NA	0.95	6	1791.55	-3570.96	27.53	0.00
-0.03	NA	NA	0.03	NA	+	NA	NA	NA	NA	0.95	7	1792.52	-3570.84	27.65	0.00
0.03	NA	+	NA	NA	+	NA	NA	NA	NA	0.95	6	1791.41	-3570.68	27.81	0.00

Table S2 AICc results for all combinations of models tested to explain variation in the reproduction to population growth pathway. Int is the intercept value, DD is strength of density dependence, life exp. Is life expectancy, +/- is whether the association between body condition and reproduction is positive or negative for that site/species, Site ave temp is the mean temperature at that site across all years while site temp var. is the variance. Size is average wing length of the species. Wgt is the weight of the model.

Int	DD	Habitat	Life exp.	Ave con	Migration	+/-	Site ave temp	Site temp var.	Size	R^2	df	Log-Lik	AICc	Delta	wgt
0.17	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.00	3	-14.56	35.15	0.00	0.43
0.17	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.00	4	-13.68	35.43	0.28	0.38
0.24	NA	NA	-0.04	NA	NA	NA	NA	NA	NA	0.00	4	-16.29	40.64	5.49	0.03
0.25	NA	NA	-0.05	NA	NA	NA	NA	NA	NA	0.00	5	-15.31	40.72	5.57	0.03
0.16	0.01	NA	NA	NA	NA	NA	NA	NA	NA	0.01	4	-16.72	41.50	6.35	0.02
0.17	0.01	NA	NA	NA	NA	NA	NA	NA	NA	0.01	5	-15.99	42.09	6.94	0.01
0.21	NA	NA	NA	NA	NA	NA	0.00	NA	NA	0.00	4	-17.25	42.56	7.41	0.01
0.17	NA	NA	NA	0.01	NA	NA	NA	NA	NA	0.00	4	-17.27	42.62	7.47	0.01

0.17	NA	NA	NA	NA	NA	NA	0.00	NA	NA	0.00	5	-16.37	42.85	7.70	0.01
0.17	NA	NA	NA	0.01	NA	NA	NA	NA	NA	0.00	5	-16.40	42.89	7.74	0.01
0.16	NA	+	NA	NA	NA	NA	NA	NA	NA	0.00	4	-17.44	42.96	7.80	0.01
0.17	NA	NA	NA	NA	NA	+	NA	NA	NA	0.00	4	-17.52	43.11	7.96	0.01
0.17	NA	+	NA	NA	NA	NA	NA	NA	NA	0.00	5	-16.51	43.13	7.98	0.01
0.17	NA	NA	NA	NA	NA	+	NA	NA	NA	0.00	5	-16.64	43.39	8.24	0.01
0.34	0.01	NA	-0.10	NA	NA	NA	NA	NA	NA	0.02	5	-16.72	43.55	8.40	0.01
0.35	0.01	NA	-0.11	NA	NA	NA	NA	NA	NA	0.02	6	-15.85	43.85	8.70	0.01
0.13	NA	NA	NA	NA	+	NA	NA	NA	NA	0.01	5	-17.91	45.93	10.78	0.00
0.14	NA	NA	NA	NA	+	NA	NA	NA	NA	0.01	6	-17.65	47.44	12.29	0.00
0.19	NA	NA	NA	NA	NA	NA	NA	0.00	NA	0.00	4	-19.85	47.77	12.62	0.00
0.26	NA	NA	-0.04	NA	NA	NA	0.00	NA	NA	0.00	5	-18.98	48.07	12.92	0.00
0.19	NA	NA	NA	NA	NA	NA	NA	0.00	NA	0.00	5	-18.98	48.07	12.92	0.00
0.24	NA	NA	-0.04	0.01	NA	NA	NA	NA	NA	0.00	5	-19.01	48.13	12.98	0.00
0.23	NA	NA	-0.05	NA	NA	NA	0.00	NA	NA	0.00	6	-18.00	48.15	13.00	0.00
0.25	NA	NA	-0.05	0.01	NA	NA	NA	NA	NA	0.01	6	-18.03	48.21	13.06	0.00
0.25	NA	+	-0.05	NA	NA	NA	NA	NA	NA	0.01	6	-18.15	48.45	13.30	0.00
0.23	NA	+	-0.04	NA	NA	NA	NA	NA	NA	0.00	5	-19.18	48.47	13.31	0.00
0.24	NA	NA	-0.04	NA	NA	+	NA	NA	NA	0.00	5	-19.25	48.61	13.46	0.00
0.25	NA	NA	-0.05	NA	NA	+	NA	NA	NA	0.00	6	-18.28	48.70	13.54	0.00
0.21	0.01	NA	NA	NA	NA	NA	0.00	NA	NA	0.01	5	-19.41	48.93	13.77	0.00
0.16	0.01	NA	NA	0.01	NA	NA	NA	NA	NA	0.01	5	-19.45	49.00	13.84	0.00
0.18	NA	NA	NA	NA	NA	NA	NA	NA	0.00	0.01	5	-19.50	49.11	13.95	0.00

0.18	NA	NA	NA	NA	NA	NA	NA	NA	0.00	0.00	4	-20.56	49.19	14.04	0.00
0.16	0.01	+	NA	NA	NA	NA	NA	NA	NA	0.01	5	-19.62	49.35	14.19	0.00
0.16	0.01	NA	NA	NA	NA	+	NA	NA	NA	0.01	5	-19.69	49.48	14.32	0.00
0.18	0.01	NA	NA	NA	NA	NA	0.00	NA	NA	0.01	6	-18.69	49.53	14.38	0.00
0.17	0.01	NA	NA	0.01	NA	NA	NA	NA	NA	0.01	6	-18.72	49.59	14.43	0.00
0.25	NA	NA	-0.08	NA	+	NA	NA	NA	NA	0.01	6	-18.78	49.71	14.55	0.00
0.16	0.01	+	NA	NA	NA	NA	NA	NA	NA	0.01	6	-18.86	49.86	14.70	0.00
0.18	NA	NA	NA	0.01	NA	NA	0.00	NA	NA	0.00	5	-19.96	50.02	14.86	0.00
0.17	0.01	NA	NA	NA	NA	+	NA	NA	NA	0.01	6	-18.96	50.07	14.92	0.00
0.14	NA	NA	NA	0.01	NA	NA	0.00	NA	NA	0.00	6	-19.07	50.29	15.14	0.00
0.18	NA	+	NA	NA	NA	NA	0.00	NA	NA	0.00	5	-20.12	50.34	15.18	0.00
0.16	NA	+	NA	0.01	NA	NA	NA	NA	NA	0.00	5	-20.16	50.43	15.28	0.00
0.13	NA	+	NA	NA	NA	NA	0.00	NA	NA	0.00	6	-19.18	50.50	15.35	0.00
0.21	NA	NA	NA	NA	NA	+	0.00	NA	NA	0.00	5	-20.21	50.53	15.37	0.00
0.17	NA	NA	NA	0.01	NA	+	NA	NA	NA	0.00	5	-20.23	50.56	15.41	0.00
0.17	NA	+	NA	0.01	NA	NA	NA	NA	NA	0.00	6	-19.23	50.61	15.46	0.00
0.17	NA	NA	NA	NA	NA	+	0.00	NA	NA	0.00	6	-19.34	50.82	15.67	0.00
0.17	NA	NA	NA	0.01	NA	+	NA	NA	NA	0.00	6	-19.34	50.84	15.68	0.00
0.16	NA	+	NA	NA	NA	+	NA	NA	NA	0.00	5	-20.41	50.92	15.77	0.00

Survival Results

These results utilised the smaller dataset, including only the sites and years with enough data to calculate adult survival estimates. We tested the model fit by the test of directional separation and found that the model represents the data well and no paths are missing (P=0.20; Lefcheck, 2016).

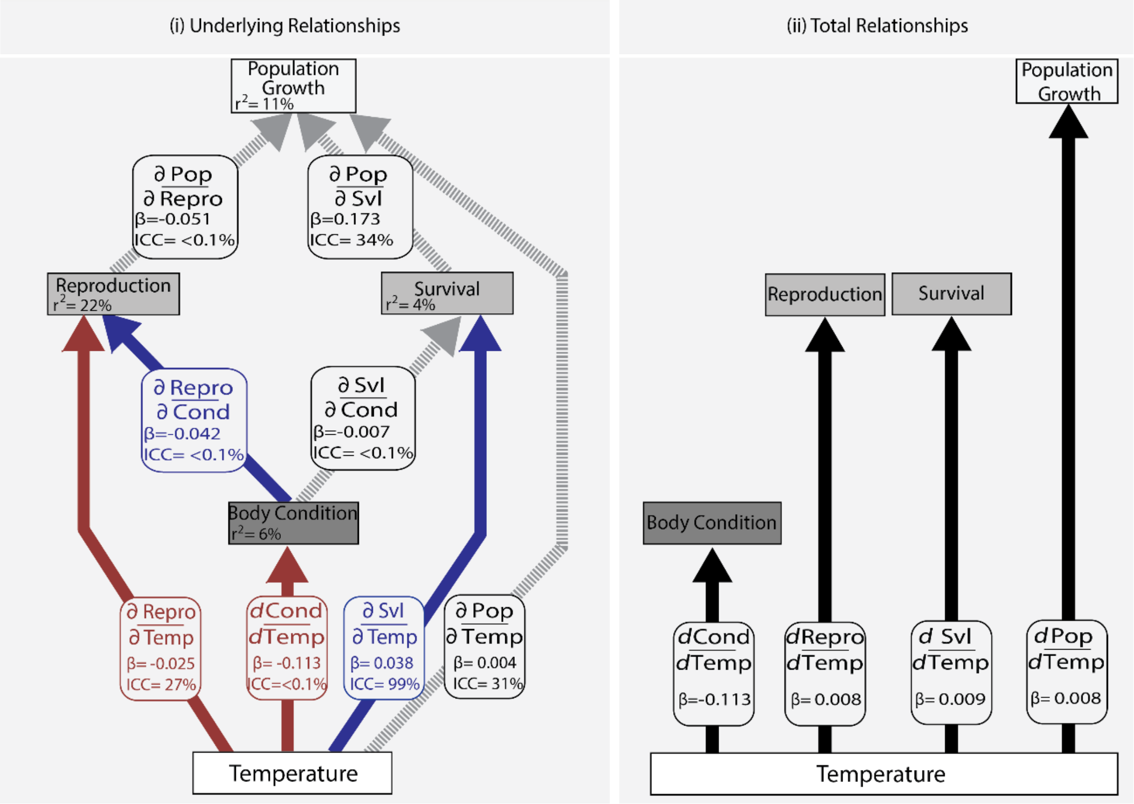

Figure S4 Decomposition of pathways in the structural equation model by which temperature-driven changes in body condition affect reproductive success, survival and population growth rate in 17 bird species (n=625). Panel (i) 'Underlying Relationships' displays the graphical model used in the structural equation analysis carried out on all species. The model includes the direct effects of temperature on reproductive success ($\frac{\partial \mathbf{Repro}}{\partial \mathbf{Temp}}$), on survival ($\frac{\partial \mathbf{Svl}}{\partial \mathbf{Temp}}$) and on population growth rate ($\frac{\partial \mathbf{Pop}}{\partial \mathbf{Temp}}$). It also includes the indirect effects of temperature on population growth rate via body condition and reproduction, as well as via body condition and survival. The red and blue solid arrows indicate significant negative and positive relationships (determined by whether the 95% confidence intervals cross zero), respectively, while the grey broken arrows indicate that there was no significant effect. Logistic models are used to describe the proportion of juveniles and annual survival rates (between 0 and 1). The r^2 values for each variable show the mean amount of variation explained by all pathways. ICC gives the ratio of the among-species variance or the intra-class correlation coefficient for each pathway. Panel (ii) 'Total Relationships' shows the total effect (indicated as full derivatives) of temperature on body condition, reproduction, survival and population growth rate, based on all direct and indirect effects.

There is no change in trends for the other pathways when survival is removed from the SEM, but the same smaller dataset is used. This means that survival is not having a strong impact on the other pathways.

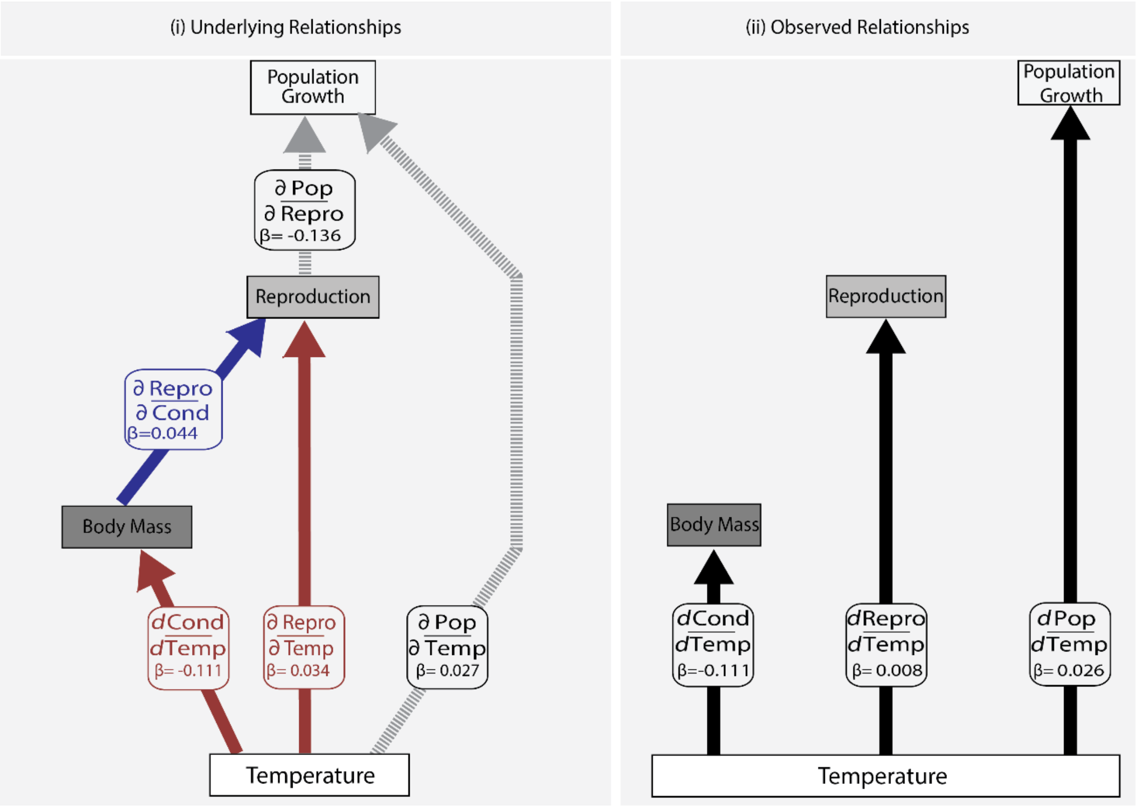

Figure S5 When survival is removed from the structural equation model, the trends in the remaining pathways remain the same (n=625).

Contradiction with previous findings about whether a species signal exists between temperature and body condition

In our previous work we found that the percentage of among-species variation in the temperature to body condition pathway was much smaller than we did here (McLean *et al.*, 2018). This difference can be attributed to several key differences in the two analyses. Firstly, in McLean *et al.* (2018) the climate sensitivities of body condition to temperature are calculated on individual-level data, whereas, here we have averaged body condition estimates per site/year +-SE because all other estimates (survival, reproduction and population growth) are not possible to investigate on individual-level data. This analysis has site nested within species, does not account for any other climate variables, and only looks at linear effects, factors that all differ from the previous study.

Chapter 4

Temperature or time? Climate warming only partly explains temporal trends in bird traits

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Abstract

Much of the ecological climate change literature investigates trends over time. Such studies assume that temporal trends accurately reflect changes due to climate change, rather than changes due to other non-climatic stressors. However, we currently have little understanding of how valid this assumption is, whether it differs among species, among populations within species or among the types of response being considered. Here, we use two large long-term datasets from the United Kingdom and the Netherlands on 60 bird species to quantify the contributions of temperature to changes over time in four key life history traits: laying date, body condition and two measures of reproductive success. We used structural equation models to distinguish between changes over time due to temperature versus those due to non-temperature effects. Non-temperature effects could include a range of effects such as habitat loss, modification or degradation, pollution, spread of invasive species but are not specifically distinguished here (i.e. non-temperature effects could be any other driver except for temperature). On average, temperature explained 47% of trends over time, with only a small amount of variation among the different traits. The contribution of temperature to long-term trends differed substantially among species, with more temperature-sensitive species showing stronger trait changes over time. Despite this, in general, non-temperature effects actually explained long-term trends far better than temperature, suggesting that temporal trends are less influenced by thermal sensitivity and depend more on the non-temperature conditions affecting species. The majority of species experienced reinforced effects from the temperature and non-temperature pathways, such that the total changes in traits over time were stronger than the change due to temperature alone. Consequently, our results indicate that non-temperature causal agents may be just as important as temperature in explaining temporal trends (if not more). As such, the assumption that long-term trends in wild animal populations are due to temperature was not met. We need to better understand the roles of both climatic and non-climatic effects on long-term trends if we are to better predict future impacts and therefore conserve those species most at risk.

Introduction

With anthropogenic climate change already impacting species around the world, and with dire predictions for species extinctions in the future (Thomas *et al.*, 2004; Urban, 2015), a key aim of much ecological research is to identify and predict species' responses to climate change. Investigating the responses of traits to changes in particular climatic variables (e.g. mean temperature, North Atlantic Oscillation, sea-surface temperature, days >35°C) arguably provides the most direct means of understanding the sensitivities of species to climate (Salewski *et al.*, 2010; van de Pol *et al.*, 2016). However, much of the literature investigating the effects of climate change on organisms does not directly relate climate variables to changes in traits such as phenology, physiology, survival or reproductive success. Instead, studies frequently assume that temporal trends accurately reflect responses to climate change, and therefore investigate trait changes over time. The decision to relate systematic variation in traits through time rather than directly to climate relies on three important assumptions: that other non-climatic causal agents are not changing over time, that climate affects the trait of interest, and that the climate experienced by the organism or system is changing over time. These three assumptions have each been tested independently by biological and climatological studies, but the relative contribution of each of these three pathways to trait change is never assessed simultaneously, let alone in a systematic study on a large scale across multiple traits, species and populations.

Non-climatic effects can often also be changing over time. Such non-climatic effects could include changes in population density, habitat loss, modification or degradation, pollution, spread of invasive species, loss of keystone species, spread of diseases carried by invasive species or overexploitation (Edinger *et al.*, 1998; Wilcove *et al.*, 1998; Mora *et al.*, 2007; Brook *et al.*, 2008). Chronic stressors (as opposed to short-term acute threats) alter the physical or biological environment on a long term basis, causing long term damage (Edinger *et al.*, 1998). Indeed as the human population continues to grow over time, it is expected that the frequency of threats and effects associated with urbanisation (e.g. infrastructure development, land development, water development and land conversion) will also increase over time (Mantyka-pringle *et al.*, 2012; Cunningham *et al.*, 2016). This can mean that changes in, for example, phenology over long periods of time will likely not be solely due to climate change.

Although the combined effects of climatic and non-climatic threats are becoming more commonly considered in studies on population and biodiversity dynamics (Mora *et al.*, 2007; Brook *et al.*, 2008; Kampichler *et al.*, 2012; Mantyka-pringle *et al.*, 2012; Duffy *et al.*, 2016), the idea that such combined effects could underlie responses in phenology, physiology or demography has been far less considered. Changes in climate have been found to have strong influences on the timing of reproduction across many taxa (Parmesan & Yohe, 2003; Parmesan, 2006; Dunn & Winkler, 2010; Poloczanska *et al.*, 2013). Yet, large-scale changes in land use or expansion into urban areas, for example, can also impact timing of reproduction for some species (Crick & Sparks, 1999). Additionally, the timing of breeding can be determined by nutritional state as determined by food availability which can be linked to habitat degradation (Drent & Daan, 2002; Low *et al.*, 2015). Body condition is similarly impacted by changes in climate (Garant *et al.*, 2004; Van Buskirk *et al.*, 2010; du Plessis *et al.*, 2012; Aubry *et al.*, 2013; Kruuk *et al.*, 2015; Gardner *et al.*, 2016), but can also be affected by changes in diet (unrelated to climate), predation, selective harvesting or habitat degradation (Lima, 1986; Garel *et al.*, 2007; Salewski *et al.*, 2010). Despite these non-climatic effects being known to be important, we currently have little understanding of how strongly such non-climatic causal agents contribute to temporal trends or how this might vary for different traits.

There are now many comparative studies that aim to explain interspecific variation in responses to climate (reviewed by Buckley & Kingsolver 2012). As many of these comparative studies use temporal trends to indicate climate change responses, they could encounter problems if the importance of temperature in explaining temporal trends differs among species. Some species can be highly sensitive to climate, while others can be climate insensitive (Thackeray *et al.*, 2016). Furthermore, different species can be affected by different climate variables, and the direction and magnitude of the response can often differ among populations within species (McLean *et al.*, 2018). In addition, different species will likely be affected by different non-climatic factors to varying degrees. For example, urban development will have a much stronger impact on some species compared to others (Cunningham *et al.*, 2016). As such, the amount of variation in temporal trends that is due to climate will likely differ among species.

Understanding how climatic and non-climatic effects each contribute to temporal trends will also be important if the two effects potentially reinforce one another and strengthen the overall response (reinforced effects), or act in opposing ways and dampen or buffer the overall change (Mora *et al.*, 2007; Radinger *et al.*, 2016a). Consequently, determining the magnitude and direction of both non-climatic and climatic causal agents will be essential not only to improve our predictive models, but also to develop appropriate conservation management strategies (Parmesan & Yohe, 2003; Wright *et al.*, 2009). However, there have been few studies that isolate individual and combined effects (Mora *et al.*, 2007).

The assumption that the climate will be changing over time is, in the majority of cases, likely to be met. Warming of the climate system is unequivocal, and since the 1950s, the atmosphere and ocean have warmed, the amounts of snow and ice have diminished, and sea level has risen (IPCC, 2014). However, the magnitude of changes in climate can vary substantially among locations and seasons (Buckley & Kingsolver, 2012). For example, the breeding times in the ring ouzels *Turdus torquatus* in Britain advanced with spring precipitation but there was no significant change in precipitation over the time at the study site, and therefore no change in laying date over time (Beale *et al.*, 2006). Similarly, finding a change in phenology with warmer temperature does not always mean that there will be any clear phenotypic change over the study period if there is high inter-annual variability which may obscure a systematic trend (Wright *et al.*, 2009; Kruuk *et al.*, 2015). Finally, identifying general patterns in changes over time across populations or species is troublesome as the direction and magnitude of change will depend on the climate in the local region (Gardner *et al.*, 2014).

Using two large long-term datasets on common bird species from the United Kingdom and the Netherlands on four important life history traits (lay date, body condition, fledglings per breeding attempt and proportion of juveniles), we ask here whether changes over time can be assumed to be due to warming temperatures. To answer this question, we use structural equation models to decompose long-term trends in traits into those due to temperature (i.e. changes over time due to the effects of temperature, termed the temperature pathway) versus those due to non-temperature effects (i.e. changes over time not due to the effects of temperature, termed the non-temperature pathway). We quantify what proportion of the changes over time are due to each effect and determine whether this varies among different types of traits, species and populations within species. Furthermore, we test whether the effects of temperature and non-temperature factors generally either counteract or reinforce one another, making the overall change over time due to their combined effects either weaker or stronger.

Methods

Biological Data

We used one long-term dataset on common bird species from the United Kingdom (UK) and another from the Netherlands (NL). The UK dataset included national averages for multiple species, while the NL dataset included data from multiple species and sites. With the UK dataset, we investigated two traits: timing of egg laying, and the number of fledglings produced per breeding attempt/brood (FPBA; a standard measure of breeding success Baillie *et al.*, 2014), using records of 35 common British bird species over 48 years (1966–2013; BTO 2015). We analysed annual estimates of mean egg laying dates and the mean number of FPBA per species recorded by the British Trust for Ornithology's Nest Record Scheme. FPBA estimates were derived as a function of maximum recorded brood size and egg and chick stage nest failure rates in each year. Therefore partial brood losses are not taken into account (Crick *et al.*, 2003), and so breeding success could be under-estimated. However, we have no reason to assume that this underestimation is dependent on the climate in any given year or that it has changed over time.

In the Netherlands, we investigated two traits: body condition and the proportion of juveniles in the population, for 47 species recorded as part of the Dutch Constant Effort Site (CES) program over 21 years (1994-2014). This dataset also allowed us to quantify intra-specific variation as it included data from over 80 sites, with each species recorded at multiple sites (see Appendix 7 Fig S1 for map; McLean *et al., 2018*). Site-level estimates were not investigated for the UK data because the data consisted of national averages. On average, each species had data from 57 sites (range 39-68; see Table S1 for site details). We estimated standardised body condition by correcting body mass for a number of factors by taking the residuals from the linear regression on wing length, age (adult or juvenile; birds are considered adults after their first year in all species), sex (if determinable based on plumage), time of day and date of capture in the year (both non-linear) and the random intercept individual ID. Therefore we effectively adjust mass for size, age, sex, capture timing and recaptures of individuals. The residuals are centred such that a body condition of 0 means that it is exactly average given its conditions. We looked at the change in body condition as a percentage of the species' mean mass to make this value comparable across species of different sizes. The proportion of juveniles (with binomial standard error) caught at each site per year was used as a relative measure of breeding productivity (Du Feu & McMeeking, 1991; Peach *et al.*, 1996; Nur *et al.*, 2000). This measure can be thought of as per capita reproduction. The mean and the standard error of body condition residuals and the proportion of juveniles were calculated for each site and year per species to match the measures of proportion of juveniles (i.e. a single measure per species per site).

Climate Data

We used daily records of mean temperatures from the Central England Temperature dataset (Parker et al. 1992) and from the Royal Netherlands Meteorological Institute (KNMI). Because we used only single estimates for populations across the United Kingdom (rather than site-level estimates) we used a single measure of climate taken from the Central England Temperature dataset. Dutch temperature data was used from 37 weather stations across the Netherlands, with biological data from each Dutch CES site matched with the closest weather station (mean distance 17 km; see Appendix 7 Table S1).

Statistical Analysis

Climate Windows

We performed climate window analyses to identify the time period during which a linear effect of mean temperature explained the most variation in the trait measures for each species and trait (laying date, body condition, FPBA, and proportion of juveniles), using the R package *climwin* (Bailey & van de Pol, 2016). This allowed us to take a systematic exploratory approach, as we considered all possible combinations of consecutive weeks for the previous two years to identify the 'best' possible window. This meant that potential climate windows could potentially differ in their periods across species, for instance from recent spring temperatures to conditions from the previous year. All analyses assumed Gaussian distributions, with the exception of the proportion of juveniles which had a binomial error distribution and logit link function. For all four response variables, the *climwin* analysis was weighted by the uncertainty of the estimates, such that estimates with larger standard errors (laying date, FPBA and body condition) or smaller sample sizes (proportion of juveniles) contributed less (respectively, using the inverse standard error or the square root of the sample size as weight). We selected the best model based on Akaike's Information Criterion modified for small samples (AICc; Burnham & Anderson, 2002).

When testing so many climate window models, the chances of spurious results are high (van de Pol *et al.*, 2016). Randomisation techniques were therefore used to assess the likelihood that the best time window might occur by chance, with fifty randomisations carried out for each species (Bailey & van de Pol, 2016). We considered there to be a temperature signal present if the best window had more than a 50% chance that it was real.

Structural Equation Modelling

After identifying the climate windows for which temperature explained most variation in our respective traits, we used structural equation models (SEMs) to decompose trends over time into those components due to temperature versus those due to non-temperature effects. Models were conducted only on those species for which we had identified temperature windows with sufficient statistical support. In our SEM, the association between year and trait was decomposed into an indirect effect on the trait via temperature (i.e. changes over time due to the effects of temperature, termed the temperature pathway) and a direct effect on the trait (i.e. changes over time not due to the effects of temperature, termed the non-temperature pathway) (see Fig 2 for graphical representation of the SEM). The direct, or non-temperature, pathway captures the change in trait over time not due to the temperature window and so is likely composed of many unknown drivers. To calculate the temperature pathway, the effect of year on temperature can be multiplied with the effect of temperature on the trait to describe the temporal change due to temperature (Fig 2, column (ii); Grace, 2006). The total change in trait over time is then calculated as the sum of the temperature and non-temperature pathways (Fig 2, col (iii)). If the total changes in trait over time are predominantly due to warming temperatures, then there are two patterns that would be expected. First, the direct, non-temperature path estimate would be expected to be weak relative to the temperature path estimate. Second, temperature would increase over time, and traits would be associated with changes in temperature. By allowing temperature to serve as both a response variable and a predictor variable, we can quantify indirect or cascading effects that would be unrecognised in alternate single models (Lefcheck, 2016).

We constructed a structural equation model for each species in either the UK or the Netherlands using the R-package *piecewiseSEM* (Duffy *et al.*, 2016; Lefcheck, 2016). Temperature was mean centred and the start year was set as zero. Similarly to the previous *climwin* analysis, all regression equations in the SEM had Gaussian distributions, with the exception of the proportion of juveniles which had a binomial error distribution and logit link function, and were weighted by the inverse of the standard error (or the square root of the sample size in the case of the proportion of juveniles). Because the slope estimates with reproductive success as the response variable were on the logit scale (i.e. nonlinear), we calculated a linear approximation to be able to calculate the combined pathways (described above). To do this, we calculated the tangent at the mean (i.e. the linear slope around mean-0.0001, and mean+0.0001). To investigate intra-specific variation, site was included as a random intercept and slope term in the analysis of the NL dataset. Species/site-specific estimates of changes with respect to temperature and time were extracted as random slope coefficients from the model.

We accounted for propagation of uncertainty when calculating the temperature pathway that is determined by the product of the underlying pathways (which each have their own imprecision). We applied a bootstrapping technique by randomly generating 10,000 data points from a normal distribution centred at the path estimate value with variance equal to the standard error and multiplied each of the newly generated estimates. To summarise the bootstrap results from the 10,000 temperature path estimates, we took the median as the temperature path estimate and the 0.025% and 0.975% quantiles as the 95% confidence intervals. In this way, estimates that are more accurate have a smaller standard error and therefore the values will remain roughly the same in each of the runs, while estimates with large error will move over a larger distribution for subsequent runs. The same bootstrapping technique was used to calculate the total pathway, where the temperature pathway is summed with the non-temperature pathway.

Our model was saturated as all path estimates were needed to answer our specific questions. This meant that the normal model fit statistics could not be calculated. In order to check that the estimates from our SEMs were likely to be reasonable, we checked the fits of each of the individual path estimates and made sure the residuals were normally distributed, the standard errors appeared reasonable (not extremely large or close to zero) and the random intercept and slope terms were normally distributed (for the site-level analysis). All models satisfied these assumptions (see Appendix 7).

The approach developed here with SEMs is similar to year-detrending undertaken by other studies (Iler *et al.*, 2017). The detrending approach detangles the potentially confounding effects of year on climate-trait relationships by carrying out a two-step approach where the residuals from two separate regressions with the trait over time, and climate over time are extracted, with the subsequent analysis carried out on the detrended climate and trait variables. Alternatively, year (as a fixed continuous linear effect) and climate can be included as predictors in a multiple regression with trait as the response variable (Iler *et al.*, 2017). The SEM approach used here has several benefits over detrending: it does not require multiple steps and can be done all in one model, it looks at partial effects and so accounts for the effects of the other variables, but most importantly, it is able to determine the trend over time due to climate (i.e. the temperature pathway) by distinguishing between the effect of year on climate, and the sensitivity of the trait to climate unrelated to year. By investigating these individual and total or combined pathways you can gain much greater insight into the trends.

Percentage of change over time explained by temperature

We calculated the percentage of change over time due to the temperature pathway as

$$\left(1 - \frac{abs\left(\beta_{Total\ pathway} - \beta_{Temperature\ pathway}\right)}{abs\left(\beta_{Total\ pathway} - \beta_{Temperature\ pathway}\right) + abs\left(\beta_{Total\ pathway} - \beta_{Non-Temperature\ pathway}\right)}\right) * 100$$

To account for the error surrounding each of these individual path estimates within the equation, we used the same bootstrapping technique as described above. By including the absolute difference between unstandardised pathway coefficients, the percentage explained is not affected by the sign of the relationship.

Results

Identifying temperature sensitive species

Not all species and traits were equally sensitive to temperature. We found significant effects of temperature on laying dates and body condition in most species (27/35=77% of species for laying dates and 22/47=47% of species for body condition), while significant temperature sensitivities in reproductive parameters were less common (12/35=34% for FBPA and 13/47=28% for proportion of juveniles; Appendix 7 Table S3). There was a significant difference in the changes in laying date over time for temperature sensitive and insensitive species, where temperature sensitive species advanced their laying dates by 0.20±0.07SE days per year on average while insensitive species delayed their laying dates by 0.05±0.06SE days per year on average over time (Fig 1; linear regression p=0.008). However, there were no significant differences in changes over time between temperature-sensitive and -insensitive species for the three other response variables.

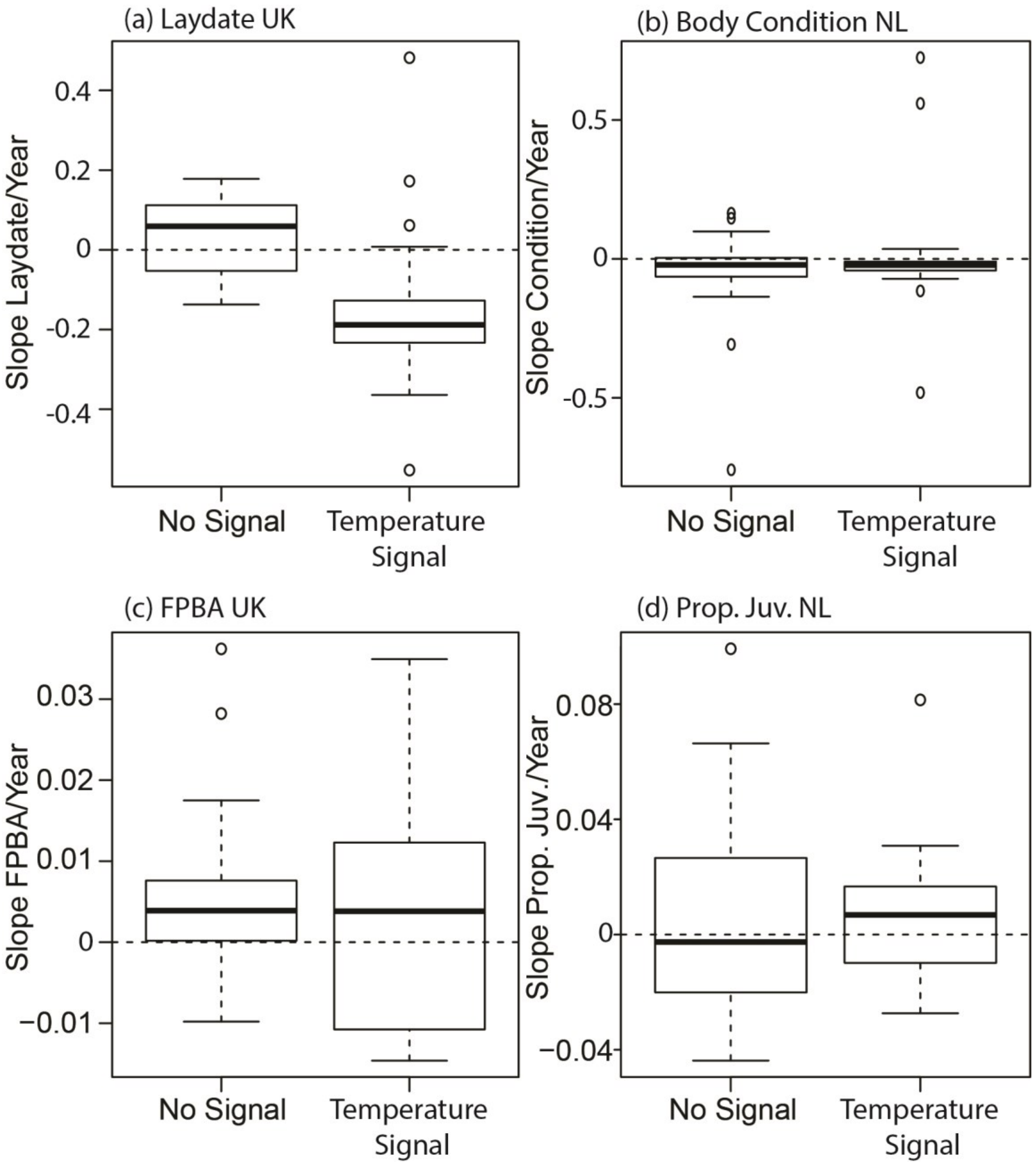

Figure 1 Distribution of slope estimates for changes in response (laying date, FPBA, body condition and proportion of juveniles) over time among species.

The direction of temperature and non-temperature pathways

Mean temperature was increasing over time across both countries. Over both time and temperature, laying date advanced (Fig 2a, Fig S3), body condition decreased (Fig 2c, Fig S4) and the proportion of juveniles increased on average (Fig 2d, Fig S6). For both body condition and laying date, the change over time due to temperature and non-temperature effects were roughly equal (birds laid eggs 0.09 or 0.07 days earlier per year due to temperature or non-temperature effects, respectively; body condition decreased by 0.012 or 0.016% grams per year respectively due to temperature or non-temperature effects). The change in the proportion of juveniles per year was larger for non-temperature effects (0.002±0.001 compared to 0.0005±0.0004 increase in the proportion of juveniles per year). However, FPBA increased over time due to non-temperature effects (Fig 2c), but the temperature pathway was not systematically negative or positive when averaged across all species.

For all traits, the temperature and non-temperature pathways reinforced each other for the majority of species (85% for laying date, 77% for body condition, 75% for FPBA and 54% for proportion of juveniles). As such, in the majority of cases, the total change in traits over time were greater than the change due to temperature alone.

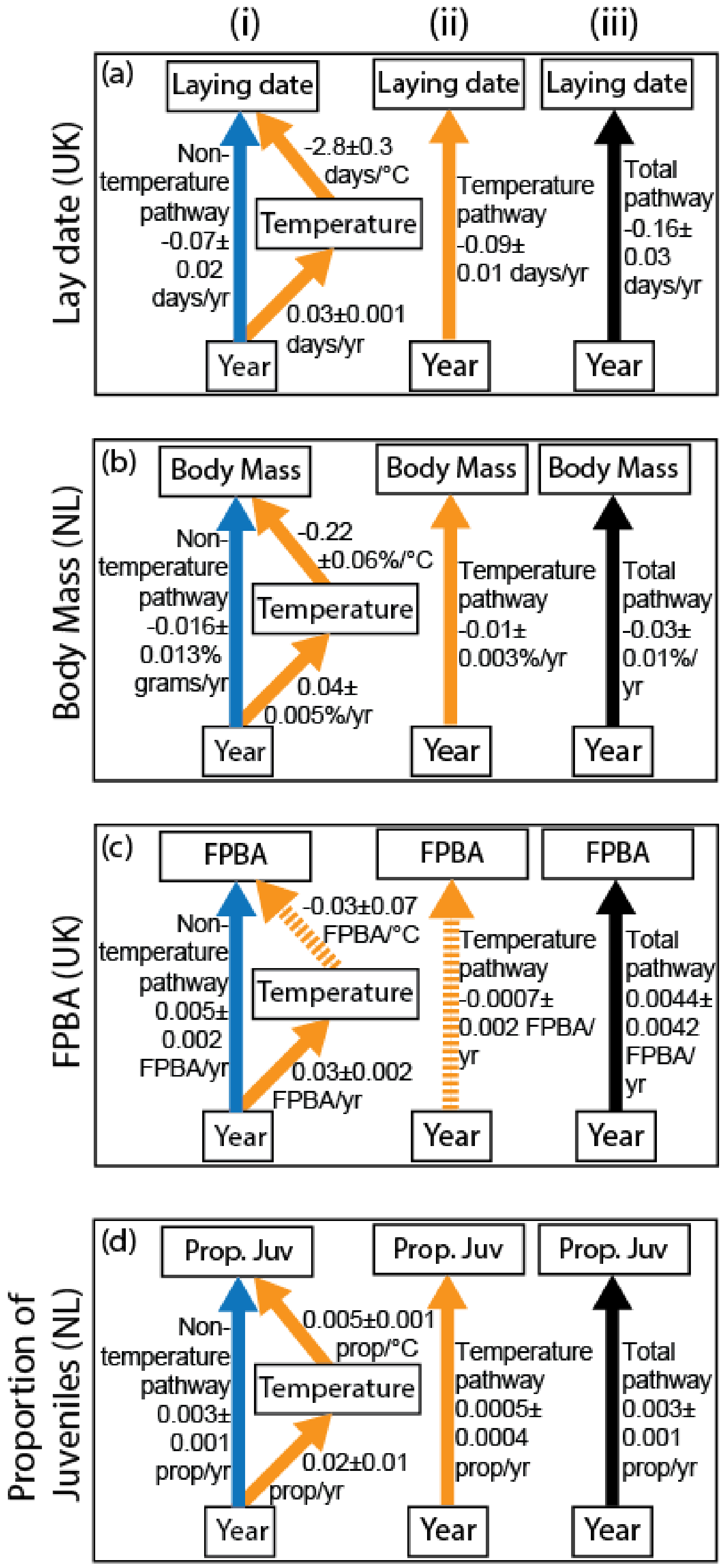

Figure 2 Graphical representations of the structural equation models used for each species and each of the four traits (a-d). Here, the path estimates are the averaged (± standard error) values across all species. The first column (i) shows the full SEM and the individual path estimates for each. The temperature pathway (in column ii) shows the change in trait over time due to temperature and is

calculated as the year to temperature pathway multiplied with the temperature to trait pathway. The total pathway (in column iii) shows the total change in trait over time due to all variables, and is calculated as the temperature pathway summed with the non-temperature pathway. Solid arrows indicate the SE did not cross zero, while the dashed arrows indicate the SE did cross zero.

Change over time due to temperature

By determining how much the temperature pathway contributed to the total temporal responses we were able to quantify the percentage of change in response due to the indirect effect of temperature. On average across all traits, 47% of changes in traits were due to the temperature windows identified in our *climwin* analysis. There was some variation among the traits, but mostly the percentage explained was around 50% (50% for lay date, 40% for body condition, 56% for FPBA and 41% for the proportion of juveniles). However, there were large differences in the percentage explained among species, with laying date showing the least interspecific variation (Fig 3).

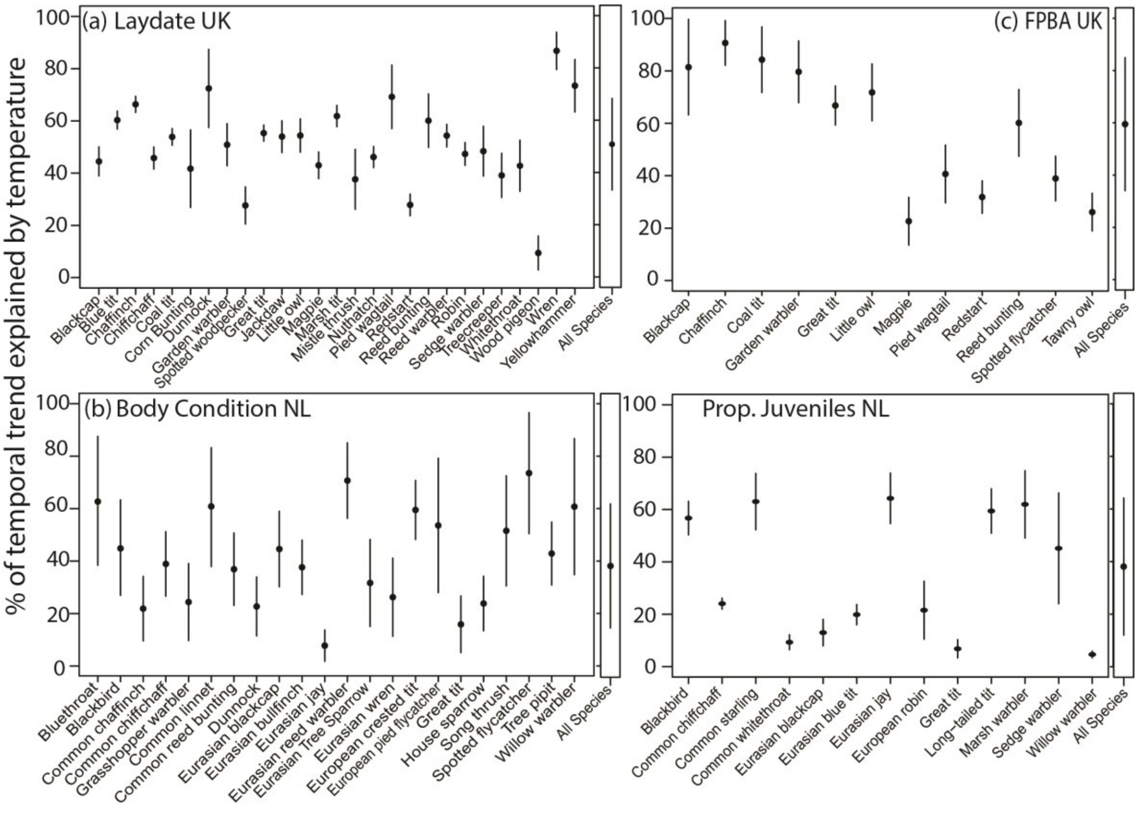

Figure 3 *Percentage of the trend over time that is due to temperature (± 95% confidence intervals) for each of the four response types across all species. The separate value for each response type listed as All Species is the average value across all species for that trait.* Interspecific variation

Interspecific variation

Comparing responses across species, the temperature and non-temperature pathway estimates were correlated. Species that showed stronger associations with temperature also showed stronger changes due to other effects (Fig 4a-d; Correlation coefficient for laying date = 0.64, for body condition = 0.13, for FPBA = 0.72 and for proportion of juveniles = -0.29). The correlation was negative for proportion of juveniles.

Species that were more sensitive to temperature or non-temperature effects had stronger total changes in traits (Fig 4e-h). For all traits, the non-temperature pathway better explained variation in the total change in trait over time among species (Fig 4e-h). Temporal changes in response types due to temperature were always more precisely estimated than those due to non-temperature effects (i.e. lower standard deviation; grey bars in Fig 4a-d). As such, although temperature explained on average about 50% of the total trend within a species (Fig 3), variation in the total temporal change (due to both temperature and non-temperature effects) among species appears to be mainly due to the varying effects of the non-temperature pathway.

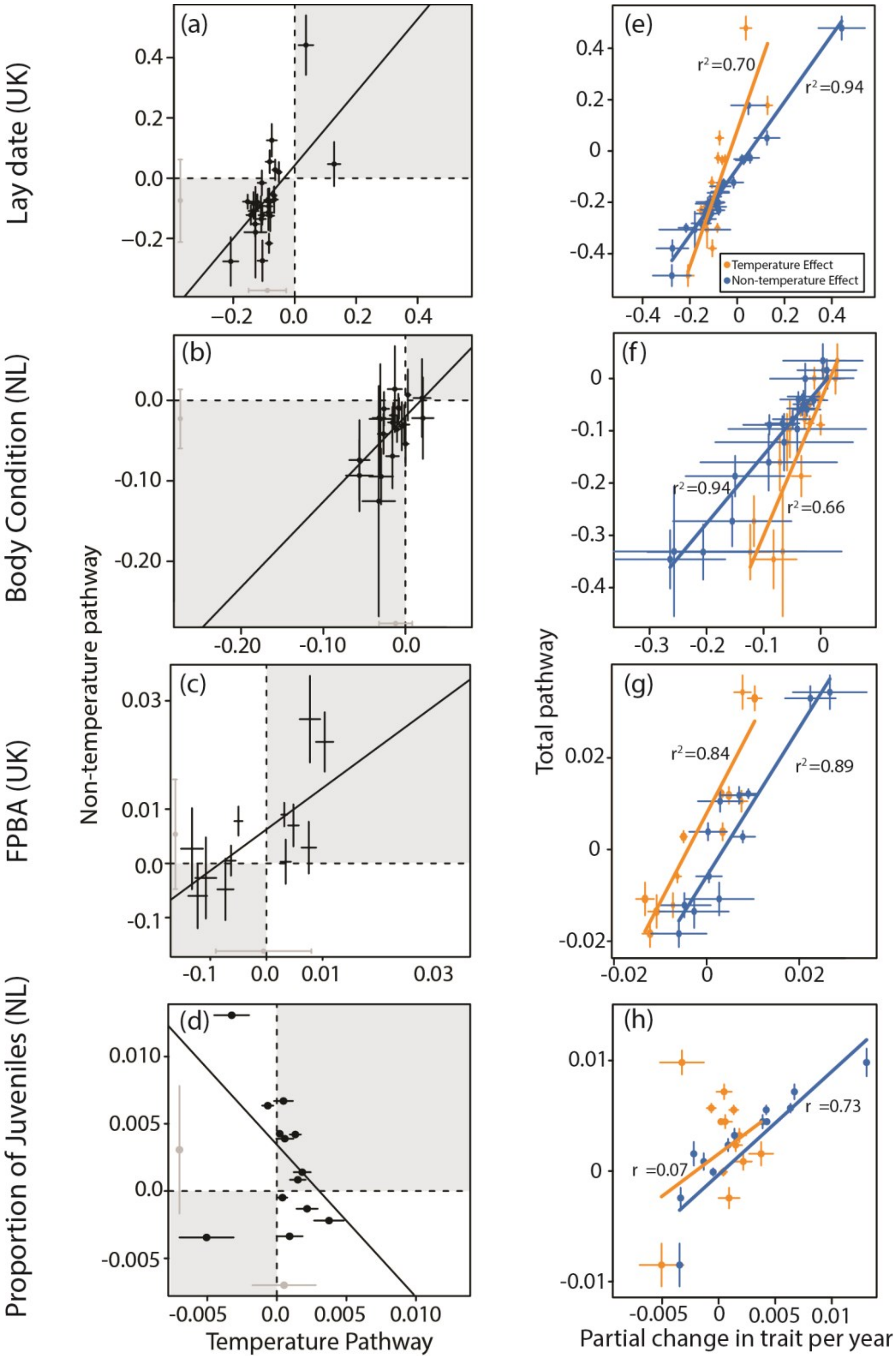

Figure 4 The left panel (a-d) shows the relationship between the temperature and the non-temperature pathway for all temperature-sensitive species, where each point represents a species and the error bars show the standard error. The solid black line shows the correlation between the two pathways. The dark shaded areas indicate when species are experiencing reinforced effects from temperature and non-

temperature effects (i.e. each pathway causes the trait to increase over time, or conversely both cause decreases over time). The unshaded areas indicate when species experience counteracting effects. The grey lines and points adjacent to the x-axis and y-axis show the mean effect across all species ± one standard deviation. The right panel (e-h) shows the relationships between the total change in trait over time (calculated as the temperature pathway summed with the non-temperature pathway) compared to the change over time due to temperature (orange; calculated as the year to temperature pathway multiplied with the temperature to trait pathway) and non-temperature (blue; i.e. the direct pathway between year and trait). Each point represents a species ± standard error. The x-axis is the estimate for the partial regression slope of trait over time accounting for either the temperature effect or the non-temperature effect. The plots (a and e) in the top row show values for laying date, the second row (b and f) for body condition, the third row (c and g) for FPBA and the bottom row (d and h) for the proportion of juveniles.

Intra-specific Variation

Considering just the NL data, for which we had observations on multiple sites per species, the percentage of the trend over time that was due to temperature differed substantially among populations when looking at responses in body condition (average standard deviation across all species was 11.3). However, there was very little intra-specific variation when looking at responses in the proportion of juveniles (standard deviation of only 2.2).

Discussion

The assumption that systematic variation in traits through time reflects responses to warming relies on three assumptions holding true: that the trait is sensitive to climate, that the climate experienced by the organism or system is changing over time and that other non-temperature causal agents are not changing over time. By using two long-term datasets from the United Kingdom and the Netherlands on multiple common bird species, we demonstrate that, even for four different types of trait responses, trait variation through time cannot be assumed to be solely due to warming. In both countries, temperature was warming over time. However, we show that non-temperature causal agents are important in explaining temporal trends, often reinforcing the effects of temperature. This suggests that non-temperature causal agents have an important contribution to trends over time.

Our results suggest that interpreting trends over time as being solely due to warming appears to be incorrect. Temporal trends were not predominantly due to temperature. In fact, not all species were found to have sensitivities to temperature, so any changes in traits over time in these species were not due to temperature at all. Less than 50% of species were sensitive to temperature for the three traits other than laying date. For those species that were sensitive to changes in temperature, only 40-50% of changes over time could be attributed to temperature. Even within one type of trait response, the percentage of changes over time due to warming temperatures varied extensively among species, and often even among populations within species. Parmesan & Yohe (2003) argue that, although competing explanations in the form of non-climatic causal agents (such as land-use change) could have impacts, it is unlikely that such factors would produce a consistent pattern of impact over space and time. Yet these results, and that of Crick & Sparks (1999) who found that only 37% of temporal trends could be statistically accounted for by changes in temperature and rainfall, suggest that trends over time can be quite strongly attributed to non-temperature effects.

Non-temperature causal agents make important contributions to trends over time. Variation in changes over time among species (i.e. the total pathway) were better explained by the effects of the other, non-temperature factors (non-temperature pathway) than temperature. Although species that were more sensitive to temperature also had larger changes over time, species' sensitivities to other factors varied considerably more, suggesting that overall temporal trends might not reflect thermal sensitivity, but instead depend more on what non-temperature conditions species are experiencing. Part of this high interspecific variability might be due to the non-temperature pathway being comprised of multiple different potential non-temperature parameters (such as habitat degradation or invasive species). Different parameters might be acting upon different species depending on their sensitivities. For example, both warmer temperatures and increased urbanisation might cause earlier egg laying in some species such as the magpie (Crick & Sparks, 1999) making the overall change over time stronger. However, in other species, urbanisation might have no effect on lay date whatsoever. Although changes in lay date over time due to temperature could be equal among species, the overall change over time would differ substantially. Given that the non-temperature pathway is potentially comprised of multiple variables while the temperature pathway was only one single parameter which explained about 50% of the temporal trends suggests that temperature is potentially one of the most important single factors influencing overall changes over time.

The idea of the world undergoing a 'deadly anthropogenic cocktail' of climate change and other effects such as habitat destruction is not new (Travis, 2003; Brook *et al.*, 2008; Mantyka-pringle *et al.*, 2012). Indeed, we identified two ways in which the combined effects of multiple stressors could result in stronger changes over time. Firstly, the effects of temperature and other non-temperature parameters reinforced overall effects on all four traits for the majority of species. This meant that the overall trend over time was frequently made more extreme by the combined climatic and non-climatic factors. Other studies looking at population dynamics and biodiversity have found similar results, where non-climatic and climatic effects increase the overall species declines (Mora *et al.*, 2007; Mantyka-pringle *et al.*, 2012). On the other hand, counteracted effects were not uncommon, where the total change over time was dampened or buffered by the opposing effects of temperature and other non-temperature parameters. Reinforcing effects are important to recognise because if changes over time are assumed to reflect the effects of warming, they would actually be overestimated, whereas for species that experience counteracting effects the importance of temperature would be underestimated.

Secondly, the combined effects of multiple stressors could result in stronger changes over time for some species than for others. Species that were more sensitive to temperature were also more sensitive to other non-temperature effects, suggesting that there may be some disturbance-sensitive taxa. This was the case for all four traits. If a species' tolerance to non-climatic disturbances is correlated with its tolerance to climatic impacts and this results in changes in population dynamics, it can influence the abundance of more and less tolerant species within a community (Côté & Darling, 2010). The synergy of threats is regarded as one of the most important challenges to biodiversity and in the construction of future projections on biodiversity change (Mora *et al.*, 2007; Brook *et al.*, 2008).

Our estimate of global warming is not representative of the full and total changes that organisms would be experiencing. Indeed, changes in mean temperature, the measure that we focus on we here, is only one aspect of the climate. We only look at a single period of temperature, where other periods could also be important. Other climate variables such as rainfall or humidity would likely also be important (van de Pol *et al.*, 2016), as well as other potential measures of temperature, such as temperature fluctuations (Briga *et al.*, 2015) or thresholds (e.g. days above 35°C; Gardner *et al.*, 2016). The choice of weather variables could have different impacts for different taxa, where other variables (e.g. precipitation, soil temperature, humidity) might be more appropriate for some species (Crick & Sparks, 1999). As such, our temperature measure as a proxy for changes in 'climate' is actually just a minimum estimate. By expanding the model to include other climatic changes, the non-temperature pathway effect would likely decrease. Similarly, our measure of other, non-temperature effects would likely be made up of many different factors which would be informative to identify and separate out. Although we did not investigate interacting effects between temperature and non-temperature effects, this would also be of interest as this is commonly thought to be important in the context of population effects (Mantyka-pringle *et al.*, 2012; Radinger *et al.*, 2016b).

Here, we made the decision to compare all temperature windows that were identified as the most important. This meant that we were sometimes comparing species with windows from the current year against species with windows from the previous year. Such different windows would likely be due to different underlying mechanisms. However, even with the particularly well-studied climate change response, laying date, the underlying mechanisms are still in question. Temperature could act as a cue for reproduction or work via changes in food availability (Phillimore *et al.*, 2016). This lack of knowledge on the underlying mechanisms makes it particularly difficult to hypothesise how such different lags from the important temperature window up until the trait occurrence might be working. Here, we were not primarily interested in the mechanisms, but instead focused on identifying correlations.

Implications

It is clear that the assumption that changes in common responses, such as phenology, body condition or reproduction, over time are due solely to the effects of warming temperatures is incorrect. Therefore, it is important that we understand the contributions of climatic and non-climatic effects to temporal trends (Both *et al.*, 2004; Wright *et al.*, 2009). Understanding more about the different causal agents behind changes in common responses is not only vital if we are to properly account for these differing effects in predictive statistical models (Grenouillet & Comte, 2014; Cunningham *et al.*, 2016), but also to develop appropriate and effective conservation strategies. For instance, if the effects of climate and other environmental changes are reinforced, stronger overall changes over time will need to be taken into account (Travis, 2003; Radinger *et al.*, 2016a). An important next step might be to tease apart exactly what is making up the non-temperature component of these trends. Decomposing changes over time due to other climate variables such as rain and humidity, but also specific non-climatic effects such as habitat quality, pollution or habitat fragmentation, would improve our understanding of exactly how these different effects contribute to temporal change substantially. Additionally, identifying species characteristics (such as migration strategy or other life-history characteristics) that might be able to predict which species are more or less strongly affected by climate or non-climatic effects would be invaluable for conservation management. If, for instance resident species are more strongly impacted by climate, then limited resources can be focused to those species at most risk. Finally, given that non-temperature factors can have strong contributions to trends over time, we caution whether studies should be considering trends over time to be due to global warming. Instead, we suggest that relating systematic variation in traits directly to climate is a more precise way to address such questions.

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Appendix 7

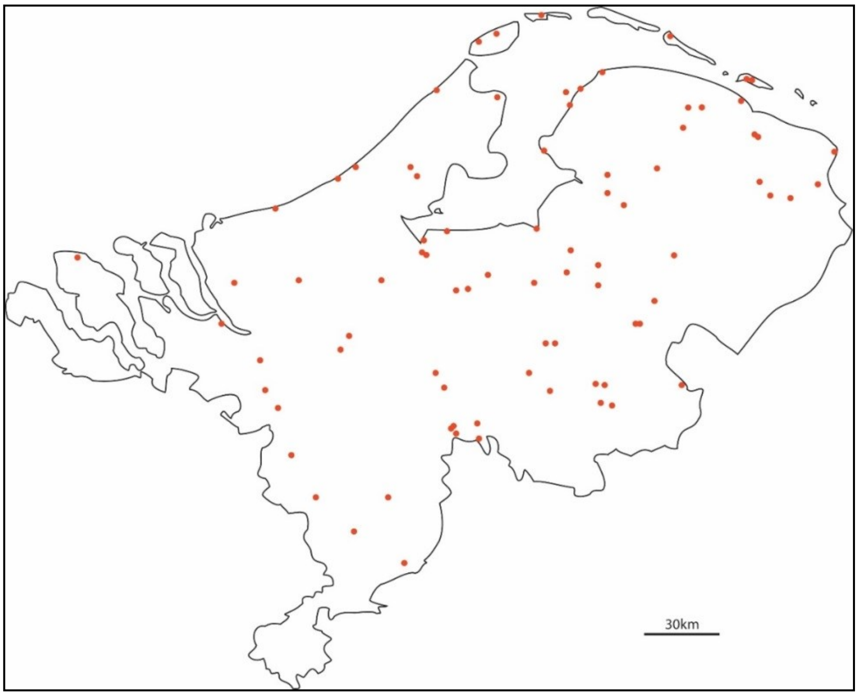

Figure S1 Map of the Netherlands with all study sites (indicated by the red dots).

Climatic data

Table S1 CES site and weather station coordinates and the distances between the two.

CES Site	Lat (CES)	Long (CES)	Weather Station	Lat (Stn)	Long (Stn)	Distance (km)
C01	52.61	5.90	273	52.70	5.89	10.1
C02	52.45	5.82	269	52.46	5.53	20.3
C03	52.34	4.52	240	52.30	4.77	17.7
C04	52.54	6.47	278	52.44	6.26	18
C05	53.21	5.44	270	53.23	5.76	21.2
C06	53.11	4.79	235	52.92	4.79	20.3
C07	53.20	6.80	280	53.13	6.59	16.8
C08	52.33	5.16	265	52.13	5.27	23.7
C09	52.91	5.83	273	52.70	5.89	23.9
C10	51.85	5.12	356	51.86	5.15	1.9
C11	52.61	5.64	269	52.46	5.53	18.2
C12	51.57	4.90	350	51.57	4.93	2.1

C13	53.04	5.40	267	52.90	5.38	15.8
C14	52.54	4.83	249	52.64	4.98	15.6
C15	53.26	4.95	251	53.39	5.35	30.9
C16	51.69	4.47	344	51.96	4.44	29.8
C17	52.23	6.61	283	52.07	6.65	17.3
C18	52.28	6.52	283	52.07	6.65	24.8
C19	52.29	6.09	278	52.44	6.26	20.5
C20	52.63	6.08	273	52.70	5.89	15.5
C21	52.42	5.23	269	52.46	5.53	20.4
C22	52.53	6.46	278	52.44	6.26	16.6
C23	51.83	5.93	375	51.66	5.71	24.5
C24	52.85	5.44	267	52.90	5.38	6.2
C25	51.84	5.96	275	52.06	5.89	25.1
C26	52.44	6.88	290	52.27	6.90	18.5
C27	51.34	5.79	377	51.20	5.76	16.1
C28	52.42	4.56	240	52.30	4.77	19.7
C29	51.44	5.24	370	51.45	5.41	12.4
C30	51.84	4.39	344	51.96	4.44	13.4
C31	52.14	4.33	210	52.17	4.42	6.8
C32	52.31	5.21	265	52.13	5.27	20.5
C33	53.33	6.42	277	53.41	6.20	16.9
C34	53.07	5.33	267	52.90	5.38	19.4
C35	52.86	6.00	273	52.70	5.89	19.1
C36	52.31	6.13	278	52.44	6.26	16.9
C37	51.57	3.57	310	51.44	3.60	14.2
C38	52.27	6.47	278	52.44	6.26	23.7
C39	53.04	4.74	235	52.92	4.79	13.2
C40	51.65	4.77	350	51.57	4.93	14.7
C41	53.33	6.43	277	53.41	6.20	17.8
C42	52.81	6.42	279	52.75	6.58	12.6
C43	52.91	5.03	235	52.92	4.79	16.3
C44	52.86	5.88	273	52.70	5.89	17.5
C45	53.31	6.05	277	53.41	6.20	14.7
C46	53.46	5.66	251	53.39	5.35	21.8
C47	53.21	6.03	270	53.23	5.76	18.8
C48	51.90	5.12	356	51.86	5.15	4.9
C49	52.54	5.95	273	52.70	5.89	18.7
C50	52.57	6.15	278	52.44	6.26	16.9
C51	51.35	6.13	391	51.50	6.20	17.4
C52	51.36	5.49	370	51.45	5.41	11.2
C53	52.14	5.09	260	52.10	5.18	7.6
C54	53.20	6.59	280	53.13	6.59	8
C55	52.27	5.48	265	52.13	5.27	20.9
C56	51.97	4.69	348	51.97	4.93	16.4
C57	53.44	6.87	286	53.20	7.15	32.6
C58	53.41	6.22	277	53.41	6.20	1.9

C59	52.22	6.55	283	52.07	6.65	17.5
C60	51.51	5.84	375	51.66	5.71	18.8
C61	52.33	5.16	265	52.13	5.27	23.7
C62	53.48	6.16	277	53.41	6.20	8.3
C63	51.91	6.03	275	52.06	5.89	20
C64	51.87	6.08	275	52.06	5.89	25
C65	51.96	5.74	275	52.06	5.89	15.4
C66	52.52	4.91	249	52.64	4.98	14.8
C67	52.53	6.15	278	52.44	6.26	12.7
C69	52.42	5.23	269	52.46	5.53	20.3
C70	52.29	5.53	269	52.46	5.53	18.3
C71	53.28	6.00	270	53.23	5.76	17.4
C72	51.82	5.94	375	51.66	5.71	24.2
C73	53.17	6.70	280	53.13	6.59	9
C74	52.37	5.58	269	52.46	5.53	10.4
C75	52.81	4.69	235	52.92	4.79	14.3
C76	53.04	6.04	270	53.23	5.76	28.6
C77	53.31	6.89	286	53.20	7.15	21.5
C78	52.57	6.14	278	52.44	6.26	16.8
C79	52.16	6.26	275	52.06	5.89	27.6
C81	51.55	5.03	350	51.57	4.93	7
C82	53.48	6.18	277	53.41	6.20	8.4
C83	52.63	6.47	279	52.75	6.58	14.7
C84	53.44	6.87	286	53.20	7.15	32.6
C85	52.31	5.20	265	52.13	5.27	20.6
C86	52.17	6.10	275	52.06	5.89	18.9
C87	51.98	5.66	275	52.06	5.89	18.2
C88	53.10	5.39	267	52.90	5.38	22.7

Check Assumptions of the Structural Equation Model

Normal distribution of residuals

Most species had clear normal distributions, while a few had outlier sections. However, these small increased densities of residuals in the outer regions of the normal distribution curve were not overly large and we decided to accept these models as fitting appropriately.

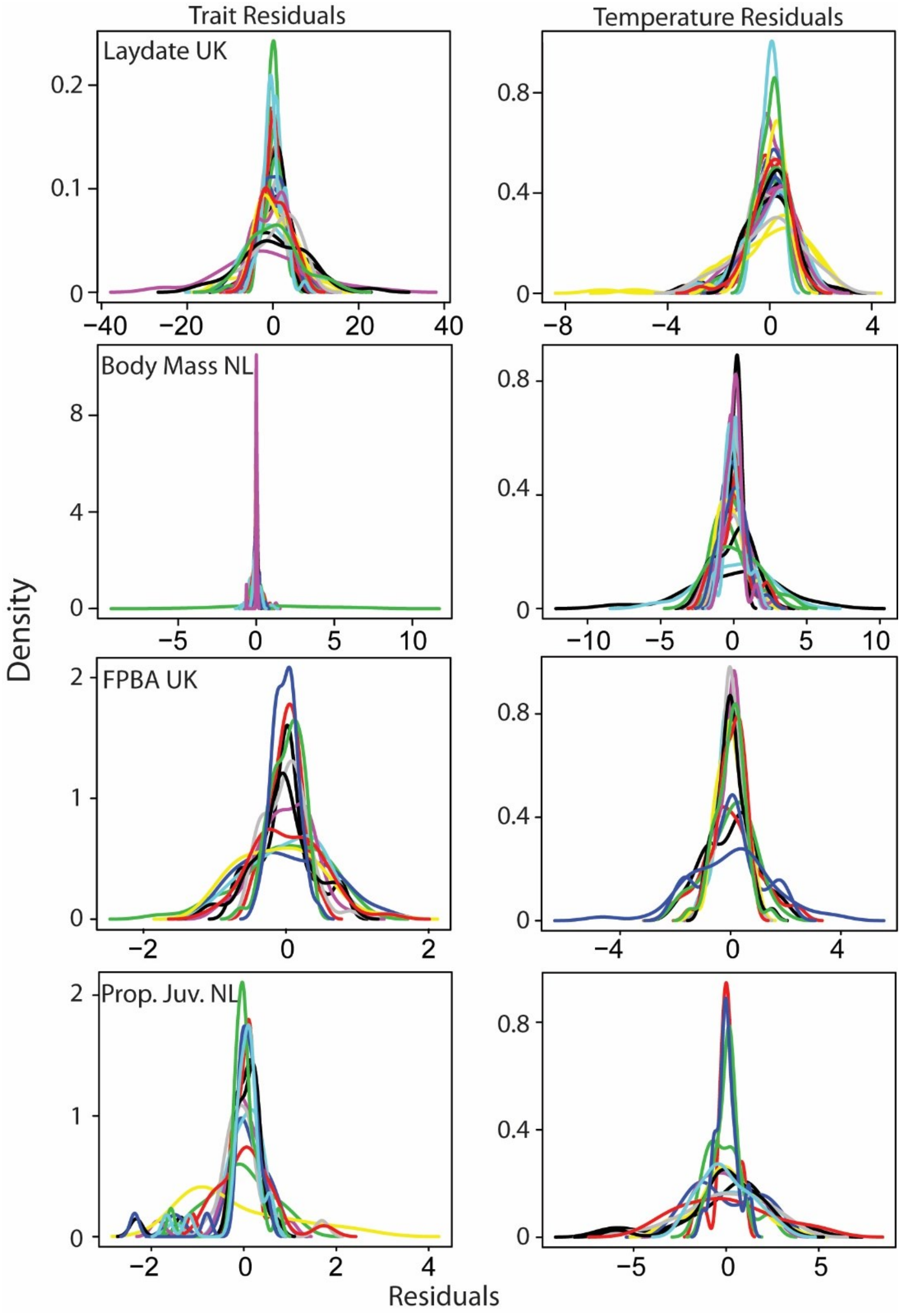

Figure S2 Distribution of residuals of traits (left column) and temperatures (right column), where each line is a different species.

Estimates and standard error

The plots below show all of the path estimates and their standard errors calculated in the SEMs for each species.

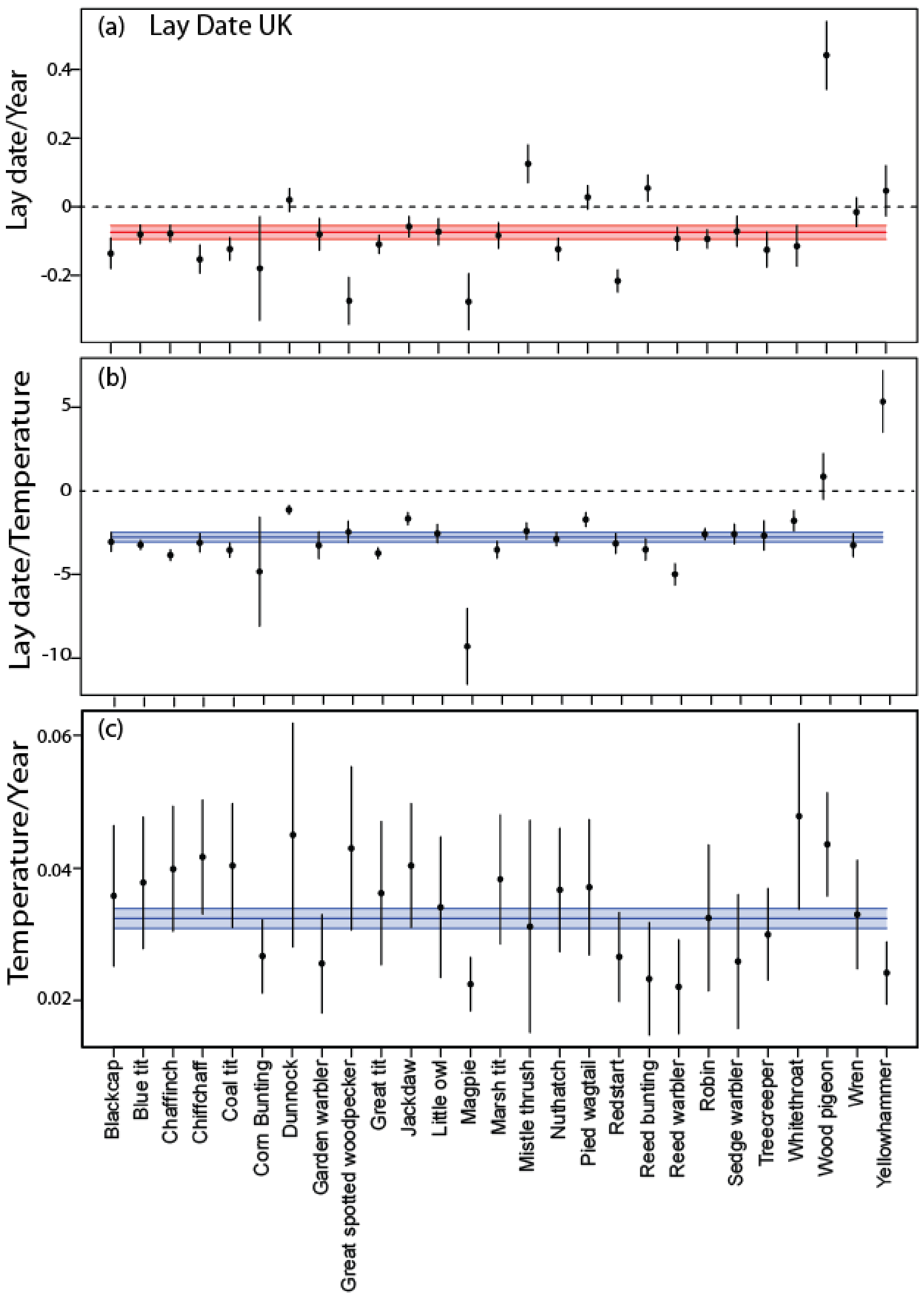

Figure S3 Pathway estimates for laying date (UK). (a) is the direct year to trait pathway (i.e. the non-temperature pathway) and the slopes show the change in lay date per year. (b) is the temperature to trait pathway (changes in lay date per degree Celsius) and (c) is the year to temperature pathway (change in temperature per year) that are multiplied to calculate the temperature pathway. The solid horizontal line shows the overall path estimate across all species ± standard error.

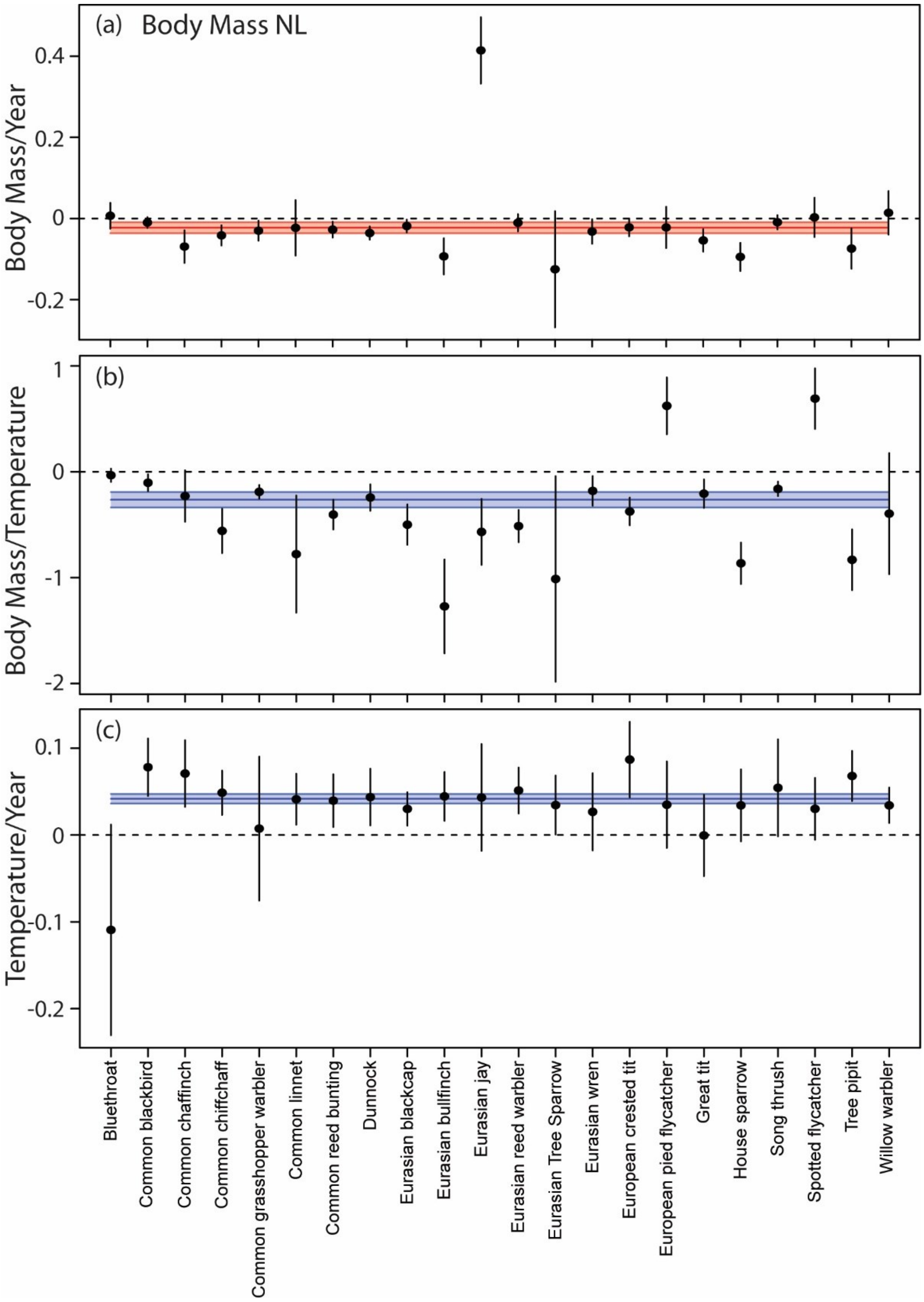

Figure S4 Pathway estimates for Body Mass. (a) is the direct year to trait pathway (i.e. the non-temperature pathway) and the slopes show the change in % body mass per year. (b) is the temperature to trait pathway (changes in body mass per degree Celsius) and (c) is the year to temperature pathway (change in temperature per year) that are multiplied to calculate the temperature pathway. The solid horizontal line shows the overall path estimate across all species ± standard error.

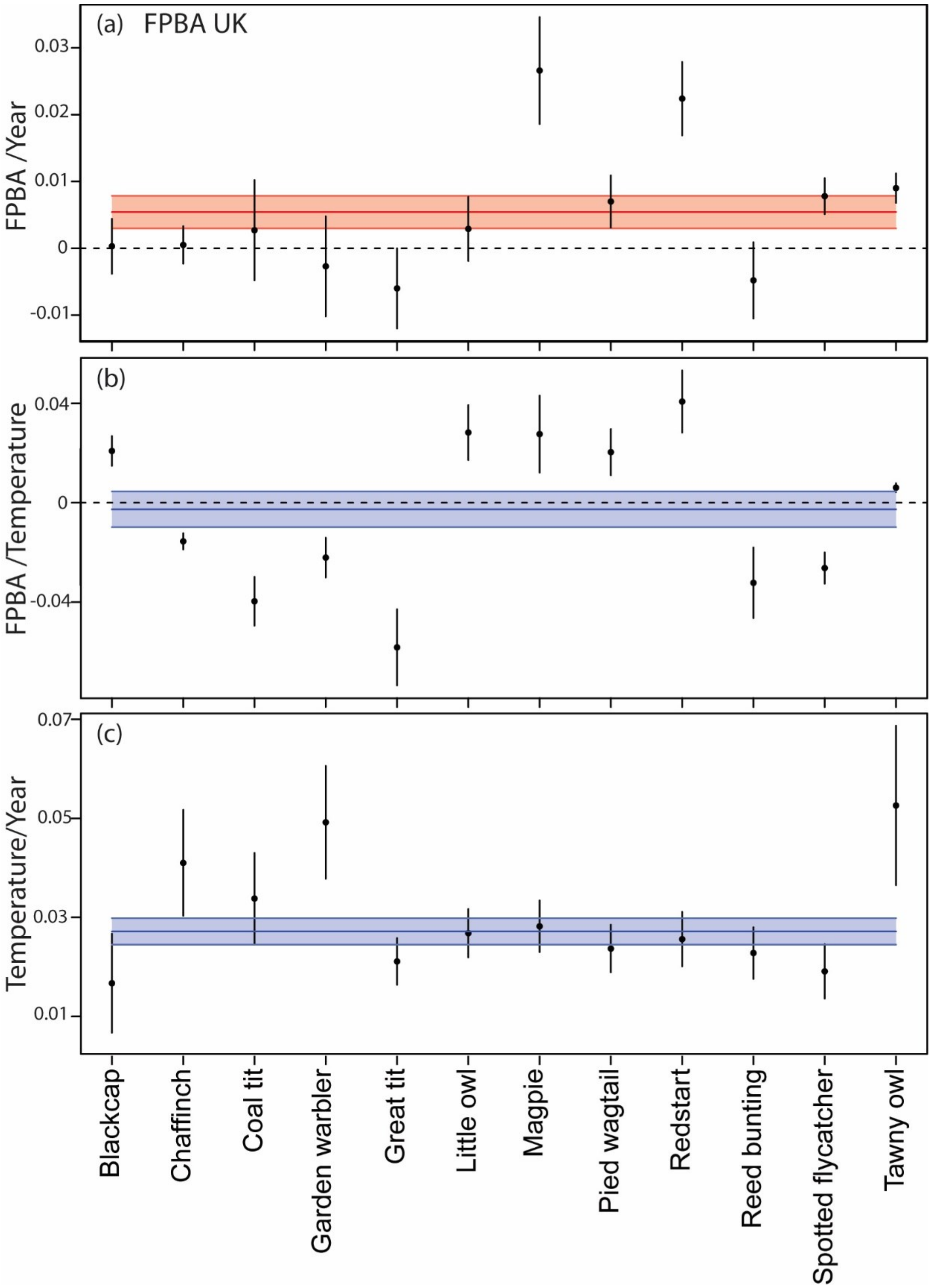

Figure S5 Pathway estimates for FPBA (fledglings produced per breeding attempt; UK). (a) is the direct year to trait pathway (i.e. the non-temperature pathway) and the slopes show the change in fledglings per year. (b) is the temperature to trait pathway (changes in fledglings per degree Celsius) and (c) is the year to temperature pathway (change in temperature per year) that are multiplied to calculate the temperature pathway. The solid horizontal line shows the overall path estimate across all species ± standard error.

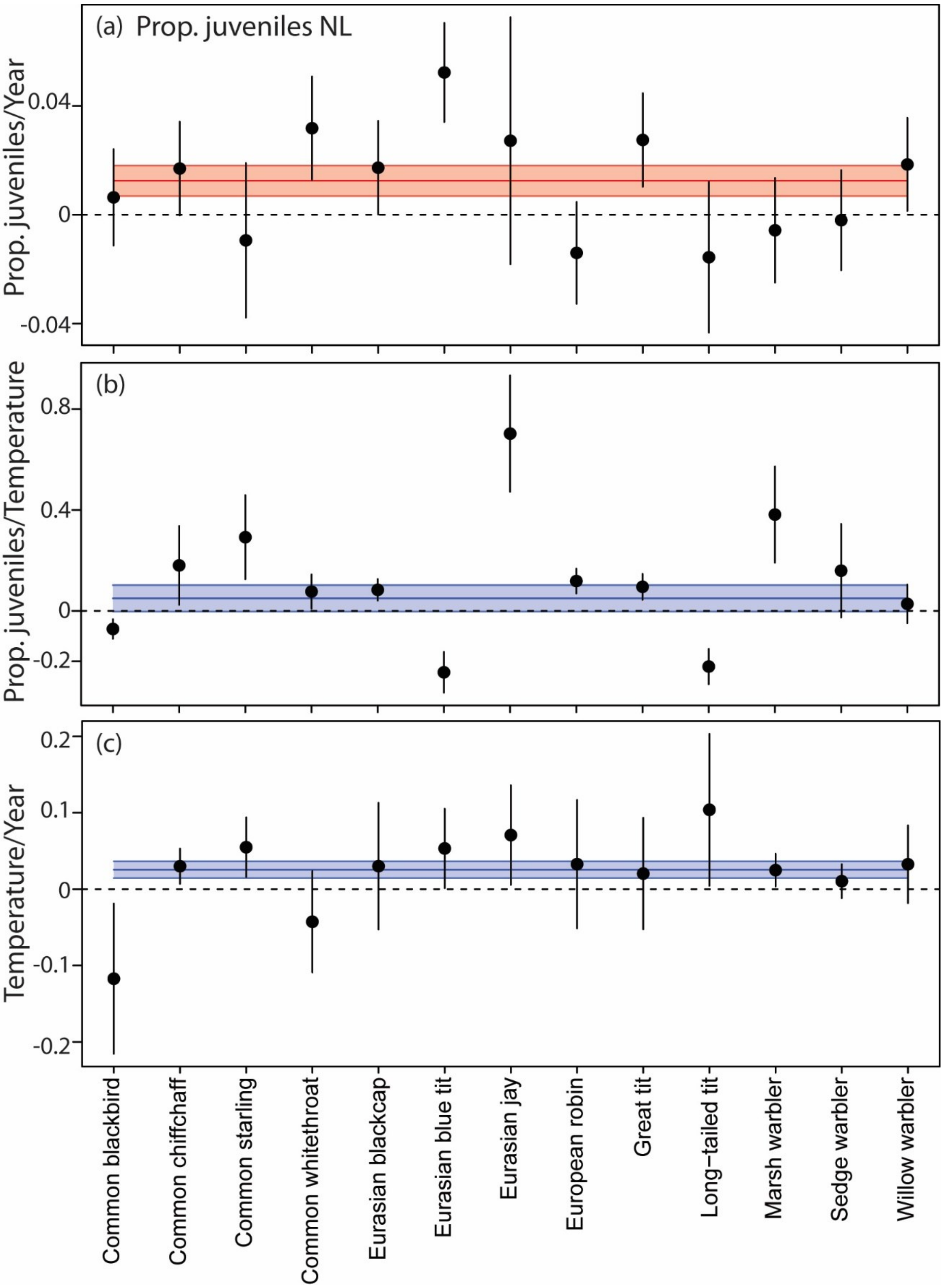

Figure S6 Pathway estimates for the proportion of juveniles (NL). (a) is the direct year to trait pathway (i.e. the non-temperature pathway) and the slopes show the change in proportion of juveniles per year. (b) is the temperature to trait pathway (changes in proportion per degree Celsius) and (c) is the year to temperature pathway (change in temperature per year) that are multiplied to calculate the temperature pathway. The solid horizontal line shows the overall path estimate across all species ± standard error.

Distribution of random intercept and slope terms

We were unable to plot all species on the same figure as the axes varied among species such that most species density curves could not be seen. Due to the high number of species and intercept and slope terms we have not published the figures here. All species appeared to be mostly normally distributed, with no species standing out as not meeting this assumption.

Temperature Windows

Table S2 Species from the United Kingdom where laying date or FPBA are either sensitive or insensitive to temperature and the p-value from the *climwin* analysis. Here, p-values less than 0.5 are considered to be real, and thus those species are considered sensitive to temperature.

	Species	Laying date p-value	Laying date Window	FPBA p-value	FPBA Window
1	Blackbird	0.723067	Insensitive	0.924515	Insensitive
2	Blackcap	8.38E-06	Sensitive	0.039492	Sensitive
3	Blue tit	4.01E-05	Sensitive	0.65349	Insensitive
4	Bullfinch	0.92441	Insensitive	0.843804	Insensitive
5	Chaffinch	6.56E-06	Sensitive	0.001587	Sensitive
6	Chiffchaff	6.77E-06	Sensitive	0.624452	Insensitive
7	Coal tit	6.62E-06	Sensitive	0.002334	Sensitive
8	Collared dove	0.768718	Insensitive	0.992527	Insensitive
9	Corn Bunting	0.000172	Sensitive	0.860345	Insensitive
10	Dunnock	0.005261	Sensitive	0.975413	Insensitive
11	Garden warbler	9.42E-06	Sensitive	0.389847	Sensitive
12	Great spotted woodpecker	0.162519	Sensitive	0.989374	Insensitive
13	Great tit	1.44E-05	Sensitive	0.003986	Sensitive
14	Jackdaw	1.08E-05	Sensitive	0.829469	Insensitive
15	Little owl	7.66E-06	Sensitive	0.318695	Sensitive
16	Magpie	3.84E-05	Sensitive	0.041115	Sensitive
17	Marsh tit	6.73E-06	Sensitive	0.721564	Insensitive
18	Mistle thrush	0.000727	Sensitive	0.746145	Insensitive
19	Nuthatch	6.90E-06	Sensitive	0.819935	Insensitive
20	Pied wagtail	0.009844	Sensitive	0.042802	Sensitive
21	Redstart	9.21E-06	Sensitive	6.86E-06	Sensitive
22	Reed bunting	9.52E-06	Sensitive	0.489953	Sensitive
23	Reed warbler	1.30E-05	Sensitive	0.979256	Insensitive
24	Robin	7.66E-06	Sensitive	0.615268	Insensitive
25	Sedge warbler	0.000378	Sensitive	0.965738	Insensitive
26	Song thrush	0.682729	Insensitive	0.927407	Insensitive
27	Spotted flycatcher	0.919559	Insensitive	0.420912	Sensitive
28	Tawny owl	0.93247	Insensitive	0.016499	Sensitive
29	Treecreeper	1.67E-05	Sensitive	0.86677	Insensitive
30	Turtle dove	0.967052	Insensitive	0.953662	Insensitive

31	Whitethroat	0.001433	Sensitive	0.967667	Insensitive
32	Wood pigeon	0.025219	Sensitive	0.960302	Insensitive
33	Wren	1.40E-05	Sensitive	0.944545	Insensitive
34	Yellow wagtail	0.906465	Insensitive	0.92501	Insensitive
35	Yellowhammer	0.007466	Sensitive	0.967573	Insensitive

Table S3 Species from the Netherlands where body mass or the proportion of juveniles (Prop. Juv.) are either sensitive or insensitive to temperature and the p-value from the *climwin* analysis. Here, p-values less than 0.5 are considered to be real, and thus those species are considered sensitive to temperature.

	Species	**Mass p-value**	**Mass Window**	**Prop. Juv. p-value**	**Prop. Juv. Window**
1	Bearded reedling	0.974274	Insensitive	0.992021	Insensitive
2	Bluethroat	0.033642	Sensitive	0.95378	Insensitive
3	Common blackbird	0.000103	Sensitive	0.027648	Sensitive
4	Common chaffinch	0.036375	Sensitive	0.951273	Insensitive
5	Common chiffchaff	4.27E-05	Sensitive	1.11E-05	Sensitive
6	Common grasshopper warbler	0.007161	Sensitive	0.525908	Insensitive
7	Common Kingfisher	0.964986	Insensitive	0.972807	Insensitive
8	Common linnet	0.009873	Sensitive	0.573736	Insensitive
9	Common nightingale	0.9732	Insensitive	0.925036	Insensitive
10	Common redstart	0.650429	Insensitive	0.970452	Insensitive
11	Common reed bunting	0.07584	Sensitive	0.968133	Insensitive
12	Common starling	0.958907	Insensitive	0.000107	Sensitive
13	Common whitethroat	0.633896	Insensitive	0.108371	Sensitive
14	Dunnock	0.216536	Sensitive	0.950149	Insensitive
15	Eurasian blackcap	0.107361	Sensitive	0.000282	Sensitive
16	Eurasian blue tit	0.772692	Insensitive	2.25E-05	Sensitive
17	Eurasian bullfinch	0.000115	Sensitive	0.93104	Insensitive
18	Eurasian jay	0.01813	Sensitive	0.000168	Sensitive
19	Eurasian nuthatch	0.923356	Insensitive	0.941814	Insensitive
20	Eurasian reed warbler	0.400956	Sensitive	0.939811	Insensitive
21	Eurasian Tree Sparrow	0.062817	Sensitive	0.951963	Insensitive
22	Eurasian wren	0.165995	Sensitive	0.972886	Insensitive
23	European crested tit	0.010937	Sensitive	0.974085	Insensitive
24	European goldfinch	0.972886	Insensitive	0.903129	Insensitive
25	European greenfinch	0.957159	Insensitive	0.926376	Insensitive
26	European pied flycatcher	0.290141	Sensitive	8.58E-05	Sensitive
27	European robin	0.940149	Insensitive	0.968638	Insensitive
28	European stonechat	0.719451	Insensitive	0.705012	Insensitive
29	Garden warbler	0.960244	Insensitive	0.934142	Insensitive
30	Goldcrest	0.949	Insensitive	0.902998	Insensitive
31	Great spotted woodpecker	0.969845	Insensitive	1.18E-05	Sensitive
32	Great tit	0.002687	Sensitive	0.990604	Insensitive

33	House sparrow	0.010446	Sensitive	0.753179	Insensitive
34	Icterine warbler	0.950854	Insensitive	0.877465	Insensitive
35	Lesser whitethroat	0.83758	Insensitive	0.000569	Sensitive
36	Long-tailed tit	0.966956	Insensitive	0.961262	Insensitive
37	Marsh tit	0.971174	Insensitive	0.004392	Sensitive
38	Marsh warbler	0.635981	Insensitive	0.967954	Insensitive
39	Savi's warbler	0.924619	Insensitive	0.949145	Insensitive
40	Sedge warbler	0.801783	Insensitive	0.21679	Sensitive
41	Short-toed treecreeper	0.954955	Insensitive	0.958312	Insensitive
42	Song thrush	0.158258	Sensitive	0.830104	Insensitive
43	Spotted flycatcher	0.490702	Sensitive	0.89298	Insensitive
44	Tree pipit	0.044876	Sensitive	0.91023	Insensitive
45	White wagtail	0.974085	Insensitive	0.992358	Insensitive
46	Willow tit	0.7075	Insensitive	0.955596	Insensitive
47	Willow warbler	0.006405	Sensitive	0.349019	Sensitive

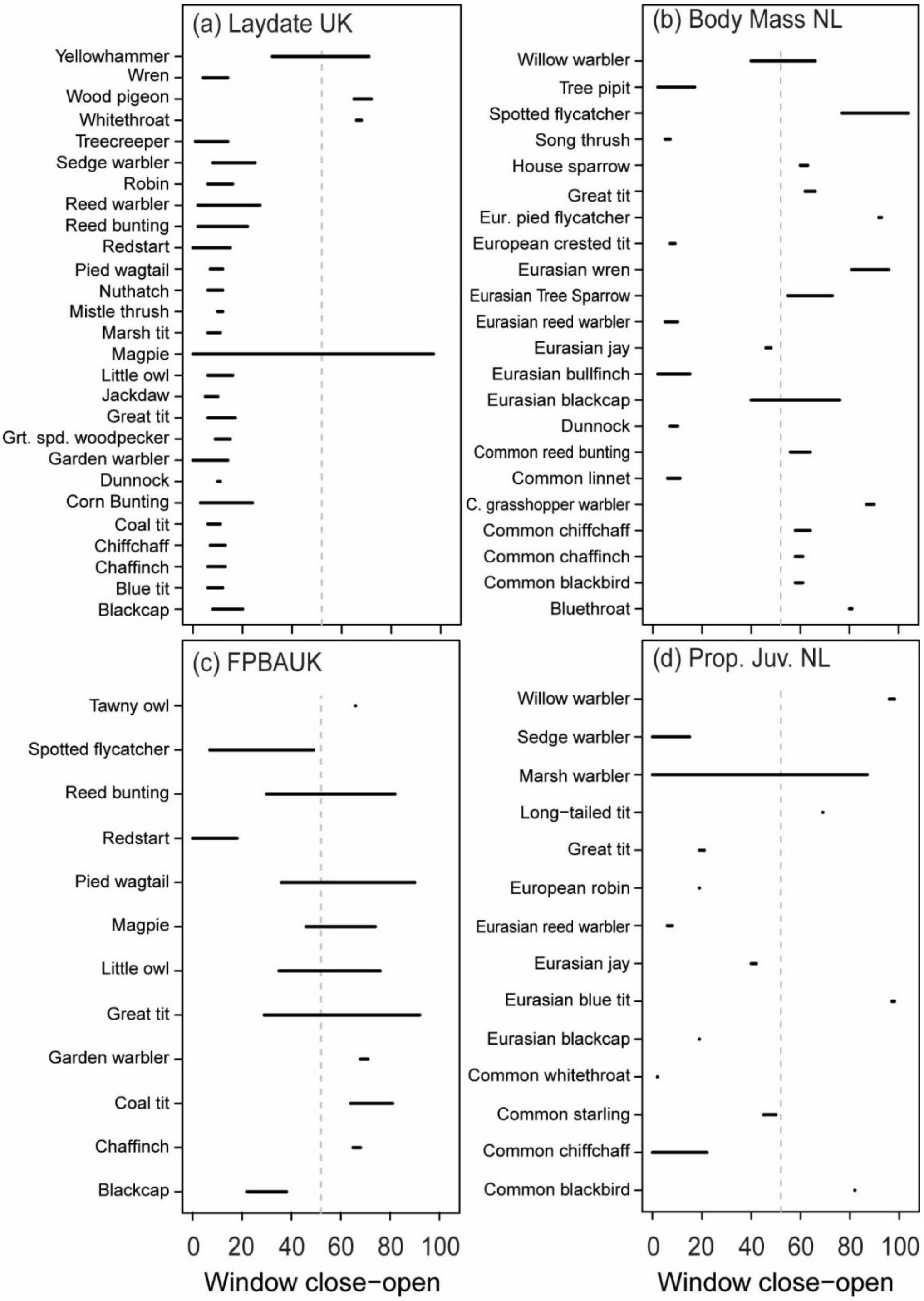

Figure S7 Temperature windows for laying date (a), body mass (b), fledglings per breeding mass (FPBA; c) and the proportion of juveniles (d) of bird species in the United Kingdom (UK) and the Netherlands (NL). For laying date, the 0 date differs among species, where it is 30 days after the maximum mean laying date for all years (early July on average across species). For FPBA, date 0 is the 1st July as this is around the end of the sampling season. For body mass and the proportion of juveniles, the date 0 is the 15th August as sampling took place from 12 April - 14 August each year. Some species names have been shortened, where *C.* stands for common, *Grt. spd.* stands for Great spotted, and *Eur.* stands for European.

Synthesis

The climate is changing at a rapid rate, which is already having observable effects on animals and plants around the world (Parmesan & Yohe, 2003; IPCC, 2013). As the climate continues to change in the future, the risk of extinctions is predicted to drastically rise, with one in six species likely to be committed to extinction (Thomas *et al.*, 2004; Urban, 2015). Consequently, it is important that we not only understand how changes in climate are affecting organisms, but also are able to make reliable predictions of which species, populations or communities are most at risk. Yet, the ability to make broad generalisations about climate impacts and identify those populations most at risk requires large scale comparative analyses based on correct assumptions. This thesis takes some steps towards addressing our knowledge gaps, focusing on how common European bird species are responding to changes in the climate, and identifying which species or populations are most at risk. I investigated the validity of several common assumptions that are frequently made throughout the climate change literature.

It is now becoming clear that changes in traits such as phenology and physiology do not always result in population level changes (Reed *et al.*, 2013; Dunn & Møller, 2014; Stopher *et al.*, 2014). For common passerine species in the Netherlands and the UK, I found that changes in laying dates or body condition did not influence population dynamics, and thus there was no change to species' extinction risks resulting from changes in climate (Chapters 1 & 3). Although understanding the effects of climate on traits is of interest for determining the underlying mechanisms of climate change, trait sensitivities will not always reflect species' sensitivities to population-level impacts. Consequently, trait sensitivities to climate may be of little use as indicators for population changes. Given that natural resource managers and policy makers are mainly interested in how climate change will affect population size and persistence (Miller-Rushing et al. 2010), one main challenge will now be to understand which traits are more likely to result in population-level effects, and which species or populations are most at risk.

Although trait changes do not appear to be impacting population-level responses currently, as the climate continues to change and reach new extremes outside of the historical data, it is uncertain whether trait changes might become more important in the future (Petchey *et al.*, 2015). Atmospheric temperatures are expected to rise by 0.3°C – 0.7°C from 2016-2035 and will likely exceed 1.5°C by 2100, while changes in precipitation will not be uniform but higher latitudes are likely to experience increased precipitation (IPCC, 2014). As temperatures continue to warm, there will likely be a threshold or tipping point where the effects that are currently observed change (Gardner *et al.*, 2014). For instance, I found that laying earlier currently improves reproductive success, but there will likely be a point at which laying any earlier will be detrimental (Chapter 1). As a result, predictions that are extrapolated beyond current conditions from correlative models will not be as reliable (Buckley *et al.*, 2010), and our ability to understand such responses in the distant future, or under novel conditions, is limited (Petchey *et al.*, 2015). Given that trait responses are often non-linear, responses could potentially change substantially as conditions continue to change (Chapter 2). Our decomposition approach estimates full and partial derivatives which reflect the effect sizes of traits, demographic rates or population growth rates on each other (e.g. how much reproductive success changes per lay date), and to climate (e.g. how much egg-laying date changes per degree Celsius). We assume that changes in the climate, traits and demographic rates are relatively small, such that we can characterize the relationships between these variables as being roughly linear around the mean current climatic conditions(Chapter 1). Consequently, the trends described in this thesis are likely to be accurate for the near future, but will likely shift as the climate continues to warm.

Empirical studies in the climate ecology literature often fail to consider variability in responses among populations of the same species, and thus assume that one population is representative of a species response (Rubolini *et al.*, 2007; Malyshev *et al.*, 2016; Thackeray *et al.*, 2016). Yet, populations can differ in their genetic structures (Phillimore *et al.*, 2010; Somero, 2010; Acker *et al.*, 2014; Abbott *et al.*, 2017), life history traits (Moran *et al.*, 2015), predation rates, parasites and presence of refuges (Aubry *et al.*, 2013; Schindler *et al.*, 2015), all of which could influence how changes in climate affect different populations. Indeed, not only did populations within species frequently differ in their responses to climate (Chapter 2), and to changes in population growth from reproduction (Chapter 3), but the contributions of non-temperature effects to trends over time also differed among sites (Chapter 4). Populations within species often varied in their responses to climate variables to such an extent that populations of the same species were often no more alike than populations of different species (Chapter 2). In such cases, a single species response value will not be meaningful (Stevens *et al.*, 2010; Malyshev *et al.*, 2016).

The ability to make generalisations about which species are more at risk from global changes based on species or population characteristics is vital for our future conservation efforts (Buckley & Kingsolver, 2012; Jenouvrier, 2013). Life history or habitat characteristics that can predict differential climate change responses are of particular importance for species about which we have limited knowledge (especially given that most species are data deficient). Such characteristics will help to determine where to prioritize conservation efforts (Sæther et al. 1996). We found that under warmer temperatures the population growth rate increased for species that have multiple broods over a season, while single-brooders showed declines (Chapter 1). Apart from this species characteristic, we were unable to identify any clear 'types' of species that were more at risk (e.g. larger, long-lived species). However, given that intra-specific variation was often high, this was perhaps not surprising. If a species does not respond consistently across populations, it suggests that other, more local factors are of more importance and that site-specific traits (e.g. habitat type) are likely having a stronger influence on population sensitivities (Moran *et al.*, 2015). Indeed, we found that populations in dry habitats had much stronger decreases in body condition with warmer temperatures and increased body condition with increased rainfall (Chapter 2).

By decomposing population responses into relationships among different underlying pathways, we can better understand the mechanisms that drive population decline (Nichols & Hines, 2002; Ådahl *et al.*, 2006; McLean *et al.*, 2016). For instance, the main effects of temperature on the population growth rate were not driven by changes in body condition, but instead by reproductive success and other unknown traits (Chapter 3). However, the phenomenological (or associative) approach taken here means that, although we know that there are important relationships between hierarchical levels (e.g. warmer temperature is associated with decreased body condition), we do not yet understand how or why these effects occur (e.g. how changes in temperature affect body condition). Because of this, extrapolating the trends and life-history and site characteristics identified here as important to other taxa or geographical regions could be problematic (Buckley *et al.*, 2010). Associative trends can often predict responses just as well, if not better, than detailed mechanistic models because they do not rely on accurate understanding of the underlying relationships that often differ among species (Buckley *et al.*, 2010; Peterson *et al.*, 2015). However, extrapolation to other situations will only work if, (1) the explanatory variables correspond to the underlying process that is resulting in change (i.e. temperature is the direct cause of changes in body condition or is a good proxy for the causal mechanism, perhaps changes in food), and (2) other environmental effects do not influence the relationship or the reliability of the proxy, and thus the magnitude and direction of the relationship does not depend on whether they are present or absent in other situations (e.g. the effect of reproduction on population growth changed depending on site-and species-specific differences in Chapter 3) (Buckley *et al.*, 2010; van de Pol *et al.*, 2016). Consequently, our approach generated many hypotheses about how passerine species are responding to climate, and the characteristics that make species or populations more sensitive, but these hypotheses now need to be tested on new species and geographic locations.

Although our knowledge of the impacts of climate on organisms grows every day, there are many assumptions made throughout the literature that are rarely tested. For instance, changes in traits over time are commonly assumed to be due to changes in the climate. Yet, we found that non-temperature effects contributed about 50% to temporal trends. Furthermore, body condition responses to a range of climate variables were typically non-linear, and many climate variables can also be important for trait responses (Chapter 2). We therefore suggest that many of the common assumptions made when studying climate change responses need to be investigated or at least acknowledged.

This thesis has expanded our knowledge and understanding of how climate change is impacting organisms. It highlights the importance of understanding the consequences of trait changes and the contributions of different non-climatic factors to changes over time in order to get a more holistic understanding of the impacts of climate change. Indeed, responses to climate are complex, often not only varying among species, but also among populations within species. This body of work will lay the foundations for broader, more holistic future climate change research that encompasses relationships among multiple types of responses, across species and populations within species. Such knowledge will be absolutely vital for future conservation efforts.

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