IDEA AND PERSPECTIVE

Predicting when climate-driven phenotypic change affects population dynamics

Nina McLean,[1]* Callum R. Lawson,[2] Dave I. Leech[3] and Martijn van de Pol[1,2]

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 that 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-parameterized 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 to predict the types of species in which climate sensitivities of phenotypic traits have strong demographic and population consequences, which is crucial for conservation prioritization of data-deficient species.

Keywords

Birds, climate change, comparative, demographic rates, functional traits, phenology, population dynamics, species responses, trait.

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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 right 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. Wilson & Arcese 2003; Chase *et al*. 2005; Pearce-Higgins *et al*. 2009; Wright *et al*. 2009; Ozgul *et al*. 2010; Plard *et al*. 2014). 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 (Miller-Rushing *et al*. 2010;

[1]*Division of Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Daley Road, Canberra, ACT 0200, Australia*

[2]*Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB, Wageningen, The Netherlands*

[3]*British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK*

*Correspondence: E-mail: nina.mclean@anu.edu.au

Reed *et al.* 2013a; Dunn & Møller 2014; 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 (Sæther & Bakke 2000; Jenouvrier *et al.* 2009; Sandvik *et al.* 2012). Such information is potentially of great value to biodiversity conservation because practitioners could use species characteristics to prioritize conservation efforts towards those most likely to be at risk of climate change. Being able to generalize 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; Morrison & Hik 2007; Jongejans *et al.* 2010). Using this conceptual framework, we identify four mechanisms that could prevent changes in traits and demographic rates from affecting population dynamics. We then synthesize 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?" (Wilson & Arcese 2003; Reed *et al.* 2013a; Dunn & Møller 2014). 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 of the factors and pathways affecting population dynamics or the need to construct population matrix models.

HIERARCHICAL FRAMEWORK

The many types of responses to changes in climate mentioned in the Introduction can be categorized 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 (Nichols & Hines 2002; Ådahl *et al.* 2006; Morrison & Hik 2007; Jongejans *et al.* 2010). 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).

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 eqn 1; Fig. 2ai, iii), three processes need to occur: (1) a change in climate (C_1) must impact the trait (T_1), (2) the change in trait must impact the demographic rate (D_1) and (3) 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).

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. First, 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
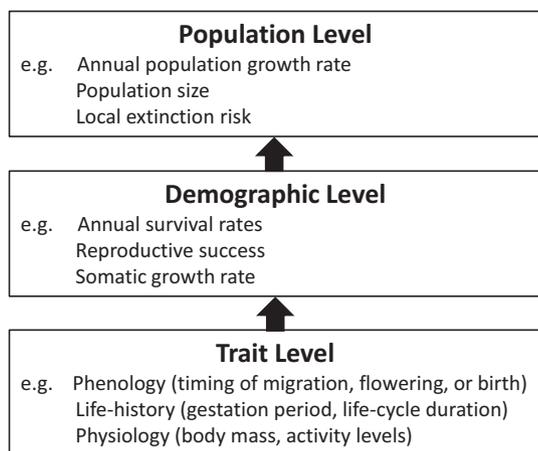

Figure 1 Hierarchical levels of responses to climate change. Changes at the trait-level can impact demographic rates, which can subsequently impact population dynamical parameters.

Box 1 Quantifying pathways from data, limitations and alternative approaches

A decomposition approach requires one to estimate the full and partial derivatives shown in Fig. 2 from data. These derivatives reflect the effect sizes of traits, demographic rates and 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. 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 direct and indirect effects to be distinguished 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 an (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 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 realized population growth rates 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 emphasize 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 nonlinear 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 refitting each of the relationships in the hierarchy with flexible functional forms that allow for nonlinear effects (e.g. using generalized 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.

demography or climate and population (Fig. 2bii). Second, 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. First, a single climate variable could affect population dynamics via multiple traits and/or demographic rates, resulting in multiple pathways (Fig. 2di). Second, 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
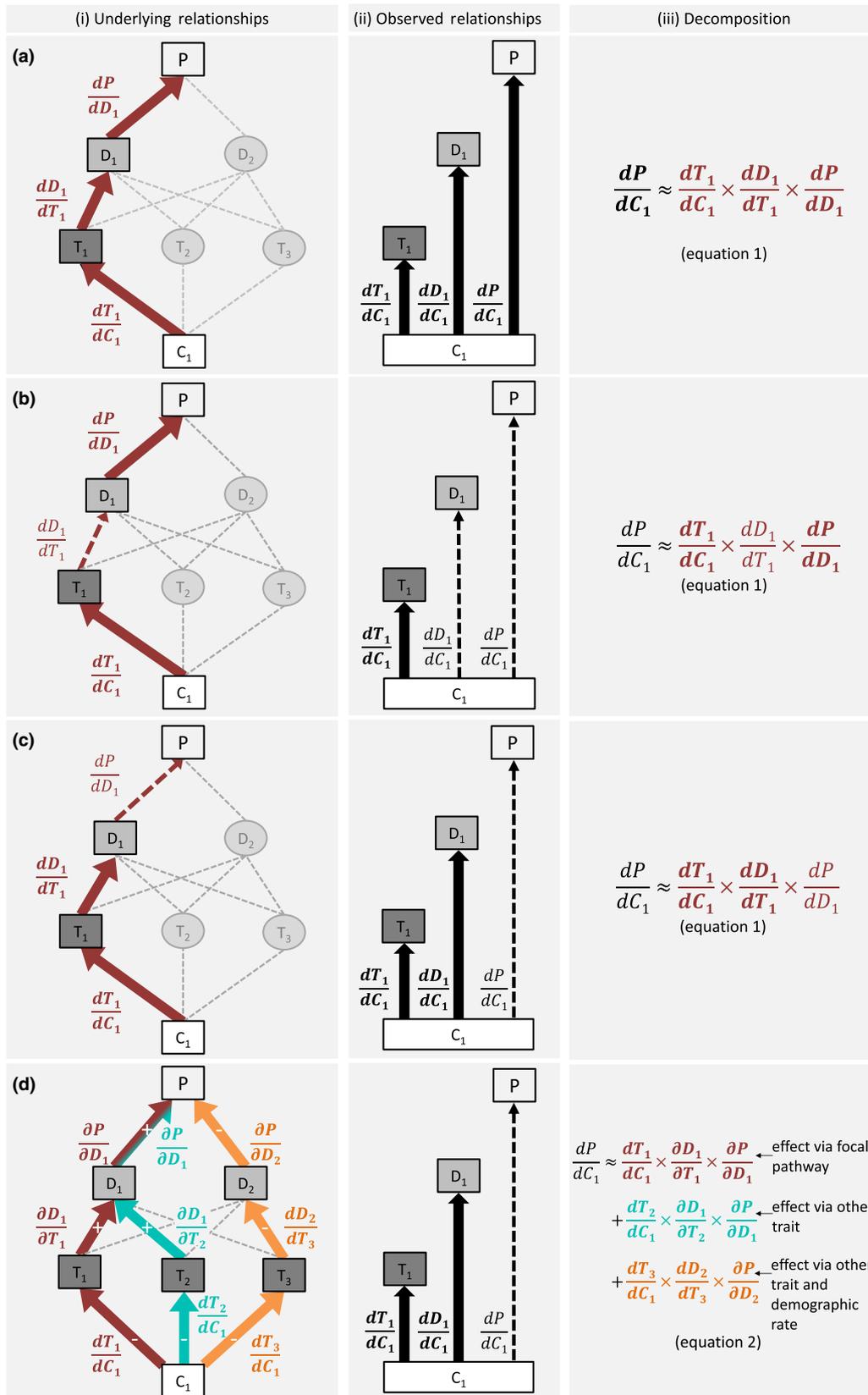
effects can be necessary to explain observed changes in population dynamics (Stopher *et al.* 2014). The climate sensitivity of population dynamics (dP/dC_1) might therefore not be accurately predicted by considering a lower-level response (dD_1/dC_1 or dT_1/dC_1) from a single pathway alone (Fig. 2diii).

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-utilized approach for identifying species characteristics that help explain species declines or extinctions (Fisher & Owens 2004; Cardillo *et al.* 2005; Buckley & Kingsolver 2012). 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 S1 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.

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 hypothesized 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 between-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 (Silvertown *et al.* 1993; Sæther *et al.* 1996; Heppell 1998; Heppell *et al.* 2000; Sæther & Bakke 2000). 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).

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

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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) and 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 Eqn 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 eqn 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. $\frac{\partial P}{\partial D_1}$ and $\frac{\partial P}{\partial D_2}$, where relationships are estimated in one pathway while accounting for effects of other pathways.

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	Specialization/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 females 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) Demographic 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, moulting, 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 due to changes in phenology can be counteracted by increased post-independence survival of offspring [10]

References from Table 1:
1. Miller-Rushing, A.J., Høye, T.T., Inouye, D.W., Post, E. (2010). The effects of phenological mismatches on demography. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 365, 3177–3186.

2. Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community interactions under climate change. *Trends Ecol. Evol.*, 25, 325–331.

3. Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. *et al.* (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.*, 8, 1–16.

4. Forcada, J., Trathan, P.N. & Murphy, E.J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Glob. Change Biol.*, 14, 2473–2488.

5. Dunn, P.O. & Møller, A.P. (2014) Changes in breeding phenology and population size of birds. *J. Anim. Ecol.*, 83, 729–739.

6. Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441, 81–83.

7. Cormont, A., Vos, C.C., van Turnhout, C.A.M., Foppen, R.P.B. & ter Braak, C.J.F. (2011). Using life-history traits to explain bird population responses to changing weather variability. *Climate Res.*, 49, 59–71.

8. Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. & Foppen, R.P.B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. Lond. [Biol.]*, 277, 1259–1266.

9. Reed, T.E., Grøtan, V., Jenouvrier, S., Sæther, B.-E. & Visser, M.E. (2013a). Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340, 488–491.

10. Reed, T.E., Jenouvrier, S. & Visser, M.E. (2013b). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *J. Anim. Ecol.*, 82, 131–144.

11. Burthe, S., Butler, A., Searle, K.R., Hall, S.J.G., Thackeray, S.J. & Wanless, S. (2011). Demographic consequences of increased winter births in a large aseasonally breeding mammal (Bos taurus) in response to climate change. *J. Anim. Ecol.*, 80, 1134–1144.

12. Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E. & Couvet, D. (2007). Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Change Biol.*, 13, 1672–1684.

13. Brinkhof, M.W.G., Cavé, A.J., Daan, S. & Perdeck, A.C. (2002). Timing of current reproduction directly affects future reproductive output in European coots. *Evolution*, 56, 400–411.

14. Gaillard, J.-M., Mark Hewison, A.J., Klein, F., Plard, F., Douhard, M., Davison, R. *et al.* (2013). How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecol. Lett.*, 16, 48–57.

15. Benton, T.G., Plaistow, S.J. & Coulson, T.N. (2006). Complex population dynamics and complex causation: devils, details and demography. *Proc. R. Soc. Lond. [Biol.]*, 273, 1173–1181.

16. Laloe, J.-O., Cozens, J., Renom, B., Taxonera, A. & Hays, G.C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nat. Clim. Change*, 4, 513–518.

17. Le Galliard, J.-F., Fitze, P.S., Ferrière, R. & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl Acad. Sci. U. S. A.*, 102, 18231–18236.

18. Jenouvrier, S., Thibault, J.-C., Viallefont, A., Vidal, P., Ristow, D., Mougin, J.-L. *et al.* (2009). Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. *Glob. Change Biol.*, 15, 268–279.

19. Sandvik, H., Erikstad, K.E. & Sæther, B.E. (2012). Climate affects seabird population dynamics both via reproduction and adult survival. *Mar. Ecol.-Prog. Ser.*, 454, 273–284.

20. Sæther, B.-E. & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81, 642–653.

21. Heppell, S.S., Caswell, H. & Crowder, L.B. (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, 81, 654–665.

22. Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.*, 31, 367–393.

23. Wilson, S. & Martin, K. (2012). Influence of life history strategies on sensitivity, population growth and response to climate for sympatric alpine birds. *BMC Ecol.*, 12, 9.

24. Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S. *et al.* (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89, 19–25.

25. Sæther, B.-E., Ringsby, T.H. & Røskaft, E. (1996). Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, 77, 217–226.

26. Dalgleish, H.J., Koons, D.N. & Adler, P.B. (2010). Can life-history traits predict the response of forb populations to changes in climate variability? *J. Ecol.*, 98, 209–217.

27. Nevoux, M., Forcada, J., Barbraud, C., Croxall, J. & Weimerskirch, H. (2010). Bet-hedging response to environmental variability, an intraspecific comparison. *Ecology*, 91, 2416–2427.

28. Jenouvrier, S., Barbraud, C. & Weimerskirch, H. (2005). Long-term contrasted responses to climate of two Antarctic seabird species. *Ecology*, 86, 2889–2903.

29. Wittemyer, G., Barner Rasmussen, H. & Douglas-Hamilton, I. (2007). Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography*, 30, 42–50.

30. Bårdsen, B.-J., Henden, J.-A., Fauchald, P., Tveraa, T. & Stien, A. (2011). Plastic reproductive allocation as a buffer against environmental stochasticity – linking life history and population dynamics to climate. *Oikos*, 120, 245–257.

31. Tynan, C.T. & DeMaster, D.P. (1997). Observations and predictions of arctic climatic change: potential effects on marine mammals. *Arctic*, 50.

32. Jenouvrier, S., Holland, M., Stroeve, J., Serreze, M., Barbraud, C., Weimerskirch, H. *et al.* (2014). Projected continent-wide declines of the emperor penguin under climate change. *Nat. Clim. Change*, 4, 715–718.

33. Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G. & Watters, G.M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc. Natl Acad. Sci. U. S. A.*, 108, 7625–7628.

34. Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P. & Ferguson, S.H. (2008). Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecol. Appl.*, 18, S97–S125.

35. McMenamin, S.K., Hadly, E.A. & Wright, C.K. (2008). Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Natl Acad. Sci. U. S. A.*, 105, 16988–16993.

36. Hunter, C.M., Caswell, H., Runge, M.C., Regehr, E.V., Amstrup, S.C. & Stirling, I. (2010). Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology*, 91, 2883–2897.

37. Donnelly, M. & Crump, M. (1998). Potential effects of climate change on two neotropical amphibian assemblages. *Clim. Change*, 39, 541–561.

38. Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C. *et al.* (2013). Temperature variation makes ectotherms more sensitive to climate change. *Glob. Change Biol.*, 19, 2373–2380.
39. Vincenzi, S. & Mangel, M. (2013). Linking food availability, body growth and survival in the black-legged kittiwake Rissa tridactyla. *Deep.-Sea Res. Pt II*, 94, 192–200.
40. Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S. *et al.* (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Glob. Change Biol.*, 17, 2455–2469.

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: (1) those due to multiple traits and/or demographic rates being affected by a single climate variable (Table 1c), or (2) 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 because 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 can 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 to 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 affected by the change in the lower-level parameter.

To the best of 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). Second, 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 (Lloyd 1999; Sæther *et al.* 2004; Altwegg & Anderson 2009). 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 (1) decompose how climate-induced changes in traits affect demographic rates and population dynamics (Fig. 3), and to (2) 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
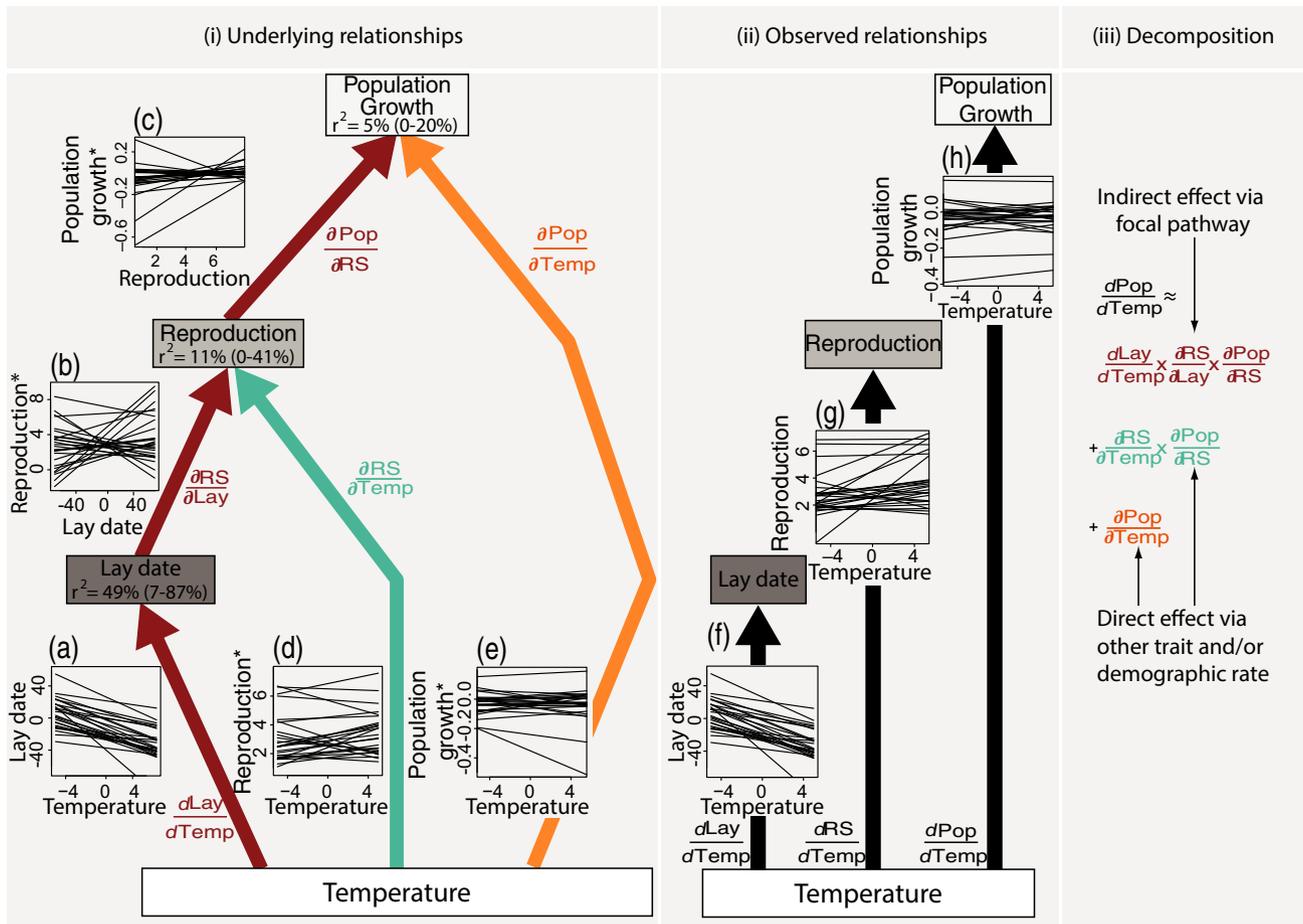
Figure 3 Decomposition of pathways by which climate-driven phenological change affects reproductive success and population growth rate in 27 bird species. Panel (i) 'Underlying Relationships' displays the graphical model used in the structural equation analysis carried out on each species. The model 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 ($\frac{\partial RS}{\partial Temp}$; green 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 $\frac{dLay}{dTemp} \times \frac{\partial RS}{\partial Lay} + \frac{\partial RS}{\partial Temp}$. 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).

mean laying date (See Appendix S1), 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 S1 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 S1 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).
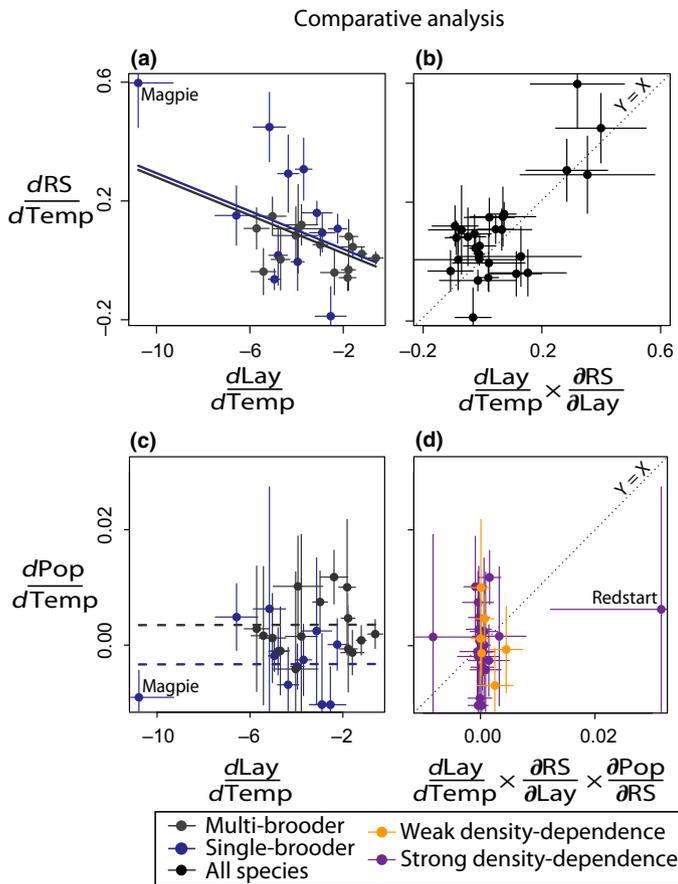
Comparative analysis

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 ($\frac{d\text{Lay}}{d\text{Temp}}$) and reproductive success ($\frac{d\text{RS}}{d\text{Temp}}$), and (c) laying dates ($\frac{d\text{Lay}}{d\text{Temp}}$) and the population growth rate ($\frac{d\text{Pop}}{d\text{Temp}}$). While (b) shows the relationship between the multiplied regression slope estimates of temperature effects on lay date and lay date effects on reproductive success ($\frac{d\text{Lay}}{d\text{Temp}} \times \frac{\partial\text{RS}}{\partial\text{Lay}}$; i.e. the indirect, focal pathway), with the total effect of temperature on reproductive success ($\frac{d\text{RS}}{d\text{Temp}}$), while (d) shows the relationship between the multiplied slope estimates of the entire indirect pathway ($\frac{d\text{Lay}}{d\text{Temp}} \times \frac{\partial\text{RS}}{\partial\text{Lay}} \times \frac{\partial\text{Pop}}{\partial\text{RS}}$) against the total effect of temperature on population growth ($\frac{d\text{Pop}}{d\text{Temp}}$). 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.

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 eight species showed no clear relationship between lay date and temperature during any period and were excluded from further analyses; Appendix S1). 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 Table S2; removing the magpie from this analysis decreases the estimate from -0.032 ± 0.011 SE to -0.019 ± 0.012 SE [model 1 in Table S4], suggesting that the magpie has a large influence but is not driving the entire relationship). Moreover, the total effects (see Fig. 3ii, iii) of temperature on reproductive success were well predicted by the (indirect) lay date pathway (Fig. 4b; $r^2 = 0.41$; model 1 in Table S2). However, there was also an important direct effect of temperature on reproduction (the green 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 Table S3). 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 Table S3; the removal of the redstart did not change this, see Table S6). 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.

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 ± 0.01 SE 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 1 vs. 3 in Table S2). 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 Table S3). 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.

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 Table S3). 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, these multiple pathway effects are unlikely to be due to density dependence.

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 and in which species or taxa these mechanisms are likely to be important. We illustrated how empirical data could be used to (1) quantify the degree to which a strong climate sensitivity of a trait results in important demographic or population-level consequences, and (2) 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 with warmer temperatures are associated with improved reproductive success, this had no apparent effect on population trends. Furthermore, temperature effects on reproduction were 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 emphasizes that even if the climate sensitivity of a trait predicts the climate sensitivity of a higher-level response, 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 by 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 that is 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 the 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 overestimate population responses if multiple effects counter-act one another, or underestimate population responses if multiple effects reinforce climate effects (Larsen *et al.* 2011; Leuzinger *et al.* 2011). Species characteristics 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 Wilson & Arcese 2003; Ozgul *et al.* 2010; Plard *et al.* 2014).

Hypothesis testing

By utilizing 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 with important food resources by reducing competition in one bird population (Reed *et al.* 2013a). However, in our analysis, the strength of density dependence was not effective in explaining variation in the effects of temperature on population growth. This suggests 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 for each species) 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 for single-brooders it declined, a trend also found by both Dunn & 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 changes in spring temperature. However, because we know that its predictive power did not stem from phenological effects on reproduction as hypothesized, there must be another reason. One reason could be that multi-brooding species are more likely to benefit from longer breeding seasons experienced under climate change (Dunn & 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 (Végvári *et al.* 2010; Buckley & Kingsolver 2012). 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, 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 lay date on reproductive success were slightly stronger in single-brooded species.

Challenges

Although many studies have suggested hypotheses for species characteristics 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 the likelihood 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 hierarchy, making relationships even more difficult to detect. If different pathways interact with one another to cause synergistic 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 levels. To help achieve this, we first 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, in order to 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 about which we have limited knowledge (most species are data deficient), as their climate sensitivity may be predicted based off their characteristics, therefore helping to determine where to prioritize conservation efforts (Sæther *et al.* 1996).

AUTHORSHIP

The project was conceived by NM and MvdP, and developed with CRL. NM performed the literature review, DL collated the empirical data. NM performed the statistical analyses, and NM, MvdP and CRL interpreted them. NM wrote the manuscript, with all authors contributing substantially to revisions.

REFERENCES

Ådahl, E., Lundberg, P.E.R. & JonzÉn, N. (2006). From climate change to population change: the need to consider annual life cycles. *Glob. Change Biol.*, 12, 1627–1633.

Alexieva, V., Ivanov, S., Sergiev, I. & Karanov, E. (2003). Interaction between stresses. *Bulg. J. Plant Physiol.*, (Special Issue), 1–17.

Altwegg, R. & Anderson, M.D. (2009). Rainfall in arid zones: possible effects of climate change on the population ecology of blue cranes. *Funct. Ecol.*, 23, 1014–1021.

Bailey, L.D. & van de Pol, M. (2015). *climwin: Climate Window Analysis. R Package Version 0.0.1.* Available at: http://cran.r-project.org/web/packages/climwin. Last accessed 10 September 2015.

Bansal, S., Hallsby, G., Löfvenius, M.O. & Nilsson, M.-C. (2013). Synergistic, additive and antagonistic impacts of drought and herbivory on Pinus sylvestris: leaf, tissue and whole-plant responses and recovery. *Tree Physiol.*, 33, 447–450.

Barraquand, F. & Yoccoz, N.G. (2013). When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theor. Popul. Biol.*, 89, 1–11.

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. & Foppen, R.P.B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. Lond. [Biol.]*, 277, 1259–1266.

Boyce, M.S., Haridas, C.V., Lee, C.T. & NCEAS Stochastic Demography Working Group (2006). Demography in an increasingly variable world. *Trends Ecol. Evol.*, 21, 141–148.

Brown, C.R. & Brown, M.B. (1999). Fitness components associated with laying date in the cliff swallow. *Condor*, 101, 230–245.

BTO (2015). *British Trust for Ornithology.* Available at: http://www.bto.org/. Last accessed 17 September 2015.

Buckley, L.B. & Kingsolver, J.G. (2012). Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annu. Rev. Ecol. Evol. Syst.*, 43, 205–226.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W. et al. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309, 1239–1241.

Chase, M.K., Nur, N., Geupel, G.R. & Stouffer, P.C. (2005). Effects of weather and population density on reproductive success and population dynamics in a song sparrow (*Melospiza melodia*) population: a long-term study. *Auk*, 122, 571–592.

Clements, M.N., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Kruuk, L.E.B. (2011). Gestation length variation in a wild ungulate. *Funct. Ecol.*, 25, 691–703.

Cotton, P.A. (2003). Avian migration phenology and global climate change. *Proc. Natl Acad. Sci.*, 100, 12219–12222.

Darling, E.S., McClanahan, T.R. & Côté, I.M. (2013). Life histories predict coral community disassembly under multiple stressors. *Glob. Change Biol.*, 19, 1930–1940.

Doyle, M.J., Picquelle, S.J., Mier, K.L., Spillane, M.C. & Bond, N.A. (2009). Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. *Prog. Oceanogr.*, 80, 163–187.

Dunn, P.O. & Møller, A.P. (2014). Changes in breeding phenology and population size of birds. *J. Anim. Ecol.*, 83, 729–739.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000). Size-specific sensitivity: applying a new structured population model. *Ecology*, 81, 694–708.

Fisher, D.O. & Owens, I.P.F. (2004). The comparative method in conservation biology. *Trends Ecol. Evol.*, 19, 391–398.

Foden, W.B., Butchart, S.H., Stuart, S.N., Vié, J.C., Akçakaya, H.R., Angulo, A. et al. (2013). Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*, 8, e65427.

Gibbs, M., Van Dyck, H. & Breuker, C.J. (2012). Development on drought-stressed host plants affects life history, flight morphology and reproductive output relative to landscape structure. *Evol. Appl.*, 5, 66–75.

Glanville, E.J. & Seebacher, F. (2006). Compensation for environmental change by complementary shifts of thermal sensitivity and thermoregulatory behaviour in an ectotherm. *J. Exp. Biol.*, 209, 4869–4877.

Heppell, S.S. (1998). Application of life-history theory and population model analysis to turtle conservation. *Copeia*, 1998, 367–375.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, 81, 654–665.

Hutcheon, J.A., Chiolero, A. & Hanley, J.A. (2010). Random measurement error and regression dilution bias. *BMJ*, 340, 1402–1406.

Jenouvrier, S., Barbraud, C. & Weimerskirch, H. (2005). Long-term contrasted responses to climate of two Antarctic seabird species. *Ecology*, 86, 2889–2903.

Jenouvrier, S., Thibault, J.-C., Viallefont, A., Vidal, P., Ristow, D., Mougin, J.-L. et al. (2009). Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. *Glob. Change Biol.*, 15, 268–279.

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E. & Couvet, D. (2007). Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Change Biol.*, 13, 1672–1684.

Jongejans, E., Huber, H. & de Kroon, H. (2010). Scaling up phenotypic plasticity with hierarchical population models. *Evol. Ecol.*, 24, 585–599.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L. et al. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.*, 21, 393–404.

Kruuk, L.E.B., Osmond, H.L. & Cockburn, A. (2015). Contrasting effects of climate on juvenile body size in a Southern Hemisphere passerine bird. *Glob. Change Biol.*, 21, 2929–2941.

Larsen, K.S., Andresen, L.C., Beier, C., Jonasson, S., Albert, K.R., Ambus, P.E.R. et al. (2011). Reduced N cycling in response to elevated CO2, warming, and drought in a Danish heathland: synthesizing results of the CLIMAITE project after two years of treatments. *Glob. Change Biol.*, 17, 1884–1899.

Lawson, C.R., Vindenes, Y., Bailey, L. & van de Pol, M. (2015). Environmental variation and population responses to global change. *Ecol. Lett.*, 18, 724–736.

Leech, D.I. & Crick, H.Q.P. (2007). Influence of climate change on the abundance, distribution and phenology of woodland bird species in temperate regions. *The Ibis*, 149, 128–145.

Leuzinger, S., Luo, Y., Beier, C., Dieleman, W., Vicca, S. & Körner, C. (2011). Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol. Evol.*, 26, 236–241.

Lloyd, P. (1999). Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. *The Ibis*, 141, 637–643.

Madin, J.S., Hughes, T.P. & Connolly, S.R. (2012). Calcification, storm damage and population resilience of tabular corals under climate change. *PLoS ONE*, 7, e46637.

Mielikäinen, K. & Sennov, S. (1996). Growth trends of forests in Finland and North-Western Russia. In: *Growth Trends in European Forests* (eds Spiecker, H., Mielikäinen, K., Köhl, M. & Skovsgaard, J.). Springer, Berlin, Heidelberg, pp. 19–27.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010). The effects of phenological mismatches on demography. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 365, 3177–3186.

Morrison, S.F. & Hik, D.S. (2007). Demographic analysis of a declining pika Ochotona collaris population: linking survival to broad-scale climate patterns via spring snowmelt patterns. *J. Anim. Ecol.*, 76, 899–907.

Nichols, J.D. & Hines, J.E. (2002). Approaches for the direct estimation of u, and demographic contributions to *u*, using capture-recapture data. *J. Appl. Statist. Sci.*, 29, 539–568.

Ozgul, A., Tuljapurkar, S., Benton, T.G., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T. (2009). The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science*, 325, 464–467.

Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E. et al. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466, 482–485.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992). A new daily Central England Temperature Series, 1772–1991. *Int. J. Clim.*, 12, 317–342.

Pearce-Higgins, J.W., Yalden, D.W., Dougall, T.W. & Beale, C.M. (2009). Does climate change explain the decline of a trans-Saharan Afro-Palaearctic migrant? *Oecologia*, 159, 649–659.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N. *et al.* (2014). Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Change*, 4, 217–221.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. *et al.* (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biol.*, 12, e1001828.

van de Pol, M., Vindenes, Y., Saether, B.-E., Engen, S., Ens, B.J., Oosterbeek, K. *et al.* (2010). Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology*, 91, 1192–1204.

Pretzsch, H., Biber, P., Schütze, G., Uhl, E. & Rötzer, T. (2014). Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.*, 5, 1–10.

Pugesek, B.H., Tomer, A. & von Eye, A. (2003). *Structural Equation Modeling: Applications in Ecological and Evolutionary Biology*. Cambridge University Press, West Nyack, NY.

Reed, T.E., Grøtan, V., Jenouvrier, S., Sæther, B.-E. & Visser, M.E. (2013a). Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340, 488–491.

Reed, T.E., Jenouvrier, S. & Visser, M.E. (2013b). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *J. Anim. Ecol.*, 82, 131–144.

Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. (2004). Demographic mechanisms of the population decline of the song thrush Turdus philomelos in Britain. *J. Anim. Ecol.*, 73, 670–682.

Robinson, R.A., Morrison, C.A. & Baillie, S.R. (2014). Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods Ecol. Evol.*, 5, 1361–1372.

Rudolf, V.W. & Singh, M. (2013). Disentangling climate change effects on species interactions: effects of temperature, phenological shifts, and body size. *Oecologia*, 173, 1043–1052.

Ruel, J.J. & Ayres, M.P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.*, 14, 361–366.

Sæther, B.-E. & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81, 642–653.

Sæther, B.-E., Ringsby, T.H. & Røskaft, E. (1996). Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, 77, 217–226.

Sæther, B.-E., Sutherland, W.J. & Engen, S. (2004). Climate influences on avian population dynamics. *Adv. Ecol. Res.*, 35, 185–209.

Sandvik, H. & Erikstad, K.E. (2008). Seabird life histories and climatic fluctuations: a phylogenetic-comparative time series analysis of North Atlantic seabirds. *Ecography*, 31, 73–83.

Sandvik, H., Erikstad, K.E. & Sæther, B.E. (2012). Climate affects seabird population dynamics both via reproduction and adult survival. *Mar. Ecol.-Prog. Ser.*, 454, 273–284.

Scherber, C., Gladbach, D.J., Stevnbak, K., Karsten, R.J., Schmidt, I.K., Michelsen, A. *et al.* (2013). Multi-factor climate change effects on insect herbivore performance. *Ecol. Evol.*, 3, 1449–1460.

Schwanz, L.E. & Janzen, F.J. (2008). Climate change and temperature-dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? *Physiol. Biochem. Zool.*, 81, 826–834.

Sheldon, B.C., Kruuk, L.E.B. & Merila, J. (2003). Natural selection and inheritance of breeding time and clutch size in the Collared Flycatcher. *Evolution*, 57, 406–420.

Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S. *et al.* (2007). Divergence of reproductive phenology under climate warming. *Proc. Natl Acad. Sci. U. S. A.*, 104, 198–202.

Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. (1993). Comparative plant demography-relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.*, 81, 465–476.

Stopher, K.V., Bento, A.I., Clutton-Brock, T.H., Pemberton, J.M. & Kruuk, L.E.B. (2014). Multiple pathways mediate the effects of climate change on maternal reproductive traits in a red deer population. *Ecology*, 95, 3124–3138.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Végvári, Z., Bókony, V., Barta, Z. & Kovács, G. (2010). Life history predicts advancement of avian spring migration in response to climate change. *Glob. Change Biol.*, 16, 1–11.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.*, 6, e325.

Wilson, S. & Arcese, P. (2003). El Niño drives timing of breeding but not population growth in the song sparrow (Melospiza melodia). *Proc. Natl Acad. Sci. U. S. A.*, 100, 11139–11142.

Wood, S. (2006). *Generalized Additive Models: An Introduction with R*. CRC Press, Florida.

Wright, L.J., Hoblyn, R.A., Green, R.E., Bowden, C.G.R., Mallord, J.W., Sutherland, W.J. *et al.* (2009). Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark Lullula arborea. *J. Anim. Ecol.*, 78, 1191–1202.

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