REVIEW AND SYNTHESIS

Environmental variation and population responses to global change

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Abstract

Species' responses to environmental changes such as global warming are affected not only by trends in mean conditions, but also by natural and human-induced environmental fluctuations. Methods are needed to predict how such environmental variation affects ecological and evolutionary processes, in order to design effective strategies to conserve biodiversity under global change. Here, we review recent theoretical and empirical studies to assess: (1) how populations respond to changes in environmental variance, and (2) how environmental variance affects population responses to changes in mean conditions. Contrary to frequent claims, empirical studies show that increases in environmental variance can increase as well as decrease long-term population growth rates. Moreover, environmental variance can alter and even reverse the effects of changes in the mean environment, such that even if environmental variance remains constant, omitting it from population models compromises their ability to predict species' responses to changes in mean conditions. Drawing on theory relating these effects of environmental variance to the curvatures of population growth responses to the environment, we outline how species' traits such as phylogenetic history and body mass could be used to predict their responses to global change under future environmental variability.

Keywords

Climate change, climate fluctuations, climate variation, demographic rates, extreme events, functional type, global warming, stochastic growth rate, temperature variation, thermal performance.

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INTRODUCTION

Species' responses to environmental changes such as global warming are likely to depend not only on what environmental conditions are like on average (Parmesan & Yohe 2003; Chen *et al.* 2011), but also on how much they fluctuate through time (Stenseth *et al.* 2002; Jackson *et al.* 2009). One reason for this is that environmental conditions are naturally highly variable: differences in temperature between consecutive years are as great as the change in average temperature over 30 years of global warming (1970–2000: Huntingford *et al.* 2013). Moreover, these natural patterns of environmental variability are being transformed by climate change: for example, in many parts of Europe and North America, interannual variance in temperature has increased by more than 25% since 1980 (Huntingford *et al.* 2013; IPCC 2013). Methods to predict how such environmental variation will affect ecological and evolutionary processes are thus sorely needed to inform biodiversity conservation strategies under global change.

Environmental variance can affect species' responses to global change via two different routes. First, changes in environmental variance may have effects that are independent of whether the mean environment is changing (Fig. 1a–c): for

example, by exposing individuals to more extreme conditions, increased environmental variance may amplify population fluctuations (Bjørnstad & Grenfell 2001; Boyce *et al.* 2006), heighten extinction risk (Ovaskainen & Meerson 2010), and select for bet-hedging adaptations that reduce temporal fluctuations in fitness (Ellner 1997; Starrfelt & Kokko 2012). Second, the effects of environmental fluctuations may interact with changes in the mean environment. Organisms may respond differently to changes in mean environmental conditions depending on whether such changes occur gradually year-on-year, as typically assumed in global change studies (Fig. 1d), or erratically, as often occurs in reality (Fig. 1e; Coulson *et al.* 2004). For example, environmental variance can introduce fluctuating selection pressures that prevent species from tracking shifting phenotypic optima (Kopp & Matuszewski 2014), and generate intermittent pulses of advance and retreat that affect the progress of range expansions (Bennie *et al.* 2013). Furthermore, if environmental variance does alter the effects of changes in the mean environment, then species are likely to respond differently to changes in environmental means and variances when such changes occur together (Fig. 1f; Vasseur *et al.* 2014). To predict how environmental variance will affect species' responses to global

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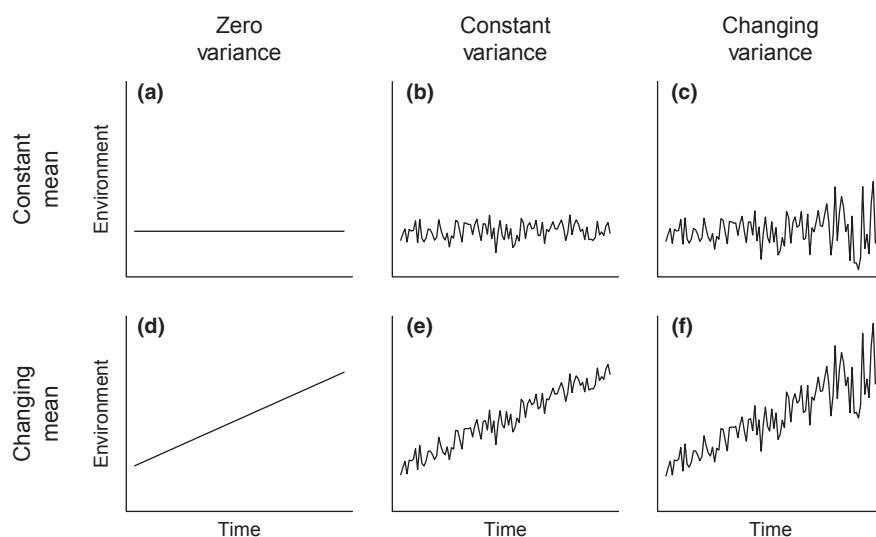*Correspondence: E-mail: c.lawson@nioo.knaw.nl*

Figure 1 Environmental change scenarios for investigating the effects of environmental variance. The effects of temporal fluctuations in environmental conditions can be explored either by comparing scenarios with and without environmental variance (a, d vs. b, e), or by examining the consequences of changes in environmental variance, such as those predicted under climate change (b, e vs. c, f). The effects of environmental variance may depend on whether the mean environment is constant (a–c) or changing (d–f): for instance, increased temperature variance may have different effects when average temperatures are higher.

change, we thus need to understand its impacts in both stationary environments, in which mean conditions remain constant, and in non-stationary environments, in which mean conditions are changing.

Of fundamental importance in this context are the effects of environmental variance on population growth rates, since these growth rates underpin a broad range of ecological and evolutionary processes including phenotypic adaptation (Roughgarden 1979), population persistence (Ovaskainen & Meerson 2010), and the colonisation of new habitats at a species' range edge (Bennie *et al.* 2013). Recent empirical studies have quantified how long-term growth rates of particular populations may be affected by changes in environmental variance (e.g. Jenouvrier *et al.* 2012; McCaffery *et al.* 2012) or by increases in the frequency of 'extreme events' such as unusually hot years (Kingsolver *et al.* 2013). However, given that such detailed demographic data are generally unavailable for most species of conservation concern, and that different populations will respond to environmental variance in different ways, there is a need to develop general principles for predicting the population dynamical consequences of environmental variance.

In this manuscript, we review theoretical and empirical population dynamical studies to assess how environmental variance affects long-term population growth rates in (1) constant mean environments and (2) changing mean environments. Our review of empirical evidence reveals that environmental variance can enhance as well as reduce long-term population growth, and that it can alter the effects of changes in the mean environment. Our theoretical synthesis shows how the direction and strength of these effects are determined by the curvatures of relationships between population growth rates and the environment. We outline how these curvatures could be inferred using species' traits such as phylogenetic history and body mass, and thus serve as a general basis for predicting species' responses to global change in a variable world.

ENVIRONMENTAL VARIANCE EFFECTS IN CONSTANT MEAN ENVIRONMENTS

Theory

Throughout this review, we focus on how *environmental variance*, defined as the temporal variance in an environmental variable (z) such as temperature, affects the long-term change in the number of individuals in a population, measured by *the stochastic growth rate* and denoted $\bar{r}$ (Box 1; Lewontin & Cohen 1969; see Box 2 for Glossary). The stochastic growth rate quantifies the mean per-capita growth rate of the population (on a log scale), indicating whether the population size is expected to grow ($\bar{r} > 0$), stay constant ($\bar{r} = 0$) or decline ($\bar{r} < 0$) in the long-term. It is thus a key measure of both mean fitness (Roughgarden 1979) and population viability (Lande *et al.* 2003). We begin by examining the effects of environmental variance on the stochastic growth rate in a constant mean environment (Fig. 1a–c); this will provide the conceptual tools necessary to investigate its effects in a changing mean environment (Fig. 1d–f).

The effects of environmental variance on the stochastic growth rate $\bar{r}$ depend on the relationship between the population growth rate r_t in a given time interval (e.g. each year) and the environment during that same time interval: we henceforth refer to this relationship as the *population growth response* (Box 1; Stearns 2000; Drake 2005). Specifically, it is the *curvature* of the population growth response that determines how environmental variance affects $\bar{r}$ (Ruel & Ayres 1999; Drake 2005). If the population growth response is *convex* (upwardly curving), environmental variance increases $\bar{r}$ because favourable environments increase the population growth rate more than unfavourable environments decrease it (Fig. 2a). Conversely, if the population growth response is *concave* (downwardly curving), environmental variance decreases $\bar{r}$ because unfavourable

Box 1 Linking population growth to the environment

Here, we describe a baseline model for the effects of environmental means and variances on population growth (for further details see Lewontin & Cohen 1969; Drake 2005; García-Carreras & Reuman 2013). During a time interval lasting from t to t + 1, a population changes in size (or biomass; Turchin 2003) N by a multiplicative factor λ_t:

$$N_{t+1} = \lambda_t N_t$$

Assuming density-independent growth and identical responses among individuals, such that the values of λ_t in different time steps are independent and identically distributed (IID), the population size after t time steps is given by the following equation:

$$N_t = N_0 \lambda_1 \lambda_2 \ldots \lambda_t$$

Switching to a log scale by defining $r_t = \ln(\lambda_t)$ (henceforth referred to simply as the *growth rate*; note that r_t is a stochastic variable) allows the growth rates in different time steps to be treated additively, such that the expected population size at time t can be calculated using the mean (expectation) of the growth rate on a log scale $\bar{r}$:

$$E[\ln N_t | N_0] = \ln N_0 + E[r_1 + r_2 \ldots + r_t] = \ln N_0 + \bar{r}t$$

The *stochastic growth rate* $\bar{r}$ indicates whether the population size is expected to grow ($\bar{r} > 0$), stay constant ($\bar{r} = 0$) or decline ($\bar{r} > 0$) in the long-term (but note that extinction risk will be additionally affected by variance in r_t; Lande *et al.* 2003). We focus on $\bar{r}$ throughout this manuscript, but many studies instead focus on the *multiplicative growth rate* on an absolute scale $\lambda_s = e^{\bar{r}}$; Appendix S1 discusses the links between these two measures.

The environment z in each time interval t is assumed IID with probability density distribution p(z), mean μ_z and variance σ_z^2. We use *environmental variance* to refer to σ_z^2, the variance in z among time intervals; environmental variance within time intervals is not explicitly included. We denote the relationship between r_t and z by the function f(z), henceforth referred to as the *population growth response*. We are interested in the effects of μ_z and σ_z^2 on $\bar{r}$, given by the following equation:

$$\bar{r}(\mu_z, \sigma_z^2) = \int p(z; \mu_z, \sigma_z^2) f(z) dz$$

The temporal scale at which environmental values from p(z) affect $\bar{r}$ depends on the length of the timestep t, which is ideally chosen to match a natural biological cycle, such as the interval between breeding seasons. We assume either that the environmental distribution p(z) is symmetrical (zero skew), or that the third derivative of the population growth response f(z) is zero, such that changes in the skew of p(z) have no effect on $\bar{r}$ (Appendix S6).

Box 2 Glossary

Environmental variability: The temporal distribution of environmental conditions, including both environmental variance and higher moments such as environmental skew.
Environmental variance (σ_z^2): The variance in environmental conditions between time intervals (Box 1).
Population growth rate (r_t): The per-capita rate of population growth during a given time interval (Box 1).
Stochastic growth rate ($\bar{r}$): The long-term (asymptotic) rate of population growth on a logarithmic scale (Box 1).
Vital rate: Any individual-level rate directly contributing to the growth rate or demographic composition of the population, such as rates of birth, death and development.
Population growth or *vital rate response*: The relationship between the population growth rate or vital rate and the environment during the current time interval (Box 1).
Population growth or *vital rate curvature*: The rate at which the population growth rate or vital rate accelerates (or decelerates) with the environment, quantified by the second derivative of the response function.
Convex: an upwardly curving (accelerating) relationship.
Concave: a downwardly curving (decelerating) relationship.
Demographic structure: subdivision of the population into different types of individuals, usually to account for between-individual differences in vital rate responses.
Mean–variance interaction: a situation in which the effect of environmental variance on the stochastic growth rate depends on the mean environment, and thus the effect of the mean environment depends on the environmental variance.

variance has no effect on $\bar{r}$ because the effects of favourable and unfavourable environments perfectly counterbalance (Fig. 2b). Quantifying the curvature at a given point on the population growth response (given by the second derivative $\frac{\delta^2 r_t}{\delta z^2}$: Fig. 2; Ruel & Ayres 1999) thus provides a way to predict both the direction and strength of environmental variance effects on the stochastic growth rate.

There is a common – and incorrect – perception amongst ecologists and evolutionary biologists that increased environmental variance always decreases the stochastic growth rate $\bar{r}$ (Appendix S1). This perception is rooted in theoretical population dynamics models (e.g. Lande *et al.* 2003 and references therein) that do not consider explicit environmental variables and instead assume that environmental variance is proportional to the variance of population growth rates on an absolute scale (λ_t). Implicit in this assumption is that population growth responses are linear on an absolute scale (λ_t), and therefore concave on a log scale (r_t), with the consequence that increased environmental variance reduces $\bar{r}$ (Fig. 1c). However, the theory discussed above shows that when explicit environmental variables are considered, increased environmental variance can actually increase the stochastic growth rate (Fig. 1a), a conclusion that is supported by the empirical studies reviewed in the next section.
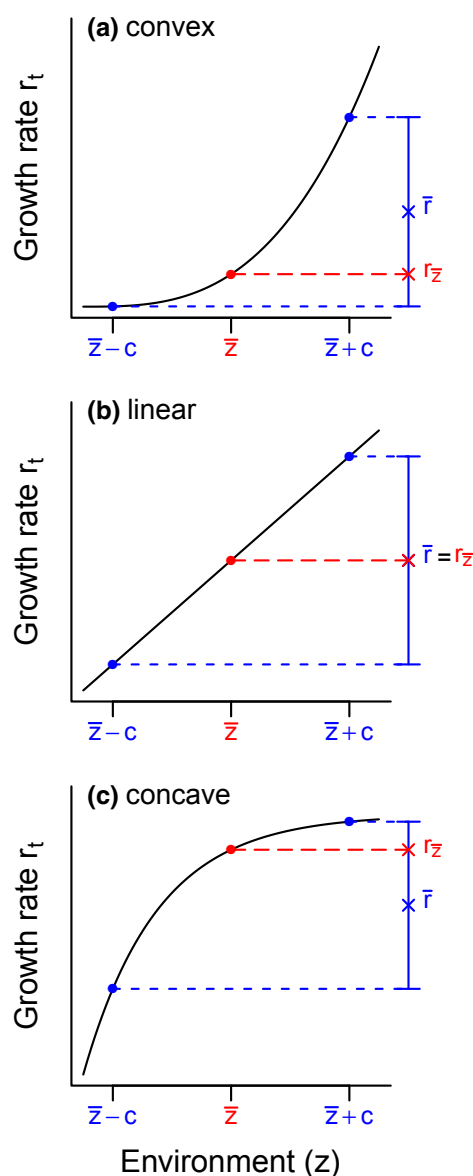
environments decrease the population growth rate more than favourable environments increase it (Fig. 2c). In the special case of a perfectly linear population growth response, environmental

Figure 2 The curvature of the population growth response determines how environmental variance affects the stochastic growth rate $\bar{r}$. Panels illustrate three relationships between population growth rates (r_t) and the environment (z), each with a different curvature (a: convex, $\frac{\delta^2 r_t}{\delta z^2} > 0$; b: linear, $\frac{\delta^2 r_t}{\delta z^2} = 0$; c: concave, $\frac{\delta^2 r_t}{\delta z^2} < 0$). When the population growth response is nonlinear, the growth rate in the mean environment $r(\bar{z})$ (red, long-dashed lines) differs from the mean growth rate in a variable environment $\bar{r}$ (here illustrated as the mean of the growth rates in two environments, $r_{\bar{z}-c}$ and $r_{\bar{z}+c}$, where c is a constant: blue, short-dashed lines). Environmental variance increases the stochastic growth rate when the population growth response is convex (a: $\bar{r} > r(\bar{z})$), decreases the stochastic growth rate when the population growth response is concave (c: $\bar{r} < r(\bar{z})$), and has no effect on the stochastic growth rate when the population growth response is linear (b: $\bar{r} = r(\bar{z})$).

A deeper understanding of environmental variance can be gained by breaking down the population's growth response into individual *vital rate responses*, including rates of birth, death and development. For example, by exploring how the stochastic growth rate (equivalent to mean fitness; Roughgarden 1979) is altered by changes in the underlying vital rate responses, we can infer how populations are likely to adapt to increasing environmental variance. We can also examine the effects of *demographic structure* by allowing vital rate responses to differ between individuals of different ages (e.g. adults and juveniles; Jackson *et al.* 2009), life history stages (e.g. dormant and germinating plants; Cohen 1993) or phenotypes (e.g. individuals of different body sizes; Vindenes *et al.* 2014). This is especially important because in such demographically structured populations, the population growth curvature approach described above may fail to predict the effects of environmental variance. The reason for this is that it assumes that rates of population growth are independent between time intervals (Box 1), which is not the case if the environment experienced in one time interval alters the population's demographic structure and thus its response to environments experienced in the future (Case 2000; Coulson *et al.* 2001; Ellis & Crone 2013). Vital rate responses could therefore provide the key to predicting the effects of environmental variance on both evolutionary adaptation and the stochastic growth rate of demographically structured populations.

The effects of environmental variance on the mean of a vital rate can be inferred from the vital rate's response curvature in the same way as for population growth rates (Boyce *et al.* 2006). For example, if the relationship between development rate and temperature is convex, temporal fluctuations in temperature will increase the mean development rate (Ragland & Kingsolver 2008; Paaijmans *et al.* 2013). It is thus tempting to use this approach to calculate the effects of environmental variance on the mean of each vital rate, and then sum up these effects to derive the net impacts of environmental variance on the stochastic growth rate. Unfortunately, however, this strategy can be thwarted by covariation between vital rates. This problem is illustrated by Barraquand & Yoccoz (2013), who use an unstructured population model to show that even when none of the vital rate responses (survival and reproduction) are convex on a log scale, it is possible to obtain a convex population growth response, and thus positive effects of environmental variance on the stochastic growth rate. Moreover, they show that if the reproduction response is convex, *decreasing* the convexity of the survival response can *increase* the convexity of the population growth response. Both of these counter-intuitive effects are due to covariation between the vital rates: changes in the survival rate have a larger effect on the rate of population growth in 'bust' years of low reproduction than in 'boom' years of high reproduction, so a higher stochastic growth rate can be achieved by decoupling high-survival years from high-reproduction years (illustrated in our Fig. 3). These findings indicate that species may adapt to increased environmental variance by evolving vital rate responses with dissimilar curvatures, and furthermore, that the different vital rate responses must be considered collectively to determine the effects of environmental variance on the stochastic growth rate.

Empirical evidence

Much of the empirical research on the population dynamical effects of environmental variance focuses on the impacts of
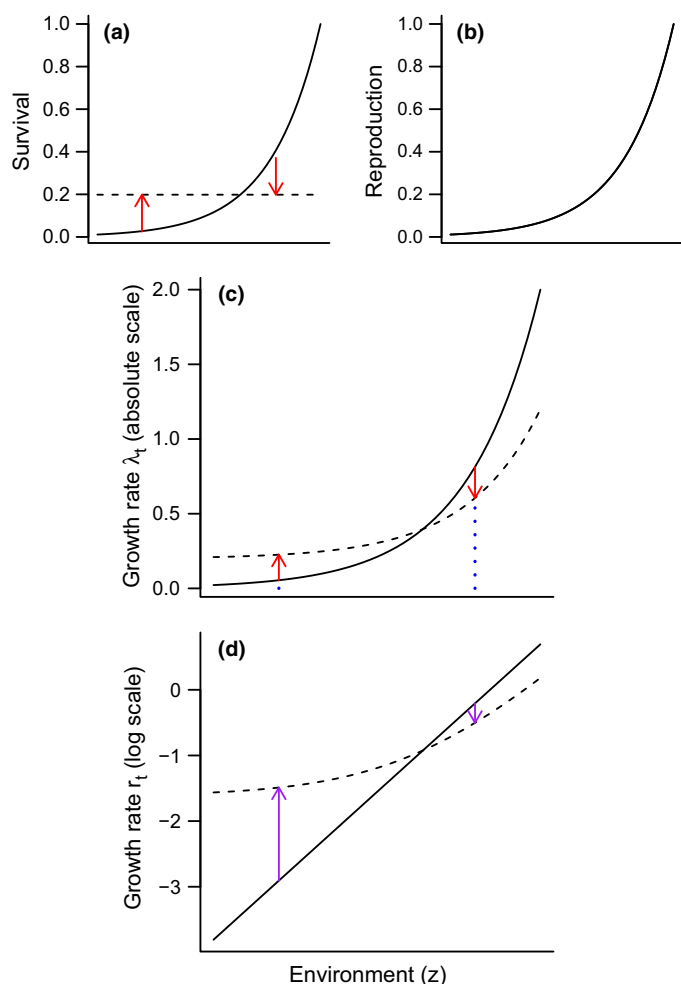
Figure 3 Diversifying vital rate responses to the environment can increase the stochastic growth rate in a variable environment. Given a convex reproduction response (b), a survival response that is flat (a: dashed line) instead of convex (solid line) results in a population growth response that is more convex on the log scale r_t (d). This is because equivalent-magnitude changes in survival have proportionally larger effects on the multiplicative growth rate (λ_t) in low-growth environments than in high-growth environments (indicated by the ratio of the red arrow to the blue dots, panel c). Thus, when the environment varies, a higher stochastic growth rate $\bar{r}$ can be achieved when the survival and reproduction responses to the environment are dissimilar. Note that the example represents a decreasing population ($\bar{r}$ is negative).

changes in climate variance (IPCC 2013), but these impacts have so far been studied on a case-by-case basis. Focussing on climatic variables, we systematically reviewed empirical studies to assess the direction and strength of environmental variance effects on the stochastic population growth rate (Appendix S2). Our literature search returned 242 studies, but 225 of these were excluded, either because they did not quantify population growth rates, or because they did not assess the effects of environmental variance *per se* (Appendix S2); the results from the remaining 17 studies are summarised in Table 1.

In contrast to the common belief that increased environmental variance always decreases the stochastic growth rate (see 'Theory', above), we found nearly as many studies

reporting positive as negative effects of increased environmental variance (4 and 5 studies respectively), as well as five studies reporting a mix of both positive and negative effects depending on context (discussed in the next section). These studies show that increased environmental variance can enhance the stochastic growth rate in a range of taxa.

The directions of environmental variance effects on the stochastic growth rate were consistent with expectations based on the curvature of population growth responses, in the sense that the effects of environmental variance on $\bar{r}$ were positive when r_t responses were convex and negative when r_t responses were concave (Table 1a). However, these expectations were generally tested using population dynamical simulations; in only one study (Estay *et al.* 2011) were they validated with independent measurements of the stochastic growth rate. In no study did all vital rates have the same direction of curvature (Table 1a), emphasising the need for theory to predict the stochastic growth rate from vital rate responses that have different curvatures.

In most studies, the authors concluded that the effects of environmental variance on the stochastic growth rate were weak. Including observed environmental variance in population dynamical simulations or increasing environmental variance or standard deviation by one unit (using sensitivity or elasticity analyses: Caswell 2001) typically changed the long-term population growth rate by less than 1% on the absolute scale (λ_s; Table 1a). Moreover, all studies that examined the effects of predicted climate changes concluded that stochastic growth rates would be more strongly affected by changes in environmental means than by changes in environmental variances (Jonzén *et al.* 2010; Nicole *et al.* 2011; McCaffery *et al.* 2012; Vindenes *et al.* 2014). Finally, although the study of copepod population growth by Drake (2005) is often considered to be the best example of positive effects of environmental variance on $\bar{r}$ (e.g. Koons *et al.* 2009), a reanalysis of the original data (Appendix S3) shows that within species, relationships between r_t and temperature are generally linear or only weakly convex, and therefore that the effects of temperature variance on $\bar{r}$ are likely to be small.

There are nonetheless three reasons that the effects of changes in environmental variance may still be large in practice. First, even small effects of a unit change in environmental variance can strongly alter the stochastic growth rate if the rate of change in environmental variance is large. Second, response curvatures measured in field studies may be 'smoothed out' due to inaccuracies in population growth, vital rate or climate measurements, weakening the inferred effects of environmental variance. Consistent with this idea, controlled experimental studies generally reported strong effects of environmental variance (Table 1; Bozinovic *et al.* 2011; Estay *et al.* 2011, 2014; but see Hart & Gotelli 2011). However, these experimental studies may also have used larger magnitudes of environmental variances than observed in field studies. Third, environmental variance can have important effects on population growth that only become apparent when considered in combination with changes in environmental means, as we discuss in the following section.

Table 1 Summary of results from a systematic review of environmental variance effects on the stochastic population growth rate r̄, divided into studies that examined a single mean environment (a), or different mean environments, to investigate mean–variance interactions (b)

Author(s)	Taxon	Study type	Environmental variable	Response curvatures		Effects of environmental variance				
				Population growth rate (r_t)	Vital rates	Direction	Effect size			
							Assessment Method	Additive change in r̄	Multiplicative change in λ_s	
(a) Studies in constant mean environments										
Altwegg & Anderson (2009)	Birds	Observational	Rainfall	–	Survival: concave reproduction: convex or linear	Zero (ns)	Comparison	−0.000050 year⁻¹	1.00 year⁻¹	
Hart & Gotelli (2011)	Insects	Experimental	Rainfall (water level)	–	–	Zero (ns)	–	–	–	
Ureta et al. (2012)	Plants	Observational	Temperature, Rainfall	–	Survival: linear reproduction: convex development: concave or linear	Zero (ns)	–	–	–	
Enright et al. (1998)	Plants	Observational	Rainfall	–	–	Positive	Comparison†	+0.0100 year⁻¹	1.0 year⁻¹	
Drake (2005)	Crustaceans	Observational	Temperature	Convex	–	Positive	–	–	–	
Troyer et al. (2014)	Mammals	Observational	Precipitation	–	–	Positive	Regression	+0.31 mm⁻¹ month⁻¹	1.4 mm⁻¹ month⁻¹	
Vindenes et al. (2014)	Fish	Observational	Temperature	–	Survival: convex or concave reproduction: concave development: concave	Positive	Simulation*	+0.0025°C⁻¹ year⁻¹	1.0°C⁻¹ year⁻¹	
Jonzén et al. (2010)	Mammals	Observational	Rainfall	–	Survival: concave or mixed reproduction: mixed	Negative	Elasticity	–	0.99 mm⁻¹ year⁻¹	
Estay et al. (2011)	Insects	Experimental	Temperature	Mixed	–	Negative	Comparison	−0.97 month⁻¹	0.38 month⁻¹	
Roland & Matter (2013)	Insects	Observational	Temperature	Concave	–	Negative	–	–	–	
McCaffery et al. (2012)	Amphibians	Observational	Snow	–	Survival: linear reproduction: linear development: convex	Negative	Sensitivity†	–	0.997 cm⁻² year⁻¹	
Nicole et al. (2011)	Plants	Observational	Temperature	Concave (λ_t linear)	Survival: linear	Negative	–	–	–	
Lawler et al. (2009)	Mammals	Observational	Rainfall	Concave (λ_t concave in model-averaged predictions)	Survival: linear or concave development: linear	Mixed (differs by model)	Simulation*	−0.025 to +0.00076 mm⁻¹ year⁻¹	0.98 to 1.0 mm⁻¹ year⁻¹	
(b) Studies in changing mean environments										
Jenouvrier et al. (2012)	Birds	Observational	Sea ice	–	Survival: mixed reproduction: mixed	Mixed	Comparison*	−0.05 to +0.055 year⁻¹	0.95 to 1.1 year⁻¹	
Bozinovic et al. (2011)	Insects	Experiment	Temperature	–	–	Mixed	Comparison	−0.60 to +1.9 day⁻¹	0.55 to 6.5 day⁻¹	
Estay et al. (2014)	Insects	Review of experiments	Temperature	Mixed	–	Mixed	Comparison*	−0.9 to +0.05 day⁻¹	0.41 to 1.1 day⁻¹	
Vasseur et al. (2014)	Invertebrates	Observational	Temperature	Mixed	–	Mixed	Sensitivity*	−1.9 to +9°C⁻¹	0.15 to 8103°C⁻¹	

'Response curvatures' describe the curvatures of the relationship between the population growth rate r_t or vital rates and the environment. 'Direction of effect' specifies the effect of increased environmental variance on the population's long-term growth rate (ns = not significantly different from zero, mixed = both positive and negative effects). 'Effect size' shows the strength of this effect on the logarithmic scale (r̄) and absolute scale (λ_s) (Box 1), together with the method used to estimate it (comparison = comparison between constant and variable environments, regression=regression of long-term growth rate against measure of environmental variance, elasticity=elasticity analysis; sensitivity=sensitivity analysis; *estimated from graph; †estimated from results).

Table 2 Environmental variance can amplify or weaken the effects of a change in the mean environment on long-term population growth $\bar{r}$, depending on the curvature of the underlying population growth response r_t around the old and the new mean environments. Environmental variance amplifies the effects of a change in the mean environment, if the growth rate curvature changes in the same direction as the growth rate, or weakens the effects of a change in the mean environment, if the growth rate curvature changes in the opposite direction to the growth rate (+, positive gradient or change in curvature; −, negative gradient or change in curvature).

Change in population growth rate $\frac{\delta r_t}{\delta z}$	Change in curvature of population growth response $\frac{\delta^3 r_t}{\delta z^3}$	Effect of mean environment on stochastic growth rate $\frac{\delta \bar{r}}{\delta z}$
+	+	Stronger positive effect
−	−	Stronger negative effect
+	−	Weaker positive effect
−	+	Weaker negative effect

ENVIRONMENTAL VARIANCE EFFECTS IN CHANGING MEAN ENVIRONMENTS

Theory

To predict species' responses to environmental changes such as global warming, we need to understand not only how environmental variance affects population growth rates when mean environmental conditions remain constant (as considered thus far; Fig. 1a–c) but also how such effects may change as mean conditions are altered (Fig. 1d–f). In this section, we will see that the direction and strength of these *mean–variance*

interactions can also be predicted based on the curvature of the population growth response.

Mean–variance interactions occur when the local curvature of the population growth response is different around the old and the new mean environments (Drake 2005; Koons *et al.* 2009; Estay *et al.* 2014; Vasseur *et al.* 2014). This is illustrated in Fig. 4, which shows how the stochastic growth rate $\bar{r}$ changes with the mean environment (*x*-axis) and with environmental variance (different lines) for three different population growth responses (taken from published case studies: Appendix S4). If the relationship between r_t and the environment is linear ($\frac{\delta^2 r_t}{\delta z^2} = 0$), environmental variance has no effect on $\bar{r}$ in any mean environment (Fig. 4a, d). If the r_t response is nonlinear but has a constant curvature (r_t is a second-order polynomial of z and thus $\frac{\delta^2 r_t}{\delta z^2}$ equals a constant), environmental variance has the same effects on $\bar{r}$ in all mean environments. In this case, changes in environmental variance alter the stochastic growth rate, but do not modify the effects of changes in the mean environment (Fig. 4b, e: the relationships between $\bar{r}$ and the mean environment in Fig. 4b are parallel). For environmental variance to have different effects in different mean environments, the population growth response must therefore not only be nonlinear, but must also have a curvature that changes with the environment (r_t must be a third- or higher-order polynomial of z, such that $\frac{\delta^2 r_t}{\delta z^2}$ changes with z; Fig. 4c, f). Importantly, such mean–variance interactions are solely due to the curvature of the underlying population growth response, rather than to any evolutionary or plastic changes in its form.
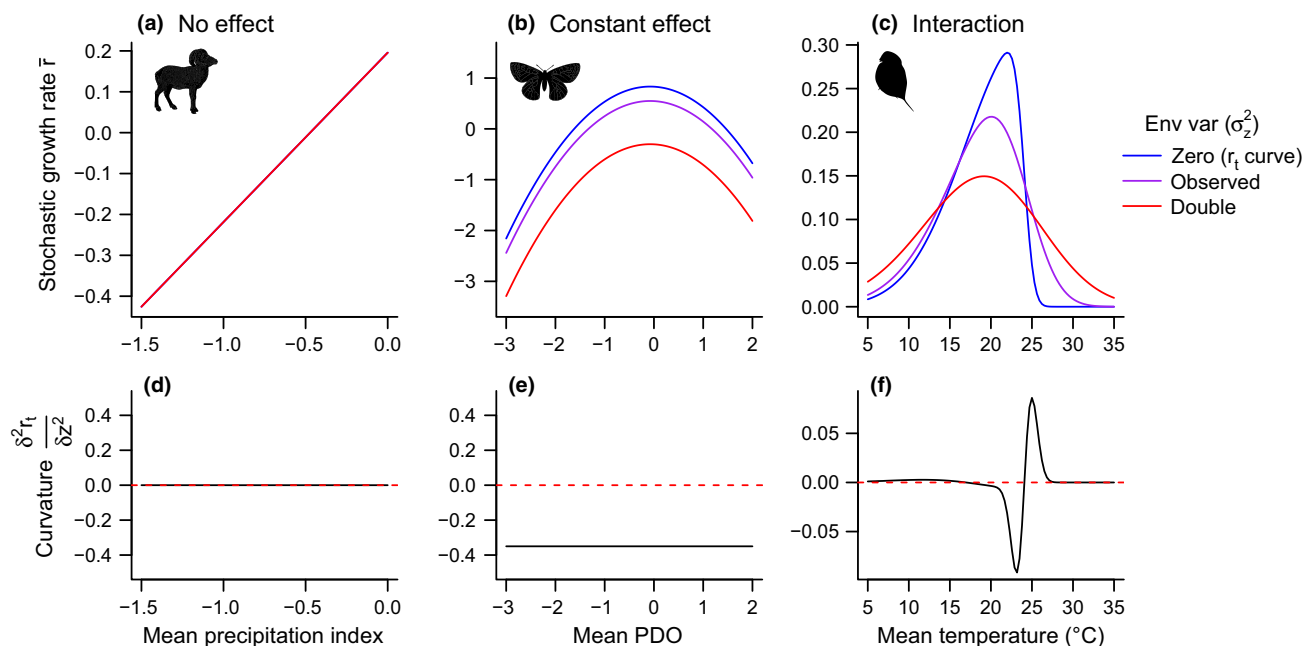

Figure 4 Differences in the curvature of the population growth response (r_t) between environments create interacting effects of environmental means and variances on the stochastic growth rate ($\bar{r}$). (a–c) Stochastic growth rates under different environmental means (*x*-axes) and variances (coloured lines) based on population growth models for three study species (a: *Ovis canadensis mexicana*; b: *Parnassius smintheus*, PDO = Pacific Decadal Oscillation; c: *Daphnia lumholtzi*; Appendix S4). For each species, three magnitudes of environmental variance are considered: (i) zero, in which case the response of $\bar{r}$ matches that of r_t; (ii) equal to the environmental variance observed in the case study; and (iii) double the observed variance. The second derivatives $\frac{\delta^2 r_t}{\delta z^2}$ (d–f) indicate how the curvature of the population growth (r_t) response changes with the environment, and thus whether environmental variance has (a) no effect on $\bar{r}$, (b) the same effect in all mean environments or (c) different effects in different mean environments.

Examining how the population growth curvature changes with the environment is key to understanding both the direction and strength of mean–variance interactions. The effects of environmental variance on $\bar{r}$ will change between positive and negative if the curvature of the r_t response changes between convex and concave ($\frac{\delta^2 r_t}{\delta z^2}$ changes in sign): for instance, in *Daphnia lumholtzi*, increased temperature variance is predicted to increase $\bar{r}$ at a mean temperature of 10°C, but decrease $\bar{r}$ at a mean temperature of 20°C (Fig. 4c). The strength of environmental variance effects on $\bar{r}$ is proportional to $\frac{\delta^2 r_t}{\delta z^2}$, and is often be most negative when the mean environment matches the 'optimum' environment in which r_t is maximised (García-Carreras & Reuman 2013), because this is the point at which population growth responses are typically most concave ($\frac{\delta^2 r_t}{\delta z^2}$ is most negative; e.g. Fig. 4c). However, the peak r_t does not always coincide with the minimum $\frac{\delta^2 r_t}{\delta z^2}$ (e.g. see Fig. 4b), so the prediction that increased environmental variance most strongly decreases $\bar{r}$ in species' optimal mean environments is a useful rule of thumb rather than a universal principle.

Conversely, the curvature of the population growth response can also be used to predict whether environmental variance accentuates or alleviates a population's vulnerability to changes in mean environmental conditions. In a variable environment, a change in the mean environment has more positive effects on $\bar{r}$, if the population growth curvature becomes more convex, or more negative effects, if the population growth curvature becomes more concave. Thus, environmental variance can accentuate or counteract the effects of a change in the mean environment, depending on whether the change in curvature works with or against the gradient of the growth response r_t (possibilities summarised in Table 2). In *Daphnia lumholtzi,* for example, the population growth response is more concave at high r_t but more convex at low r_t, such that environmental variance weakens the effects of a change in the mean environment on $\bar{r}$ (Fig. 4c). When the population growth curvature is asymmetrical, environmental variance can also shift the optimum mean environment in which $\bar{r}$ is maximised. For example, when temperature variation is higher, lower mean temperatures are better for long-term growth because they reduce the frequency of catastrophic population crashes that occur in rare extreme hot periods (e.g. Fig. 4c; Martin & Huey 2008). Thus, conditions perceived to be ideal for population growth when environmental variation is low may in fact be detrimental for population growth when environmental variation is high.

Empirical evidence

Our systematic review of the literature revealed only four empirical studies that tested for interacting effects of environmental means and variances on the stochastic growth rate (Table 1b). Nonetheless, in all cases the magnitudes of these effects were statistically and biologically significant, with changes in the mean environment altering the effects of environmental variance on the absolute rate of long-term population growth (λ_s) by 15% or more (Table 1b).

The strongest evidence for mean–variance interactions comes from experimental studies on ectotherms, which showed that increasing environmental variance increased $\bar{r}$ at low mean temperatures but decreased $\bar{r}$ at high mean temperatures (Bozinovic *et al.* 2011; Estay *et al.* 2014). These findings were consistent with the curvature of the population growth responses to temperature, which were convex at low mean temperatures but concave at high mean temperatures (Bozinovic *et al.* 2011; Estay *et al.* 2014). They also corroborate predictions of mean–variance interactions from a modelling study based on published ectotherm population growth responses, in which the combined effects of changes in the mean and variance in temperature on $\bar{r}$ differed from the sum of their separate effects (Vasseur *et al.* 2014, their figure 3). Available evidence thus suggests that, at least in ectotherms, interacting effects of mean and variance in temperature might be common.

The only study to investigate mean–variance interactions in a demographically-structured population was Jenouvrier *et al.* (2012, their figure 6). Using an empirically-derived model of emperor penguin *Aptenodytes forsteri* population growth, the authors predicted that interannual variation in sea ice concentration anomalies (SICa) would increase $\bar{r}$ at low and high SICa but would decrease $\bar{r}$ at intermediate SICa. This mean–variance interaction appears to be at least in part due to the adult survival response to SICa, which is convex at low and high SICa but becomes concave at intermediate SICa as the annual survival rate approaches its maximum of 1. This study thus suggests a potential link between mean–variance interactions and changes in the curvature of vital rate responses.

PREDICTING RESPONSE CURVATURES

We have seen that under certain assumptions (Box 1), the effects of environmental variance on stochastic population growth rates may be predicted from the curvatures of the population growth responses. Estimating these curvatures using species' traits might therefore provide a general means to infer their responses to changes in environmental variance, informing strategies to conserve species whose population growth rates have not or cannot be measured in the field.

In many cases, population growth responses may take forms that are consistent among taxa, if the environmental variable concerned affects population growth rates via the same mechanism. For example, temperature affects population growth by altering the rates of key metabolic processes involved in development (Paaijmans *et al.* 2013) or resource consumption (Dell *et al.* 2011): consequently, population growth responses to temperature often follow a typical form dictated by biochemical reaction rates, with an accelerating (convex) response at low temperatures (as predicted by the Arrhenius equation) that decelerates to a concave maximum at high temperatures as enzymes become denatured (Fig. 4c, 5a; Drake 2005; Angilletta 2009; Kingsolver 2009). Furthermore, the responses of consumer population growth rates to resource density typically become increasingly concave at high resource density, because the rate of population growth reaches a ceiling at which individuals are consuming resources as fast as they can (Fig. 5b; Turchin 2003). These classic growth response forms consistently and successfully describe population growth responses to temperature (Angilletta 2009; Dell *et al.* 2011;
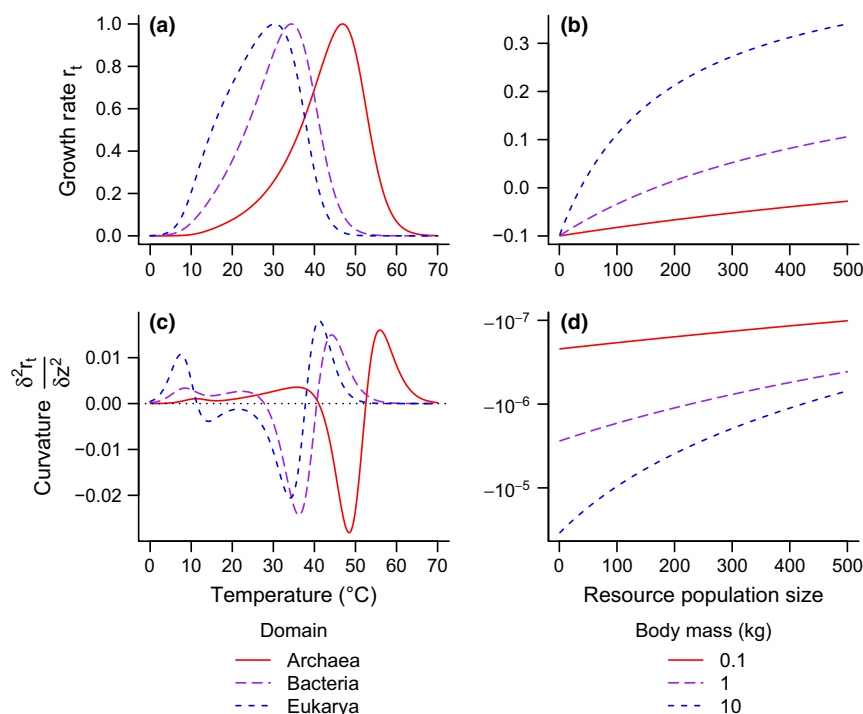
Figure 5 Species' traits determine the curvature of their population growth responses to temperature and resource abundance. Relationships between population growth and temperature are typically convex at low temperatures but reach a concave peak at higher temperatures (a), whereas relationships with resource density generally become increasingly concave at high resource densities (b; curvature shown by second derivatives in panels c and d). Species' traits create predictable differences in these response curvatures: differences in protein stability produce distinct thermal optima in unicellular organisms from the different domains of life (a,c), whereas physical constraints on feeding rates mean that consumer population growth responses to resource density are more concave when the body masses of both consumers and prey are scaled up by a common factor (b, d; Appendix S5). These differences in response curvatures could potentially be used to predict differences in species' responses to environmental variance.

Corkrey *et al.* 2012) and resource density (Rall *et al.* 2012), suggesting that species may respond to variance in these environmental variables in broadly similar ways.

Differences in species' traits may create consistent differences in population growth curvatures. For example, differences in protein stability create distinct thermal optima in unicellular organisms from the different domains of life (Corkrey *et al.* 2012), suggesting that temperature variance may begin to decrease population growth rates at lower mean temperatures in eukaryotes (10°C) than in archaea (40°C; Fig. 5a, c). Moreover, a meta-analysis of feeding rates (Rall *et al.* 2012) reports that when the body masses of consumer and resource species both become larger (i.e. are scaled up by a common factor), consumers encounter resource items more frequently but take longer to handle them; this suggests that larger species may have more quickly saturating (more concave) population growth responses to resource density, and thus that variance in resource density may more strongly reduce their stochastic growth rates (Fig. 5b, d). These examples indicate that species' traits such as phylogenetic history and body mass might be used to predict differences in the curvature of their population growth responses.

In demographically structured populations, environmental variance effects will generally need to be predicted directly from vital rate responses (see 'Theory' in section a), and the curvatures of these responses may also follow predictable patterns. For example, offspring survival responses may be more convex in cooperative breeders than in non-cooperative breeders, if help with parental care boosts offspring survival in unfavourable years but has little effect in favourable years (Jetz & Rubenstein 2011). More generally, natural upper and lower bounds can force vital rate responses to be concave or convex respectively. For instance, survival responses may be more convex in short-lived species in which annual survival rates are close to the minimum of 0, but concave in long-lived species in which annual survival rates are close to the maximum of 1 (Boyce *et al.* 2006; Van de Pol *et al.* 2010). However, there is as yet little theory for using these vital rate curvatures to predict the effects of environmental variance on the stochastic growth rate (see Discussion).

DISCUSSION

Implications for species' responses to global change

This review presents a synthesis of theoretical and empirical studies on population responses to temporal environmental variation. In general, we have found that population responses to changes in environmental variance are more diverse than often supposed. Empirical and theoretical studies show that increasing environmental variance does not always reduce long-term population growth, but can instead have a range of positive, neutral and negative effects, depending on the curvature of the population growth

response (Table 1a, Fig. 2). This suggests that conservation actions designed to buffer populations against temporal environmental variance (e.g. Turlure *et al.* 2010) could in some cases actually reduce their long-term growth rates and viability.

New empirical evidence also indicates that differences in environmental variance can greatly alter and even reverse the effects of changes in the mean environment on long-term population growth (Table 1b). One consequence of such mean–variance interactions is that the separate effects of changes in environmental means and variances may poorly approximate their combined effects: for example, increases in either the mean or the variance in temperature may increase the long-term growth of temperate ectotherm populations, whereas simultaneous increases in both the mean and the variance in temperature decrease their long-term growth by carrying individuals beyond their thermal limits (Fig. 4c; Kingsolver *et al.* 2013; Vasseur *et al.* 2014). Species might therefore be able to deal with changes in either the mean or the variance of the environment, yet be overwhelmed by simultaneous changes in both.

A second consequence of mean–variance interactions is that even in the absence of local adaptation, populations in different locations may respond differently to environmental change. For instance, increased temperature variance may have more severe effects on populations at the centre of species' ranges, where it deprives individuals of optimal conditions, than at the range edge, where it can introduce the higher temperatures needed for individual development and reproduction (García-Carreras & Reuman 2013). This implies that conservation actions to counteract environmental change may be more successful in particular regions: for example, increasing spatial heterogeneity in microclimates (Hodgson *et al.* 2009) may be most beneficial for populations at the centre of species' ranges.

A third implication of mean–variance interactions is that even if the magnitude of environmental variance remains constant, accounting for its effects may nonetheless be critical to predict population responses to changes in the mean environment. This is concerning, because most existing population dynamical models either omit temporal environmental variation entirely (Boyce *et al.* 2006; Bennie *et al.* 2013), or assume linear or quadratic population growth responses which dictate that the effects of environmental variance will be identical in all mean environments (e.g. Fig. 4a, b). The predictive accuracy of such models could thus be improved by incorporating stochastic variation in environmental conditions and allowing for more complex population growth response forms (see below).

The effects of environmental variance discussed above occur without any changes in individual vital rate responses to environmental conditions; in the long-term, however, such responses are likely to shift as species adapt to global change. Recent work suggests that species may adapt to environmental variance by diversifying their vital rate responses (Fig. 3; Barraquand & Yoccoz 2013), for instance by mixing 'labile', convex vital rate responses (Koons *et al.* 2009), which accelerate population growth in favourable years, with 'buffered', environmentally insensitive vital rate responses (Pfister 1998;

Boyce *et al.* 2006), which provide a safety net that limits population declines in unfavourable years. This diversification is consistent with the prediction from evolutionary bet-hedging theory that environmentally-insensitive lifestages such as long-lived adults (Schaffer 1974), diapausing eggs (Ellner 1997) and dormant seeds (Cohen 1993) act as adaptations to environmental variance by reducing between-individual correlations in reproductive success (Starrfelt & Kokko 2012). However, further work is needed to determine the circumstances under which diversified vital rate responses will be favoured by selection, which are likely to depend on whether covariation between vital rates enhances or reduces the population's long-term growth rate.

Using response curvatures to infer environmental variance effects

By altering long-term population growth rates, environmental variance could fundamentally alter the success of strategies to conserve biodiversity under global change – but how can such effects be anticipated in many different species when they have been quantified in only a handful of study systems (Table 1)? We suggest that the effects of environmental variance on long-term population growth rates could be inferred from species' traits such as phylogenetic history or body mass, by (1) determining how the trait affects the curvature of population growth or vital rate responses, and then (2) using these response curvatures to predict the effects of environmental variance on the long-term population growth rate. This approach capitalises on existing knowledge of the biological mechanisms underpinning population growth and vital rate responses to environmental variables. It would also make efficient use of available data, because such responses are more widely documented than population responses to environmental variance *per se*.

Although few studies have explicitly examined whether response curvatures can be predicted using species' traits, available empirical evidence nonetheless suggests that population growth responses to two major environmental drivers of population dynamics – namely, temperature and resource availability – have characteristic curvatures that differ predictably with phylogenetic history and body mass (Fig. 5). Additional relationships between traits and response curvatures could be assessed through meta-analyses of published population growth and vital rate responses to environmental variables (e.g. Porter & Semenov 2005; Angilletta 2009; Dell *et al.* 2011; Rall *et al.* 2012). Differences in response curvatures could be tested by fitting flexible response functions using generalised additive models (Wood 2006), by competing pre-defined functional forms that imply different effects of environmental variance (e.g. first-, second- and third-order polynomial functions to test for zero, constant and interactive effects of environmental variance respectively; Fig. 4), or by testing for differences in underlying parameters such as resource consumption rates (Fig. 5b; Appendix S5). The main practical challenge would be to estimate response curvatures with sufficient accuracy, which becomes difficult if population growth has been measured on too few occasions (e.g. typically fewer than four times in plant matrix population models: Crone *et al.* 2011), or in too few distinct environments (e.g.

typically fewer than six temperatures in experimental studies: Deutsch *et al.* 2008). Nonetheless, these data limitations could be accounted for by propagating uncertainties in curvature estimates through to meta-analysis results, whilst gaps in available data could be filled by new experiments quantifying response curvatures across a continuous range of environments (Inouye 2005).

How well can estimated response curvatures approximate the effects of environmental variance on the population's long-term growth rate? For unstructured populations, in which vital rate responses are identical among individuals, there is now a rapidly maturing theory linking population growth curvatures to the effects of environmental variance on the stochastic growth rate. Empirical evidence tentatively supports the use of this theory to infer the direction of environmental variance effects, but its quantitative accuracy is yet to be assessed. In comparison, theory to predict effects of environmental variance on the stochastic growth rate of demographically-structured populations remains relatively undeveloped. In this case, environmental variation typically drives transient fluctuations in demographic structure that preclude the use of population growth curvatures. Moreover, whilst vital rate curvatures can be used to separately estimate the effects of environmental variance on the mean of each vital rate, these effects can be poor predictors of long-term population growth if vital rates covary within or between demographic classes (Fig. 3; Coulson *et al.* 2005; Doak *et al.* 2005). Future theoretical work could aim to resolve this difficulty by developing ways to predict the effects of environmental variance from vital rate curvatures whilst accounting for covariance between them.

Extensions to more realistic scenarios

We have depicted complex patterns of environmental variability using the temporal variance of a single environmental variable, but this simplified picture can be fleshed out with more realistic details such as changes in the symmetry (skew) of the environmental distribution or changes in the variance of multiple environmental variables. Changes in environmental skew alter the stochastic growth rate when the curvature of the population growth response differs between environments (i.e. when its third derivative $\frac{\delta^3 r_t}{\delta z^3}$ is non-zero; Appendix S6); these effects become stronger when the environmental variance is higher, but are generally small relative to those of environmental means or variances (Appendix S6; Vasseur *et al.* 2014). Multiple environmental variables can be incorporated piecemeal by separately summing their effects on the stochastic growth rate, or together by constructing a joint population growth response function which accounts for interactions between their effects: for example, drought might reduce population growth more when it is warm than when it is cold. These more detailed descriptions of environmental variability come at the expense of increased model complexity, and thus require more population growth measurements.

Other studies have bypassed measurement of the environment entirely and instead directly examined how long-term rates of population growth or persistence depend on the temporal distribution of population growth or vital rates (e.g.

Morris *et al.* 2008; Jongejans *et al.* 2010). This 'environment-blind' approach can be used to explore what-if scenarios that incorporate the full range of observed variability of population growth or vital rates (Crone *et al.* 2011), which can only be partially captured by responses to specific environmental variables. In general, however, variation in population growth cannot be directly equated with variation in the environment (except under the strong assumption of a linear population growth response: Fig. 2b), so for examining the consequences of changes in environmental variance, there is no substitute for explicit measurements of environmental conditions. Where environmental variables are explicitly included, careful characterisation of residual temporal variance in growth rates can help to capture the full range of observed variability in population dynamics. If independent of the effects of measured environmental variables, such residual variance will not affect the population's long-term growth rate, although it will reduce its persistence time (Ovaskainen & Meerson 2010).

Throughout this review, we have assumed that population growth is density-independent, but in most natural populations the stochastic growth rate will approach zero as negative density-dependence in vital rates restricts the population to an equilibrium size (the carrying capacity). Are population growth or vital rate curvatures still useful for predicting the effects of environmental variance in this context? Empirical studies of density-dependent population dynamics have suggested links between vital rate curvatures and environmental variance effects on mean population size or persistence time (e.g. Van de Pol *et al.* 2010, McCaffery *et al.* 2012), but these links are yet to be systematically tested. Theoretical studies indicate that increased environmental variance typically reduces population persistence (reviewed in Ovaskainen & Meerson 2010) and can either increase or decrease mean population size depending, on whether the population size is restored to the carrying capacity more quickly when perturbed above vs. below the carrying capacity (Levins 1969; Roughgarden 1979); however, these studies have generally assumed linear population growth responses to the environment. Nonetheless, studies relaxing this assumption have shown that vital rate curvatures determine the effects of environmental variance on the mean population size (Barraquand & Yoccoz 2013), and that nonlinear population growth responses can facilitate the persistence of competing populations in variable environments (reviewed in Chesson 2000). These results indicate that response curvatures can continue to provide insight into the effects of environmental variance when population dynamics are density-dependent.

CONCLUSION

Recent theoretical and empirical work shows that fluctuations in environmental conditions can have important effects on species' responses to global change. In particular, changes in environmental variance can increase as well as decrease long-term population growth rates, and the magnitude of environmental variance can greatly alter population responses to changes in the mean environment. We suggest that these effects of environmental variance could be anticipated by studying the biological mechanisms underpinning the curva-

ture of population growth and vital rate responses to the environment, providing a general basis to forecast species' responses to global change in a variable world.

AUTHORSHIP

The project was conceived by CRL and MvdP, and developed with YV and LB. CRL wrote the manuscript and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION