Ecological and evolutionary impacts of changing climatic variability

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ABSTRACT

While average temperature is likely to increase in most locations on Earth, many places will simultaneously experience higher variability in temperature, precipitation, and other climate variables. Although ecologists and evolutionary biologists widely recognize the potential impacts of changes in average climatic conditions, relatively little attention has been paid to the potential impacts of changes in climatic variability and extremes. We review the evidence on the impacts of increased climatic variability and extremes on physiological, ecological and evolutionary processes at multiple levels of biological organization, from individuals to populations and communities. Our review indicates that climatic variability can have profound influences on biological processes at multiple scales of organization. Responses to increased climatic variability and extremes are likely to be complex and cannot always be generalized, although our conceptual and methodological toolboxes allow us to make informed predictions about the likely consequences of such climatic changes. We conclude that climatic variability represents an important component of climate that deserves further attention.

Key words: climate change, community structure, demography, fitness, geographic range limits, phenological mismatches, phenotypic plasticity, physiological traits, population dynamics, species interactions.

CONTENTS

I. INTRODUCTION

The Earth's climate is changing rapidly. Available data indicate a trend towards increasing global temperatures. Causes for these temperature changes are intricate and associated with a network of events in which human activities appear to play a determinant role (Trenberth, 2011). In addition to increased temperature averages, human-caused climate change is expected to lead to increased climatic temporal variability and increased occurrence of climatic extremes in many places (e.g. droughts, excessive precipitation, heat waves; Easterling *et al*., 2000; Burroughs, 2007; Meehl *et al*., 2007; Coumou & Rahmstorf, 2012). Under some climate change scenarios, climatic variability and extremes are expected to increase more than climatic averages for some regions (Meehl *et al*., 2007).

A mechanistic understanding of the biological consequences of climate change requires the integration of physiology, ecology, and evolutionary biology (Spicer & Gaston, 1999). Although biologists widely recognize the potential impacts of changes in average climatic conditions, relatively little attention has been paid to the potential impacts of changes in climatic variability and extremes (Benedetti-Cecchi, 2003; Jentsch, Kreyling & Beierkuhnlein, 2007; Bozinovic, Calosi & Spicer, 2011*b*; Thompson *et al*., 2013), and we know relatively little about the mechanisms underlying these potential impacts. Enhancing this understanding and highlighting gaps in our knowledge is the main goal of this review.

When discussing the ecological and evolutionary implications of increased climatic variability and climatic extremes, it is important to define precisely these attributes of climate. Climatic variability can be defined as the standard deviation or the variance of a climate variable such as temperature, or by a relativized measure of variability such as the coefficient of variation. Defining the frequency of occurrence of extreme climatic events in statistically precise terms is more elusive. Often extremes are defined in relation to a climate record for a certain period (e.g. three standard deviations away from the mean temperatures from 1960 to 2010). However, this definition is problematic, as it implies that an increase in the mean temperature, with no change in the shape of the distribution around the mean, would increase the frequency of high extremes and decrease the frequency low extremes, whereas a change in climatic variability might lead to increased extremes at both ends of the distribution. Alternatively, extremes can be defined as events that influence the shape of the distribution of a climatic variable without influencing the mean and the variance—i.e. the kurtosis (Fig. 1). Thus, an increase in the frequency of extreme events would make the distribution of the climatic variable more leptokurtic, while a decrease in the frequency of extreme events would make the distribution more platykurtic, without necessarily changing the mean or the variance of the climatic variable.

Here we review the evidence on the impacts of increased climatic variability and extremes on physiological, ecological and evolutionary processes at multiple levels of biological organization, from individuals to populations and communities. Specifically, we consider the responses to increased climatic variability and extremes in terms of (*i*) physiology and performance including Darwinian fitness, (*ii*) phenotypic plasticity, (*iii*) demography and population dynamics, and (*iv*) community structure and dynamics.

II. PHYSIOLOGY, INDIVIDUAL PERFORMANCE AND FITNESS

(1) Individual performance and fitness

Recent models of the physiological, ecological and evolutionary responses of organisms to climate change indicate that a change in thermal variance could have as much (or more) of an impact on fitness as does a change in the mean temperature (Bozinovic *et al*., 2013*a*; Bozinovic, Catalán & Kalergis, 2013*b*; Estay, Lima & Bozinovic, 2014). The typically unimodal, asymmetric shape of the relationship between temperature and performance, which tends to accelerate below the optimum temperature but decelerate above the optimum, implies that the impact of thermal variation on physiological performance will depend on the mean temperature in relation to the temperature at which performance peaks (Bozinovic *et al*., 2011*a*). When mean temperature is below the thermal optimum, thermal variation can either enhance or reduce physiological performance; by contrast, when mean temperature is equal to or greater than the thermal optimum, thermal variation will always impair performance (Fig. 2). Thus, the mean and variance of temperature will interact predictably to determine Darwinian fitness in a variable environment.

Several studies provide experimental evidence for the influence of thermal variance on individual performance. Bozinovic *et al.* (2011*a*) observed that thermal variation enhanced the population growth rate of the fruit fly *Drosophila melanogaster* at a low mean temperature, while it decreased this rate at the thermal optimum, despite the fact that flies improved their heat and cold tolerances through environmental acclimation. Siddiqui, Barlow & Randolph (1973) reported significantly different effects of constant and alternating temperatures on population growth of the pea aphid *Acyrthosiphon pisum*; in addition, the net reproductive rate (R_0) and the intrinsic rate of increase (r) differed in their response to different temperature regimes. More recently, Clavijo-Baquet *et al.* (2014) found similar results for the effects of thermal mean and variability on R_0, r and the generation length T_g, of *D. melanogaster*, with no effects of temperature variation on r despite strong effects on R_0 and T_g. Thus, considering that $r \approx \ln\left(R_0\right)/T_g$, thermal effects on R_0 and T_g cancel each other. Likewise, Kjaersgaard *et al.* (2013) reported that increased temperature variability decreased the individual performance of yellow dung flies *Scatophaga stercoraria*. Furthermore, some studies have shown that moderate amounts of environmental variability do not necessarily have detrimental effects on performance, compared to greater levels of variability (Pétavy *et al*., 2004; Folguera *et al*., 2011). Although experimental approaches cannot capture the wide range of abiotic and biotic conditions in nature, they help us to understand the mechanisms by which climate change may impact organisms. This kind of experiment can also shed light on geographic variation in phenotypes, because diel and seasonal patterns of environmental temperature change along latitudinal and altitudinal gradients (Angilletta, 2009). Indeed, Kjaersgaard *et al.* (2013) advocate the use of more relevant fluctuating temperatures in experimental studies of the ecological impact of climate change.

It is important to note that individual performance can change with increased temperature variability even if average temperature does not change. This is because of Jensen's inequality, a property of nonlinear functions, which states that, for a sample of x values with mean $\bar{x}$ and a nonlinear function $f(x)$, $\overline{f(x)} > f(\bar{x})$ if $f(x)$ is accelerating (second derivative is positive) and $\overline{f(x)} < f(\bar{x})$ if $f(x)$ is decelerating (second derivative is negative; Ruel & Ayres, 1999). Thus, the typically unimodal, asymmetric shape of the relationship between body temperature and physiological performance (Fig. 2) should lead to complex effects of thermal variance (Estay *et al.*, 2011): close to the peak of the function, greater temperature variability should decrease physiological performance, whereas at the lower tails of the function greater temperature variability should increase performance. For example, Siddiqui & Barlow (1972), conducted a now classic study that showed that thermal fluctuations, within the range of temperatures favourable for reproduction, enhanced the rate of population growth. Later, Orcutt & Porter (1983) observed a slightly positive effect of thermal variation on the population growth rate of water fleas *Daphnia* sp. This result could be attributed to the range of experimental temperatures used, which was in the accelerating (left tail) part of the performance curve. In turn, Estay *et al.* (2011) found that thermal variation had a negative effect on the population growth of flour beetles *Tribolium confusum* when mean temperature was in the decelerating part of the performance curve. Similar interactions between the mean and the variance of temperature have been observed in other studies (Dallwitz, 1984; Paaijmans *et al.*, 2010; Bozinovic *et al.*, 2013*a*; Estay *et al.*, 2014).

A mechanistic understanding of organismal responses to climatic variability requires elucidating the underlying cellular and physiological processes that allow animals to cope with such variation. When exposed to stress, organisms respond in multiple ways, including DNA and protein repair, apoptosis, removal of cellular and molecular waste generated by stress, and changes in cellular metabolism to switch from cellular growth to repair (Kassahn *et al.*, 2009). Thus, organisms are constrained by a trade-off between response to stress and allocation to growth and reproduction (Somero, 1995). A key component of such responses are heat shock proteins, which have an important function in cells under stressful conditions and are necessary for the survival and recovery of organisms, often by rescuing critical metabolic enzymes from destruction (Parsell & Lindquist, 1994). Experiments have shown that small amounts of induced heat shock proteins can influence development, life span, fecundity and stress resistance (Sørensen *et al*., 1999). Therefore, the influence of heat shock proteins has the potential to scale up to populations and communities. The very existence of these molecular and integrative responses to climate suggests that thermal fluctuation may be an important selective factor in nature. In addition, the effects of different thermal conditions are directly related to the thermal safety margin—i.e. the difference between an organism's thermal optimum and its current environmental temperature (Deutsch *et al*., 2008; Folguera, Bastías & Bozinovic, 2009). Future interpopulation comparisons might reveal higher sensitivity to thermal amplitude in, for instance, lowland than in highland populations, indicating that important effects on biodiversity may be expected in the context of increasing thermal amplitude.

(2) Macrophysiological patterns

Macrophysiology seeks to explain how physiological traits are affected by environmental variation over large geographic scales. For instance, compared to tropical taxa, species from temperate latitudes are thought to experience selection for greater plasticity because they live in more seasonal environments (Chown, Gaston & Robinson, 2004; Ghalambor *et al*., 2006). The latter is the case particularly in northern latitudes, where differences between absolute maximum and absolute minimum temperatures are greatest (Addo-Bediako, Chown & Gaston, 2000; Chown *et al*., 2004). Supporting evidence of a hemispheric asymmetry in physiological tolerance (with assumed underlying plasticity) has been reported for insects (Addo-Bediako, Chown & Gaston, 2002; Sinclair, Addo-Bediako & Chown, 2003) and terrestrial isopods (Bozinovic *et al*., 2014), but evidence for other taxa is lacking.

Data on latitude and thermal amplitude show that the increased temperature variation in temperate regions results from the pattern of variation of minimum temperatures, with maximum temperatures being equally variable across latitude (Chown *et al*., 2004*b*; Ghalambor *et al*., 2006). Therefore, the expected increased selection on plasticity in temperate species—compared to tropical taxa—should occur for responses to cold and not to warming. This prediction has been corroborated for insects, frogs, and lizards (see Ghalambor *et al*., 2006). In addition, Vasseur *et al.* (2014) recently demonstrated the independent and interactive effects of mean temperature and its variability on thermal performance curves for nearly 40 ectothermic invertebrates with worldwide distributions. With the use of fine-grained, site-specific historical temperature data, Vasseur *et al.* (2014) showed how changes in the mean, variance and positive skewness of historical temperatures have significant influences on organismal performance. Furthermore, for ectotherms, thermal performance—and hence fitness—tends to decline or remain unchanged under future climate scenarios, with greater declines occurring at mid to low latitudes (see also Deutsch *et al*., 2008).

III. PHENOTYPIC PLASTICITY

(1) Phenotypic plasticity and adaptation to changing environments

Increased climatic variability may be envisioned as a particular case within the general phenomenon of changing environments. Adaptation of organisms to changing environments occurs mainly by two mechanisms: (*i*) genetic differentiation, i.e. across-generations phenotypic adjustment to the prevailing environmental conditions as a result of selection on heritable traits, and (*ii*) phenotypic plasticity, i.e. within-generation phenotypic changes induced by the environment (Schlichting & Pigliucci, 1998; Réale *et al*., 2003). Evidence strongly suggests that phenotypic plasticity, which may even be reversible (Garland & Kelly, 2006), is essential for adaptation to climate change and increased climatic variability, and that evolutionary rates cannot always keep up with climate change (Jump & Peñuelas, 2005; Davis, Shaw & Etterson, 2005; Gienapp *et al*., 2008; Charmantier *et al.*, 2008; Ozgul *et al.*, 2010; Hoffmann & Sgrò, 2011; but see Visser, 2008). For instance, the advancement in parturition date of the North American red squirrel, *Tamiasciurus hudsonicus*, in response to climate change is mostly due to phenotypic plasticity (62%), while microevolutionary changes account for 13% of the phenotypic change (Berteaux *et al.*, 2004; Anderson *et al.*, 2012). In a modelling study, Chevin, Lande & Mace (2010) found that the critical rate of environmental change, i.e. the maximum rate of sustained environmental change that allows population persistence, increases with decreasing absolute difference between phenotypic plasticity and the environmental sensitivity of selection (the change in the optimum phenotype with the environment). In other words, the closer plastic responses in a given population track the shift in the favoured phenotype that occurs when the environment changes, the greater magnitude of sustained environmental change this population will tolerate. Nonetheless, it is likely that rapid responses to environmental change *via* phenotypic plasticity may be followed by selection and microevolution (Matesanz, Gianoli & Valladares, 2010; Godoy *et al.*, 2011; Brunet & Larson-Rabin, 2012).

Phenotypic plasticity is expressed in the reaction norm: the repertoire of phenotypic responses to environmental variation of a given genotype, population, or species (Pigliucci, 2001; Gianoli & Valladares, 2012). The reaction norm itself may evolve by natural selection (Scheiner & Lyman, 1991; Pigliucci & Schlichting, 1996; Scheiner & Callahan, 1999; Garland & Kelly, 2006; Baythavong & Stanton, 2010). Selection on reaction norms and performance curves in a population should be driven by the frequency (and predictability) of the environments experienced by organisms (Weis & Gorman, 1990; Gilchrist, 1995; Alpert & Simms, 2002; Kingsolver *et al.*, 2007). Phenotypic plasticity should be important not only to deal with the increasing rate of climate change, but also with the increased unpredictability of climatic anomalies (Arias, Poupin & Lardies, 2011). An experimental study with ten sub-Antarctic weevil species found that phenotypic plasticity accounted for most of the between-population variation in critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) (Klok & Chown, 2003). Weevils acclimated for only one week at

15 ºC raised their CT_{max} by 2.4 ºC, compared to those maintained at 0 ºC (Klok & Chown, 2003). Interestingly, Skelly *et al.* (2007) estimated the potential for evolutionary response in CT_{max} in ectotherms and predicted an increase in 3.2 ºC across 10 generations (50 years). Thus, within a single generation plastic responses drive an increase in CT_{max} that is 75% of that calculated for 10 generations when only evolutionary responses are considered. Furthermore, an extreme environment may allow the expression of formerly 'hidden' parts of the reaction norm, which may reveal the existence of cryptic genetic variation upon which natural selection may act (Schlichting, 2008). Overall, in view of the problem of decreased performance in ectotherms caused by climatic variation illustrated in Fig. 2, adaptive phenotypic plasticity may be conceived to function as a buffer to minimize the coupling of environmental temperature and body temperature, in a context of increased climatic variability.

(2) Patterns of phenotypic plasticity at the population level

Theory predicts that increased environmental variation should select for increased phenotypic plasticity (Schlichting & Pigliucci, 1998; Alpert & Simms, 2002). Some studies have proved the increased magnitude and adaptive value of phenotypic plasticity in spatially heterogeneous environments (Lind & Johansson, 2007; Hollander, 2008; Baythavong, 2011), but in the context of climatic variation associated with climate change it is more relevant to focus on temporal heterogeneity. We surveyed published studies to evaluate this theoretical prediction in plant populations from habitats with contrasting temporal environmental heterogeneity. Plants are appropriate study subjects to evaluate this prediction because they are sessile, which means they cannot migrate to avoid harsh climatic conditions (Post *et al*., 1999; Réale *et al*., 2003; Battisti *et al*., 2006). We specifically focused on those studies reporting plant responses to temperature and soil moisture, which are the components of climate change that are more relevant to plants (Matesanz *et al*., 2010). We found 11 studies that met these conditions, including 14 cases from 12 species (Table 1). Phenotypic plasticity data included physiological, morphological, and life-history traits (references in Table 1).

Results support the theoretical expectation that increased plasticity is selected for in more variable environments. There was a significant positive association between phenotypic plasticity in plant populations and temporal heterogeneity in rainfall or temperature (10 out of 14 cases; Table 1). These preliminary results with plant species suggest that increased phenotypic plasticity may drive adaptation to increased climatic variability in natural populations. A broader sample of studies is needed to determine whether other taxa respond similarly, and whether the detection of this relationship is influenced by the type of traits studied or the intrinsic characteristics of the organisms.

(3) Evolution of increased plasticity

How could increased climatic variability select for increased phenotypic plasticity? Schlichting & Pigliucci (1998) discuss two general models for genetic control of plastic responses: allelic sensitivity and gene regulation. Allelic sensitivity refers to changes in the amount of a given gene product in response to changes in the environment, and is considered a 'passive' form of plastic response that is not necessarily adaptive (Schlichting & Pigliucci, 1998). This mechanism has been found in insects (Schmalhausen, 1949), bacteria (Hartl & Dykhuizen, 1981), plants (Kliebenstein, Figuth & Mitchell-Olds, 2002) and nematodes (Gutteling *et al.*, 2007), and is expected to be involved in plastic responses to temperature because of the close link between enzyme activity and temperature (Schlichting & Pigliucci, 1998). By contrast, gene regulation involves the existence of an environment-dependent regulatory switch in gene expression, resulting in a threshold response, and is considered an 'active' form of plastic response, most likely of adaptive nature (Schlichting & Pigliucci, 1998). Examples of taxa in which this mechanism has been observed include plants (Doebley, Stec & Gustus, 1995), insects (Fairbairn & Yadlowski, 1997), molluscs (Egg *et al.*, 2009), and bacteria (Rivera-Gómez, Segovia & Pérez-Rueda, 2011). These two mechanisms are not mutually exclusive, as shown by Wu (1998) for growth traits in poplar trees. Furthermore, epigenetic phenomena, i.e. heritable changes in gene expression that are not mediated by changes in DNA sequence (Richards, 2006), may mediate functional responses to the environment (Bossdorf, Richards & Pigliucci, 2008; Chinnusamy & Zhu, 2009; Bräutigam *et al*., 2013; Herman *et al*., 2014). Examples of epigenetic modifications driving phenotypic plasticity include flowering regulation in response to cold exposure in *Arabidopsis thaliana* (Kim & Sung, 2012), biomass allocation responses to water shortage in poplars (Gourcilleau *et al*., 2010), niche width in a flower-living yeast (Herrera, Pozo & Bazaga, 2012), and transgenerational induction of plant defences against herbivores and pathogens (Holeski, Jander & Agrawal, 2012).

Gene regulation should be particularly advantageous for non-instantaneous plastic responses, such as those involving biomass allocation, whose complete expression involves a time lag between the appearance of the environmental cue (the stimulus) and the deployment of the target phenotype in the selective environment. Several studies indicate that reliable cues triggering plastic responses and somewhat predictable environments are required for plasticity to be adaptive (DeWitt, Sih & Wilson, 1998; Langerhans & DeWitt, 2002; Alpert & Simms, 2002; Van Kleunen & Fischer, 2005; Ghalambor *et al*., 2007; Reed *et al*., 2010; Scheiner & Holt, 2012; van den Heuvel *et al*., 2013). Pigliucci (2001) provides a detailed analysis of evolutionary outcomes concerning phenotypic plasticity in the presence and absence of environmental cues, considering the duration of temporal fluctuation as compared to generation time. In some masting plant species (those that show sporadic reproductive outbreaks that satiate herbivores) synchronous fruiting was associated with anomalously high temperatures in the summer before seedfall, a cue linked with the La Niña climatic phenomenon (Schauber *et al*., 2002). If the frequency of such anomalously high temperatures increases, masting might no longer be adaptive in terms of realized herbivore satiation (McKone, Kelly & Lee, 1998). In fact, in most of the reported cases of successful tracking of climate change, including species from diverse phyla, the climatic shift has been rather monotonic (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Cleland *et al.*, 2007; Walther *et al.*, 2007; Charmantier *et al.*, 2008). In general, if in order to adapt to seasonal changes species rely on photoperiod alone (e.g. Lambrechts & Perret, 2000), they are likely to fail to adjust to the actual environment because of the recent shift (or even uncoupling) in the relationship between temperature and photoperiod driven by climate change (Visser, Both & Lambrechts, 2004). Alternatively, if species rely on temperature alone (e.g. Condon, Chenoweth & Wilson, 2010), anomalous high-temperature periods may induce maladaptive responses (Powell & Logan, 2005), depending on the threshold of response. A mixed control on plasticity of phenology, by both photoperiod and temperature, could be a better strategy; this has been shown for several moth species at high latitudes (Valtonen *et al.*, 2011). The interaction between resource availability and climate as environmental cues is also a potentially advantageous alternative to track climate change-driven anomalies better (Visser *et al.*, 2004).

Returning to the question of how increased climatic variability could select for phenotypic plasticity, and assuming a gene regulatory system underlying the plastic responses, we show in a conceptual model (Fig. 3) the likely outcomes for two climate change scenarios: (*i*) a temporal shift in environmental quality, and in its corresponding cue for the initiation of the plastic response (Fig. 3A), and (*ii*) a temporal shift in environmental quality plus climatic variability (a short-term anomaly counteracting the climatic trend; Fig. 3B). Our analysis considers three genotypes with different phenotypic responses to the environment across the season (Fig. 3C,D). The black genotype is not responsive to climate change or climatic variability, thus maintaining the phenotypic trajectory that matches the historical climate. The red genotype tracks both climate change and climatic variability, adjusting its reaction norm accordingly. The purple genotype adjusts its reaction norm, as for the red genotype, and shows increased plasticity, envisioned as a likely response to an increasingly heterogeneous environment. We then estimate the relative advantage of each strategy (genotype) considering two possible adaptive landscapes: directional and stabilizing selection (Endler, 1986). When directional selection prevails, increased phenotypic plasticity (purple) is favoured under both climatic scenarios, especially under climatic variability (Fig. 3E,F). By contrast, if stabilizing selection prevails, increased plasticity is not beneficial, being as (mal)adaptive as the unresponsive black genotype under both climatic scenarios; the red genotype is favoured instead. Therefore, whether increased plasticity is favoured would ultimately depend on the form of natural selection acting at the end of the season. The latter is influenced by both the selective factors operating and the traits involved (Endler, 1986; Kingsolver *et al*., 2001; Geber & Griffen, 2003), which may show ontogenetic variation in their environmental sensitivity (e.g. Arias *et al*., 2011). Thus, temperature-related performance traits regularly show an optimum, with low and high levels having a lower adaptive value (Huey & Kingsolver, 1989; Angilletta, Niewiarowski & Navas, 2002; Seebacher, 2005); by contrast, water-economy traits often show linear relationships with performance (Dudley, 1996; Heschel *et al*., 2004; Saldaña *et al*., 2007). Nonetheless, stabilizing selection is less frequent and usually weaker than directional selection in natural populations (Kingsolver *et al*., 2001). In any event, increased levels of climatic complexity (the particular sequence and duration of environmental states) may complicate patterns of selection on thermal performance curves and other continuous reaction norms (Valladares, Gianoli & Gómez, 2007; Kingsolver *et al*., 2007). Moreover, a comprehensive and realistic analysis must take into account the role of correlations between characters of functional value, which may constrain the evolution of adaptive responses to climate change (Etterson & Shaw, 2001; Gianoli & Palacio-López, 2009).

The above analysis may allow identifying the different targets involved in adaptive evolution of phenotypic plasticity to deal with climatic variability. First, it may entail the evolution of responsiveness (the red genotype), i.e. a shift in the environmental threshold of response or a change in the eliciting cue. This has been shown for the flowering time in an annual plant, with summer drought selecting for early flowering and causing adaptive evolution in a few generations (Franks, Sim & Weis, 2007). Second, it may involve the evolution of increased plasticity (the purple genotype), i.e. a reaction norm with a steeper slope. This has been demonstrated for an insectivorous bird, which was able to change the duration of components of breeding behaviour in order to track the temporal shift in food availability (Charmantier *et al*., 2008). Finally, adaptation to climatic variability may include the arrestment or reversion of phenotypic changes, once the climatic anomaly is detected (the red and purple genotypes). Of course, this is possible only for certain traits, with behaviour appearing as a suitable candidate. Besides the above-mentioned study on adaptive responses to climate change in bird breeding behaviour (Charmantier *et al*., 2008), it has been reported for the same species that (*i*) there is no response of birds to warming in physiological or morphological traits (Visser *et al*., 2011), (*ii*) the cue is increased temperature and not mean temperature (Schaper *et al*., 2012), and (*iii*) there is genetic variation for cue sensitivity (Visser *et al*., 2011), thus providing the basis for an evolutionary response to natural selection. In a related species, Vedder (2012) recently showed experimentally that birds are able to advance offspring hatching in response to increased temperature after the start of laying. Can other groups do equally well when the trait is other than behaviour? Further research is needed to address this question (see Parmesan, 2006; Skelly *et al*., 2007; Visser, 2008; Hoffmann & Sgrò, 2011).

IV. DEMOGRAPHY AND POPULATION DYNAMICS

(1) Review of relevant theory

Population theory has primarily examined how changes in environmental variability will influence the average rate of annual population growth over the long term, the so-called stochastic population growth rate, λ_s (Caswell, 2001). This rate represents the appropriate average multiple by which the size of the population changes from one year to the next over a long period of time during which the actual population growth rates differ from year to year because of environmental variation. If

$\lambda_s > 1$, the population tends to increase over the long term, while if it is below one, the population tends to decline. Year-to-year variation in the population growth rate arises because of variation in the 'vital rates' (survival, somatic growth, and reproduction of individuals in all life stages, plus recruitment of new individuals) that collectively govern the loss of existing individuals and the addition of new individuals to the population. Temporal variation in the vital rates is in turn driven by year-to-year variation in environmental conditions (e.g. Doak & Morris, 2010).

Ideally, we would like to be able to say whether an increase in the variance of the vital rates driven by changes in environmental variability (keeping the mean vital rates constant) would either increase or decrease λ_s. Unfortunately, population theory demonstrates that a categorical statement about the effects of increasing environmental variability on the population growth rate is impossible to make. Instead, the answer is that increasing variability can either increase or decrease the rate of population growth over the long term, depending on numerous details about how the environment varies and about the demography of the species in question (Fig. 4). We now briefly summarize the most important of these details.

The first thing we need to know to predict if increasing environmental variability would increase or decrease the long-term population growth rate is how the environment varies. The simplest case is that environmental variability is independently and identically distributed (IID), meaning that environmental conditions (or more precisely the resulting vital rates) are drawn each year from a statistical distribution with a constant (i.e. 'identical') shape and in which the value in one year is drawn 'independently' from the values in all previous years. We would then be asking how a step-like increase in the variance of the distribution (i.e. a one-time change in the variance to a new, higher value) affects λ_s. In the simplest case in which the population is 'unstructured' (i.e. all individuals contribute equally to population growth) and generations do not overlap, increasing the variance of the annual population growth rate (i.e. the degree to which births exceed deaths) decreases λ_s, because λ_s is the geometric mean of the annual population growth rates, and the geometric mean of any set of numbers decreases as the variance of those numbers increases (Lewontin & Cohen, 1969). This argument, which ignores the complexity of demography in a structured population, would suggest that increasing environmental variability is detrimental to long-term population growth.

However, in the case of a structured population, even in the simple and often unrealistic case of IID environmental variability, increased variance of a single vital rate can either increase or decrease λ_s, depending on two demographic factors. First, it depends on whether that vital rate covaries, either positively or negatively, with other vital rates. Positive covariation means that the two rates tend to be relatively high in the same years (and both relatively low in the other years), and negative covariation means that one vital rate tends to be low when the other is high (and *vice versa*). A number of biological factors can determine whether vital rates covary, and if so, whether the covariation is positive or negative. For example, vital rates that represent the same type of demographic process (e.g. survival of newborns and survival of adults) might respond similarly to environmental conditions, creating positive covariation between those rates. Negative covariation may arise when rates represent opposing types of demographic processes (e.g. years of high individual growth are also years of low shrinkage to smaller size in plants), or it may reflect life history trade-offs (e.g. high investment in reproduction leads to low growth in the same year). The second demographic factor that determines how λ_s will respond to an increase in vital rate variance are the 'sensitivities' of the deterministic population growth rate to changes in that vital rate and in all other vital rates with which it covaries (de Kroon *et al.*, 1986; Caswell, 2001). Graphically, a sensitivity represents the slope of a graph of the population growth rate versus the value of a vital rate, with all vital rates at their current mean values (see Chapter 9 in Morris & Doak, 2002). The sensitivities play an important role, because they govern the degree to which year-to-year variability in the vital rates translates into variability in the annual population growth rate, which in turn influences λ_s. Specifically, variation in vital rates with high-magnitude sensitivity produces greater variation in the population growth rate. The sign of the sensitivity also indicates whether increasing a vital rate increases (as for individual growth rate) or decreases (as for shrinkage) the population growth rate. When two vital rates covary, we must know if the signs of their sensitivities are the same or different to predict the effect of increasing the variance of one of those rates. But if we know the environment is IID, and have estimated the means, variances, covariances, and sensitivities of all the vital rates, we can predict whether increased variance in a vital rate will increase or decrease λ_s, as laid out in Fig. 4. These results rely on Tuljapurkar's (1990) 'small-noise' approximation for λ_s, as explained in greater detail in Appendix A1 (see Section IX).

However, environmental variation may not be IID. One common case in which it is not is represented by ecosystems influenced by repeated cycles of disturbance (such as fires or hurricanes) and recovery. Here, environmental conditions, and therefore vital rates, are correlated across years because, following a disturbance, recruitment opportunities and individual growth tend to be high for several years running, while late in the disturbance cycle when competition is intense, recruitment and growth are both persistently low (e.g. Menges & Quintana-Ascencio, 2004; Menges *et al*., 2006). In such Markovian environments (so-called because we use a Markov matrix to govern the choice of next year's environmental state—for example, the number of years since the last fire—given the environmental state this year, which may influence the probability of another fire), variation even in high-sensitivity vital rates can be adaptive, and thus greater—not less—variation can lead to higher population growth (Tuljapurkar, Horvitz & Pascarella, 2003; Haridas & Tuljapurkar, 2005). For example, in a fire-prone ecosystem, high survival of seedlings immediately after a fire followed by low seedling survival once full vegetation cover has been restored and opportunities for recruitment have vanished may yield a higher long-run population growth rate than would the same average rate of seedling survival every year, regardless of the stage in the fire cycle. If so, climate change leading to less variation in survival among the phases of the fire cycle could be detrimental to population growth, as Morris *et al.* (2006) predicted for two species of fire-adapted plants. But to add further complication, greater environmental variation at *each* stage of the disturbance/recovery cycle (e.g. due to an increase in precipitation variability unrelated to fires) could reduce population growth even while greater variation *between* disturbance phases increases population growth. Morris *et al.* (2006) also observed this conflicting effect of increasing the two kinds of variability in the two study plants, although the effect of changing between-phase variability was greater, suggesting that reducing both kinds of variability simultaneously would depress population growth.

An important caveat is that the results in the preceding paragraph assume no change in the frequency of disturbance; they apply only to changes in the between- and within-disturbance phase variabilities of the vital rates at a fixed disturbance frequency. Yet changes in climatic variability will often drive changes in the frequency of disturbance (e.g. making fires or hurricanes more or less likely). When the disturbance frequency changes, it becomes meaningless to ask how changing vital rate variability *per se* will affect λ_s . The reason is that changing the disturbance frequency will simultaneously change the means and the variances of the vital rates, so we can no longer assess the effect of changing the variance while holding the mean constant, as we have done so far. Changing disturbance frequency will also change the temporal correlations within and between vital rates (these correlations measure how similar a vital rate's values are from one year to the next, as well as the similarity in one vital rate in one year to all the other vital rates in the next year). All of these changes to means, variances, and temporal correlations will collectively result in changes to λ_s (Tuljapurkar & Haridas, 2006).

Given this complexity, it is possible for changing disturbance frequency to change the variance of a vital rate and λ_s in the same or in opposite directions. For example, consider the situation in which conditions are best for a species immediately after a disturbance, as would likely be the case for a fugitive species. Increasing the disturbance frequency would then be expected to increase the long-term population growth rate, but decrease the vital rate variances (e.g. Caswell & Kaye, 2001; Tuljapurkar *et al.*, 2003; Horvitz, Tuljapurkar & Pascarella, 2005; Tuljapurkar & Haridas, 2006). Other species may show poorer population performance immediately after a disturbance but better performance at intermediate times since the last disturbance. For example, a fire may kill aboveground plants but spur recruitment from the seed bank. If recruits take several years to reach reproductive size, too high a fire frequency would preclude reproduction and prevent replenishment of the seed bank. In this scenario, an increase in disturbance frequency could decrease both λ_s and the vital rate variances (e.g. see Gross *et al.*, 1998; Satterthwaite, Menges & Quintana-Ascencio, 2002; Menges & Quintana-Ascencio, 2004; Menges *et al.*, 2006). In general, the variance of a vital rate as a function of the disturbance frequency should follow a unimodal curve, being low when disturbance frequency is low (and environmental conditions are almost always in the undisturbed state) or when it is high (and the environment is nearly always disturbed), but highest at an intermediate disturbance frequency (when disturbed and undisturbed environmental states alternate frequently). Whether increasing disturbance frequency will increase or decrease λ_s and the vital rate variances will depend on the current disturbance frequency as well as whether the population performs best at low, high, or intermediate disturbance frequency.

Finally, environmental variability may be neither IID nor Markovian. One important example is temporal trends in the mean and/or the variance of a climatic driver of demography, resulting in shifts in the means and/or variances of vital rates. Importantly, the mean and variance of a vital rate need not both increase or both decrease, but may change in opposite directions (Fig. 5). When the distribution from which annual environmental conditions are drawn is continuously shifting, the results summarized above may only serve as a general guide to the short-term response of the population growth rate, and computer simulations with changing means and/or variances would be required to predict the effective population growth rate—or population size—over time (Fig. 4).

To summarize what population theory has to say about the likely effect of changing environmental variability, greater variability can either increase or decrease the long-term rate of population growth. To predict the outcome, in addition to characteristics of the environmental variability and of the demography of the species in question, we may also need to consider simultaneous changes in the means and temporal correlations of environmental drivers, especially in the face of changing disturbance frequency or of long-term trends in the distribution of environmental conditions.

(2) Empirical estimates of population sensitivity to increased environmental variability

Another way to assess the potential effects of increased climatic variability on population growth is to compute the so-called stochastic sensitivities of the long-run population growth rate to the standard deviations of the vital rates (Tuljapurkar *et al*., 2003). These are different from the sensitivities of the deterministic population growth rate to the vital rate means that were described in the preceding section; they represent the slope of the long-run stochastic growth rate with respect to the temporal standard deviation of a vital rate, evaluated at the current standard deviation. The computation of the stochastic elasticities (Tuljapurkar *et al*., 2003) can account for any temporal correlations in environmental conditions, and therefore vital rates, in a Markovian—indeed in any auto-correlated—environment. Using multi-year demographic data, Morris *et al.* (2008) computed the stochastic sensitivities to changes in the means and standard deviations of vital rates for 36 animal and plant species ranging from insects to mammals and annual to long-lived perennial plants. In general, the population growth rates of these species are more sensitive to climate-driven changes in the vital rate means than they are to changes in vital rate standard deviations driven by changes in climatic variability. Nevertheless, short-lived species showed relatively greater sensitivity to increasing vital rate variability than did long-lived species. This result suggests that an increase in climate variability might have a disproportionately negative impact on the demography of short-lived species. Conversely, in regions expected to experience reduced climatic variability, problems for humans and other species posed by (mostly short-lived) agricultural pest insects and disease vectors, and by invasive annual plants, may worsen.

It is important to emphasize that the preceding paragraph describes what *could* happen to the study populations should climatic variability change. We still have no definitive examples in which a change in the temporal variability of vital rates has been demonstrated to have resulted from a change in climatic variability. Showing that variability in vital rates has changed is substantially more difficult than documenting a trend in the mean of a vital rate over time, because we need a series of years of demographic data just to make one reliable estimate of the variability of a vital rate, and at least two such series to assess whether variability has changed. But as the number of long-term demographic studies has increased in recent years (Crone *et al*., 2011), we may eventually be able to correlate changes in vital rate variability with changes in climate variability. In the shorter term, if we can correlate particular vital rates with specific climatic drivers, then is it probably safe to conclude that changes in the variabilities of those drivers will cause the variabilities of the vital rates to change, with the likely population consequences reviewed above.

A less direct way to assess whether increasing climatic variability will elevate variation in vital rates is to compare the temporal vital rate variances in central and peripheral populations. A species may more often experience climatic conditions that are farther from optimum at the range margin compared to the range centre (although another possibility is that conditions are always less suitable at the margin, or that climate plays no role in setting a particular range limit). If so, vital rate variances *may* be higher in peripheral populations, suggesting that even higher climatic variability beyond the margin may be contributing to the range limit. While some studies have found higher demographic variation in peripheral populations (Angert, 2009; Doak & Morris, 2010), others have not (Villellas, Morris & García, 2013*b*; Villellas *et al*., 2013*a*).

(3) Summary and future directions

In summary, we cannot make any blanket statements about whether increasing demographic variability driven by increasing variability in climate would be detrimental for the rate of population growth (or, conversely, whether decreasing variability would be beneficial). The answer depends on such factors as the organism's life history (which influences the sensitivities of the vital rates), the precise vital rates whose variabilities are changing, whether those vital rates are correlated with one another, whether the environmental variability is IID *versus* Markovian (as it would likely be in a disturbance-prone environment), and if the latter, whether climate change alters the frequency of disturbance, the variation between disturbance phases, or the variation within phases. But with sufficient demographic data, the modelling tools, some of which have been summarized here, exist to predict the effects of changing variability *per se* on population growth.

But changes in vital rate variability alone may not capture all of the effects of climate change on population growth. Changes in the frequencies of extreme values of the vital rates driven by changes in climatic extremes may affect long-run population growth in ways that are not well captured by measures of population growth based on small-noise approximations. Instead, the demographic consequences of changes in the frequency of extremes may be better explored by means of computer simulations, drawing vital rates from the 'normal' range of variation with occasional (and perhaps increasingly frequent) extreme values 'thrown in', or by slowly changing the kurtosis (as well as the mean and variance) of the probability distribution from which each vital rate's values are drawn. A yet more promising approach is to link vital rates to environmental drivers, so that climatic extremes will produce vital rate extremes directly. Simulating changes in climatic means, variabilities, and extremes, and then predicting in turn the resulting vital rates, population growth (including density-dependent effects), and population size is perhaps the most comprehensive way to assess the likely effects of changes in all aspects of climate for the dynamics of populations (Ehrlén & Morris, 2015).

V. SPECIES INTERACTIONS AND COMMUNITY STRUCTURE

(1) Phenological mismatches, species interactions and geographic range limits

Climate change will influence species interactions and communities either by directly affecting the abundances of interacting species through demographic effects, or by affecting their phenology, which may disrupt the phenological matching among interacting species. We have already discussed demographic effects in the previous section. Below we discuss how climate change, and particularly increased climatic variability, can lead to phenological mismatches among interacting species, and how those mismatches can influence geographic range limits.

Climate change should lead to phenological mismatches among interacting species if species respond idiosyncratically to climatic variables. If so, changes in one climatic variable may influence the phenology of one species but not of its interaction partners (Harrington, Woiwod & Sparks, 1999; Visser & Both, 2005; Parmesan, 2006; Devoto, Zimmermann & Medan, 2007; Memmott *et al*., 2007; Tylianakis *et al*., 2008; Hegland *et al*., 2009; Yang & Rudolf, 2010). For example, a plant could respond to increased average temperature by advancing its flowering period (as has been frequently observed; Cleland *et al*., 2007; Gordo & Sanz, 2010; CaraDonna, Iler & Inouye, 2014), while an insect pollinator may respond more strongly to photoperiod (which is determined by latitudinal position, not climate), so that its developmental phenology remains unaffected in spite of increased average temperature; this differential response to climate change would result in a phenological mismatch between these species. There are several examples in the literature of how gradual changes in climatic averages have led to phenological mismatches and concomitant demographic consequences for the interacting species (Visser *et al*., 1998; Visser & Both, 2005; Both *et al*., 2009; Plard *et al*., 2014). Of course, a partial phenological mismatch between interacting species does not necessarily indicate the influence of climate change, as mismatches are known to have occurred naturally before the onset of human-driven climate change, even for relatively specialized interactions (Singer & Parmesan, 2010); however, such mismatches are likely to be exacerbated by climate change, which may in turn exacerbate the demographic vulnerability of the interacting species.

The ecological consequences of climate-driven changes in the phenological matching of interacting species are likely to be qualitatively different under changes in climatic averages and changes in climatic variability and extremes. A change in a climatic average may lead to a slow adjustment of phenologies over decades or centuries (Parmesan *et al*., 1999; Easterling *et al*., 2000; Parmesan & Yohe, 2003; Root *et al*., 2003; Thomas *et al*., 2004; Pounds *et al*., 2006), which may allow species to adapt to changes in the phenology of their interaction partners to minimize mismatches (Harrington *et al*., 1999; Visser & Both, 2005; Parmesan, 2006; Visser, 2008; Hegland *et al*., 2009). By contrast, increased inter-annual variability and the increased occurrence of climatic extremes may lead to high temporal variation in the phenological matching of interacting species, which may impose conflicting selective pressures on interacting species, preventing adaptation and maintaining mismatches in the long run. Furthermore, the magnitude of mismatches generated by year to year climatic variation is likely to be substantially greater than that generated by gradual changes in average climatic conditions.

Mismatches in the phenologies of interacting species generated by climate change should influence the limits of geographic ranges if they influence demography, and if such influence is stronger at range limits than away from them. Under such circumstances, it is at least possible that increased climatic variation could lead to a shrinkage of geographic ranges, even if average climatic conditions remained unchanged. A greater influence of phenological mismatches on demography at range limits may occur through at least two distinct mechanisms likely to operate with particular strength at range limits: the greater influence of extreme climatic events, and the decreased sampling probability of phenological tails.

First, phenological shifts may expose populations to harsh, extreme climatic events, which are likely to be particularly frequent at range limits; this greater exposure to extreme climatic events at range limits may impose strong constraints on resource availability and, therefore, should have more detrimental demographic effects (Fig. 6A). For example, earlier flowering because of increased temperature may also mean a greater likelihood of flower damage due to early spring frosts or snows at the upper altitudinal or latitudinal range limits (Inouye, 2008); thus, the same phenological shift in flowering may have greater consequences for an animal feeding on these flowers at its range limit.

Second, if the abundance of resources, mutualists or antagonists decreases towards range limits, the demographic consequences of phenological mismatches should also be particularly strong at range limits. This is because the high likelihood of not sampling from the tails of the phenological distribution when abundance is low leads to a shortening of the phenological period (Fig. 6B); this is the same sampling issue that makes dates of first flowering unreliable to study phenological shifts (van Strien *et al*., 2008; Miller-Rushing, Inouye & Primack, 2008). A similar effect is expected if climatic conditions decrease resource abundance without shifting phenology. Thus, for example, if resources are rarer at range limits, a bad year with lower-than-average resource abundance may leave individuals with too few resources, sending populations into decline.

(2) Community structure and dynamics

Although many studies have discussed the potential effects of climate change on community structure and dynamics (e.g. Memmott *et al*., 2007; Hegland *et al*., 2009; Woodward *et al*., 2010), the focus of the vast majority of these studies is on climatic averages. Only recently have a few studies begun to consider how climatic variability and climatic extremes can influence communities (e.g. Knapp *et al*., 2002; Stireman *et al*., 2005; Benedetti-Cecchi *et al*., 2006; Jentsch *et al*., 2007; Post, 2013; Reyer *et al*., 2013; Thompson *et al*., 2013). For example, Knapp *et al*. (2002) found that increased variability in precipitation leads to increased plant diversity in a temperate North

American grassland, while Benedetti-Cecchi *et al.* (2006) showed that temporal variance mitigates the impact of mean intensity of stress in climate change in Mediterranean algal and invertebrate intertidal assemblages. In turn, Stireman *et al.* (2005) have shown that parasitism by insect parasitoids on multi-species assemblages of host caterpillars decreases with increasing inter-annual variation in precipitation. As is usual in community ecology (see, e.g. Lawton, 1999), our ability to draw generalizations about the potential effects of such climatic changes is likely to be contingent upon the way the community is organized and the type of ecosystem considered. Yet, the few available studies give us some hints as to how increased climatic variability and extremes may influence community structure and dynamics.

One way in which environmental variability can influence community structure and dynamics is through the storage effect, an ecological mechanism that promotes coexistence among competing species in variable environments (Chesson, 1994, 2000). Three conditions must be met for the storage effect to operate. First, species must have some kind of 'storage' ability to persist during unfavourable periods, such as a seed bank or diapause. Second, species must have idiosyncratic (i.e. species-specific) responses to the environment. Third, the effects of intraspecific competition on each species must covary with the effects of environmental conditions, so that competition is stronger in favourable years. Thus, under the storage effect, greater climatic variability should promote coexistence and enhance species diversity. Several studies provide evidence that the storage effect may be a common, albeit not universal, mechanism promoting community stability and diversity. In a North American temperate grassland, Adler *et al.* (2006) found that interannual climatic variability promoted the coexistence of three common grass species. By contrast, a similar analysis in a temperate sagebrush steppe found only weak effects of climatic variability on species coexistence (Adler, HilleRisLambers & Levine, 2009). In experimental aquatic microcosms, several studies have shown that species coexistence is favoured by increased temperature fluctuation (Eddison & Ollason, 1978; Descamps-Julien & Gonzalez, 2005; Jiang &

Morin, 2007); however, the type of environmental fluctuation appears to determine the type of mechanism involved, with the storage effect operating under red (positively autocorrelated) fluctuations and other mechanisms (particularly relative non-linearity; Chesson, 1994, 2000) under white (random) fluctuations (Jiang & Morin, 2007).

The type of interaction dominating the organization of the community is likely to influence the community's response to climate change. For example, analysing communities with a simple, tri-trophic structure, Post (2013) found that the trophic level with the weakest self-regulation exhibited the strongest response to climatic variation, which may in turn cause instability of the entire community. By contrast, in communities structured mainly through competitive interactions, climatic variation may help to prevent instability. A similar result was found by Kuang & Chesson (2009) for an annual plant assemblage, in which generalist seed predation shifted plant–plant interactions from resource competition to apparent competition (i.e. potential competitors interacting indirectly through common predators; Holt, 1977), thus weakening the storage effect that promotes coexistence among plant species.

The size of the community (i.e. the number of species) may also influence the community's response to increased climatic variability. In a simulation study of model communities, Kaneryd *et al*. (2012) found that the likelihood of extinction cascades increased with increasing community size, particularly under low correlation in species' responses to environmental fluctuations. These results suggest that species-rich communities may be less robust to increasing levels of environmental variability than their species-poor counterparts.

The breadth of resource use and the degree of specialization/generalization of interactions are also likely to influence how community structure and dynamics are influenced by climatic variability. In particular, greater variability should affect specialists more strongly, because they depend on fewer resources and hence should be more susceptible to environmental variability, all of which should favour generalists (MacArthur, 1972; Reyer *et al*., 2013). In turn, the differential negative effect of climatic variability on specialists could lead to decreased species richness in the community (MacArthur, 1972; Vázquez & Stevens, 2004), and to a re-arrangement of the interaction structure of the community (e.g. increased connectance—the proportion of potential links that actually occur).

Different functional groups are also likely to respond differently to increased climatic variation. In an analysis of the responses of North American grassland communities to interannual variation in precipitation, Cleland *et al.* (2013) concluded that systems dominated by perennial plants should be more stable to increasing interannual climatic variation, while systems with many rare, annual species should exhibit the greatest temporal variability in species composition in response to increased climatic variability, especially increased interannual variability in precipitation. In aquatic systems, increased temperature variability has been found to lead to increased richness of zooplankton in lakes (Shurin *et al.*, 2010), while it led to decreased richness of phytoplankton in experimental aquatic microcosms (Burgmer & Hillebrand, 2011). Of course, the contrasting results of the above studies might simply reflect methodological differences of the studies; but it is also possible that they partly reflect the underlying mechanisms that govern the dynamics of different functional groups.

In consumer–resource interactions, the relative size of the consumer and the resource species might also determine the effects of climatic variability on the outcome of interactions and, therefore, species coexistence. Rohr *et al.* (2013) have argued that parasites are typically smaller and their metabolisms faster than their hosts, which would allow them to achieve faster acclimatization to temperature shifts than their hosts, facilitating their transmission and successful infection. Several studies provide evidence in favour of this conjecture. For example, increased climatic temporal variability appears to increase transmission of a fungal parasite of amphibians believed to be partly responsible for the drastic declines of many amphibian species worldwide (Rohr & Raffel, 2010; Hamilton *et al.*, 2012; Raffel *et al.*, 2013). Similarly, increased climatic variability may enhance the transmission of malaria (Zhou *et al*., 2004; Paaijmans *et al*., 2010), dengue (Lambrechts *et al*., 2011), avian influenza (Liu *et al*., 2007), and cholera (Rodó *et al*., 2002).

In addition to the ecological characteristics of the community and the interacting species, the community's response is also likely to depend on the magnitude of changes in climatic variability and extremes. Based on an extensive review of the literature on dryland ecosystems, McCluney *et al*. (2012) predicted that modest increases in the variability of water availability should lead to strong bottom-up effects in dryland communities, whereas greater increases in the variability of water availability should lead to a dominance of top-down effects, and more non-linear and unpredictable community dynamics.

VI. CONCLUSIONS

(1) Our review indicates that climatic variability can influence biological processes at multiple scales of biological organization, from individuals to populations and communities, and from physiological to ecological and evolutionary processes. Although responses to climatic variability are usually complex and cannot always be generalized, climatic variability represents an important component of climate with potentially profound biological consequences.

(2) At the level of individual performance, the nonlinear relationship between temperature and performance implies that the impact of thermal variation on physiological performance will be contingent on the temperature at which performance peaks. Thus, close to the peak of the performance function, greater temperature variability should decrease physiological performance, whereas at the tails of the function greater temperature variability should increase performance. The relationships among thermal environments, thermal tolerance and population growth may reflect natural selection on developmental acclimation. Many researchers have examined geographic variation in thermal tolerance, which indicates that genotypes from higher latitudes tolerate low temperatures better and recover from thermal shock more rapidly, which probably provides a fitness

advantage. In addition, the ability to recover from thermal shock covaries with environmental conditions, suggesting that temperature acts as a selective agent. Because environmental temperature varies over space and time, organisms are continually challenged to maintain homeostasis. Thus, populations are expected to evolve physiological adaptations to local climatic conditions in heterogeneous environments.

(3) Functional phenotypic adjustments to changing environmental conditions may occur *via* adaptive evolution across generations and/or within-generation adaptive phenotypic plasticity. Increased environmental variation should select for increased phenotypic plasticity, a prediction supported by our review of studies on plants. Evolutionary responses to selection on plasticity may include a shift in the environmental threshold of response, a change in the eliciting cue, increased magnitude of plasticity (steeper slope of the reaction norm), and even the arrestment or reversion of phenotypic changes. The mechanisms underlying such phenotypic patterns may include allelic sensitivity, gene regulation, and epigenetic control. Our conceptual model suggests that the extent to which increased plasticity is favoured by increased climatic variation would ultimately depend on the type of selection operating. Thus, directional selection would clearly favour increased plasticity, while stabilizing selection may render enhanced plasticity maladaptive. However, directional selection often prevails over stabilizing selection in the wild. Therefore, the advantageous nature of increased plasticity in the context of increased climatic variation should be verified in most cases.

(4) At the level of populations, the effects of changing climatic variability on population growth can be predicted with the appropriate modelling tools. Whether the effects of increased climatic variation are positive or negative depends on such factors as the organism's life history, the precise vital rates whose variabilities are changing, the degree of correlation among vital rates, the type of environmental variability involved (IID *versus* Markovian), the impact of climate change on disturbance frequency, and the degree of variation between *versus* within phases of the disturbance recovery cycle. Furthermore, changes in the frequencies of extreme values of the vital rates driven

by changes in climatic extremes are also important, as they may affect long-run population growth in ways that are not well captured by measures of population growth based on ‘small-noise’ approximations. In this case, an alternative approach is the use of computer simulations, drawing vital rates from the ‘normal’ range of variation with occasional (and perhaps increasingly frequent) extreme values ‘thrown in’, or by slowly changing the kurtosis (as well as the mean and variance) of the probability distribution from which each vital rate’s values are drawn. A yet more promising approach is to link vital rates to environmental drivers, so that climatic extremes will produce vital rate extremes directly. Computer simulations may be the only feasible way to link complex changes in climatic means, variabilities, and extremes, as well as biotic interactions and intraspecific density, to their effects on vital rates, population growth, and the future abundance and distribution of species.

(5) At the level of species interactions and communities, climate-driven phenological mismatches are a key mechanism underlying the potential effects of increased climatic variability and extremes. Increased inter-annual variability and the increased occurrence of climatic extremes may lead to high year to year variations in the phenological matching of interacting species. The magnitude of such mismatches is likely to be substantially greater than that generated by gradual changes in average climatic conditions, which may impose conflicting selective pressures on interacting species, preventing adaptation and maintaining mismatches in the long run. These climate-driven phenological mismatches are likely to be especially strong towards the limits of geographic ranges; thus, it is possible that increased climatic variation could lead to a shrinkage of geographic ranges, even if average climatic conditions remain unchanged. Our ability to draw generalizations about the potential effects of increased climatic variability at the level of entire communities is rather limited, given their inherent complexity; the response of communities to increased climatic variability will be most likely influenced by the mechanisms regulating coexistence among interacting species, the type of interaction dominating the organization of the community, the community's species richness,

the relative size and the degree of specialization of the interacting species, the functional groups involved, and the magnitude of the climatic changes.

(6) To conclude, our review shows that although increased climatic variability is likely to have important biological consequences, this aspect of climate change has received little attention compared to changes in climatic averages. Given the prospect of increased climatic variability as a component of climate change in many locations, there is a clear need to increase research efforts to understand how this component of climate change influences physiological, ecological and evolutionary processes.

VII. ACKNOWLEDGMENTS

Funded by grants from FONCYT (PICT-2010-2779) to D.P.V., FONDECYT (1140070) to E.G., U.S. National Science Foundation LTREB program to W.F.M., and FONDECYT-1130015 and CAPES-FB002 line 3 to F.B. The CYTED network ECONS (410RT0406) promoted the discussions that gave rise to this manuscript.

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IX. APPENDIX A1: USING TULJAPURKAR'S (1990) 'SMALL-NOISE' APPROXIMATION TO UNDERSTAND THE INFLUENCE OF INCREASED VARIANCE OF VITAL RATES ON THE STOCHASTIC POPULATION GROWTH RATE

In this appendix, we explain how, in the case of independently and identically distributed (IID) environmental variation, the predictions about whether increased variance of a vital rate will increase or decrease the long-term stochastic population growth rate λ_s can be understood in terms of Tuljapurkar's (1990) 'small-noise' approximation.

A population projection matrix integrates the effects of the vital rates into a single measure of the population growth rate. Much of the population theory that describes the effect of environmental variation on population growth relies on Tuljapurkar's (1990) 'small-noise' approximation, derived using a stochastic projection matrix model and assuming the vital rate variances are not too large (hence 'small noise'). In its simplest form, Tuljapurkar's approximation relates the long-run stochastic population growth rate λ_s to the means, standard deviations, and correlations among vital rates as follows:

$$\log \lambda_s \approx \log \bar{\lambda} - \frac{1}{2\bar{\lambda}^2} \sum_{i,j} S_i S_j \sigma_i \sigma_j \rho_{i,j}.$$

[Note that this version of the approximation is written in terms of the underlying vital rates, accounting for the effects that each vital rate may have on multiple elements in the projection matrix; see Doak *et al*. (2005). For an alternative version based directly on the matrix elements, see Caswell (2001).] The means of the vital rates affect $\bar{\lambda}$, the asymptotic population growth rate predicted by the average of all the annual projection matrices. The sum is taken over all the vital rate pairs *i,j*. The sensitivity S_i is the slope of a graph of $\bar{\lambda}$ *versus* vital rate *i* at that vital rate's current value (mathematically, it is the partial derivative of $\bar{\lambda}$ with respect to the vital rate, evaluated at that rate's current value and keeping all other vital rates fixed). Sensitivity measures the influence that each vital rate has on the population growth rate. The sensitivities appear in the 'small-noise' approximation because we must weigh the impact of variation in the vital rates by the influence that each vital rate has upon annual population growth rate in order to predict the amount of temporal variation in annual population growth, which is what affects the long-run growth rate λ_s . Temporal variation in low-sensitivity vital rates will produce less variation in the annual population growth rate than will variation in high-sensitivity vital rates. The sensitivities are computed directly from the mean projection matrix, just as $\bar{\lambda}$ is, so they are influenced only by the means of the vital rates. The parameters σ_i and σ_j are the standard deviations of the two vital rates, and ρ_{ij} is the coefficient of correlation between vital rates *i* and *j*, positive values indicating that the two rates tend to be relatively high in the same years (and relatively low in the same years), and negative values meaning one tends to be low when the other is high. This simple version of the 'small-noise' approximation assumes that there is no correlation in environmental conditions across years (that is, we imagine choosing at random from a set of vital rate values each year, without regard to whether we chose favourable or unfavourable rates in the previous year).

The 'small-noise' approximation becomes even simpler in the special case in which vital rates vary independently of one another, so that the correlation ρ_{ij} is zero except when $i = j$, and then it equals one. Thus, the term for vital rate *i* within the sum becomes simply $S_i^2 \sigma_i^2$, the product of the squared sensitivity and the variance of the vital rate, which is always positive. Because the entire sum is then positive, the minus sign in front of it means that an increase in the variances of the vital rates will cause a *decrease* in the long-run population growth rate relative to the rate ($\bar{\lambda}$) that would occur in the absence of environmental variability. So, independent environmental variation in the vital rates is detrimental to population growth. Furthermore, the greater is S_i, the sensitivity of vital rate *i*, the greater is the depressive effect on population growth of increasing its variance. This is the basis of the prediction that natural selection should favour life-history traits that reduce temporal variation in those vital rates that have the greatest influence on population growth, a prediction that has some empirical support (Pfister, 1998; Morris & Doak, 2004).

The picture is somewhat more complex when variation between vital rates is correlated, positively or negatively. If the sensitivities of two vital rates are both positive but the vital rates covary negatively, the term in the sum for that vital rate pair will be negative, which when multiplied by the minus sign outside the sum yields a positive term that *increases* the long-run population growth rate when the temporal variance (or standard deviation) of each vital rate increases. This positive contribution to long-run growth must be weighed against the $S_i^2 \sigma_i^2$ terms in the sum for the two vital rates, which will still be positive, depressing growth. But taking both the positive and negative contributions in this case into account, it is possible for increasing variance in a vital rate with a relatively low sensitivity to cause the long-run growth rate to *increase*, by acting as a counterweight against variation in higher-sensitivity vital rates (Doak *et al.*, 2005). Another way that increasing vital rate variance can increase the long-run population growth rate is when a vital rate (such as one that represents shrinkage to a smaller size, or the rate of entering a dormant state) has a small negative sensitivity and a positive correlation with higher (but positive) sensitivity rates. Thus we cannot say categorically that increasing the variance of a demographic rate will invariably depress the population growth rate; it depends on the details of the life history (which influence the sensitivities) and on the way in which different vital rates co-vary.

Table 1. A sample of studies addressing phenotypic plasticity in plant functional traits in response to treatments of water or temperature. Experimental plants came from populations with contrasting temporal heterogeneity in soil moisture or temperature. In Outcome, + indicates greater plasticity in the population(s) from the more variable habitat(s), – indicates the opposite, and 0 refers to no differences in plasticity among populations. *N* pop = number of populations. Overall, there was a statistically significant trend for populations from more heterogeneous environments to show increased phenotypic plasticity ($P < 0.05$, sign-test).

Species (*N* pop)	Environmental factor	Scale of temporal heterogeneity	Outcome	Reference
Artemisia californica (5)	Water	Between years	+	Pratt & Mooney (2013)
Artemisia frigida (2)	Water	Between years	+	Liu *et al*. (2014)
Convolvulus arvensis (2)	Water	Within year	+	Gianoli (2004)
Convolvulus chilensis (3)	Water	Between years	+	Gianoli & González-Teuber (2005)
Leymus chinensis (5)	Water	Between years	+	Liu *et al*. (2014)
Plantago lanceolata (29)	Temperature	Within year	–	Lacey *et al*. (2010)
Polygonum persicaria (2)	Water	Between years	0	Sultan & Bazzaz (1993)*
Polygonum persicaria (3)	Water	Within year	0	Heschel *et al*. (2004)
Ranunculus flammula (10)	Water	Between years	+	Cook & Johnson (1968)

Species (*N* pop)	Environmental factor	Scale of temporal heterogeneity	Outcome	Reference
Senna candolleana (4)	Water	Between years	+	Lázaro-Nogal *et al*. (2015)
Stipa grandis (2)	Water	Between years	–	Liu *et al*. (2014)
Stipa krylovii (3)	Water	Between years	+	Liu *et al*. (2014)
Taraxacum officinale (2)	Water	Within year	+	Molina-Montenegro *et al*. (2010)
Taraxacum officinale (5)	Temperature	Within year	+	Molina-Montenegro & Naya (2012)

* The authors did not compare plasticity levels between populations; the outcome was inferred after statistical comparison of *F*-ratios.

FIGURE LEGENDS

Fig. 1. An example to illustrate the difference between changing the variance and the kurtosis (occurrence of extreme events) of a climatic variable. (A) Three contrasting distributions of a climatic variable are shown, one following the normal distribution with a variance of 1 (black), another following the normal distribution with a variance of 5/3 (blue), and the last following Student's *t* distribution with a variance of 5/3 (green). Thus, the black curve has lower variance than the blue curve but both have the same kurtosis, as by definition the normal distribution has zero kurtosis. In turn, the green curve has the same variance as the blue curve (5/3) and is leptokurtic, with a kurtosis value of 6. Thus, it exhibits greater occurrence of extreme events than the other curves and has greater kurtosis than the black and blue curves. The three curves are centered on the same mean. (B) The same three curves shown in A with the ordinates in log scale, which helps when comparing the frequency of extreme events among the curves.

Fig. 2. Given the nonlinear relationships between performance and body temperature, mean performance differs between ectothermic organisms inhabiting constant and fluctuating environmental conditions. Coloured circles symbolize the performance of individuals kept at either a low (blue circle) or a high (red circle) constant temperature. Green circles denote performances of individuals kept at thermal cycles following a step function; arrows indicate the range of the step function. When the mean temperature lies below the thermal optimum (T_0), thermal variation increases the mean performance. Contrarily, when the mean temperature exceeds the thermal optimum, thermal variation reduces the mean performance. Modified from Bozinovic *et al*. (2011*a*).

Fig. 3. The adaptive value of phenotypic plasticity under two different scenarios of climate change: (*i*) a temporal shift in environmental quality (and in its corresponding cue for the initiation of the

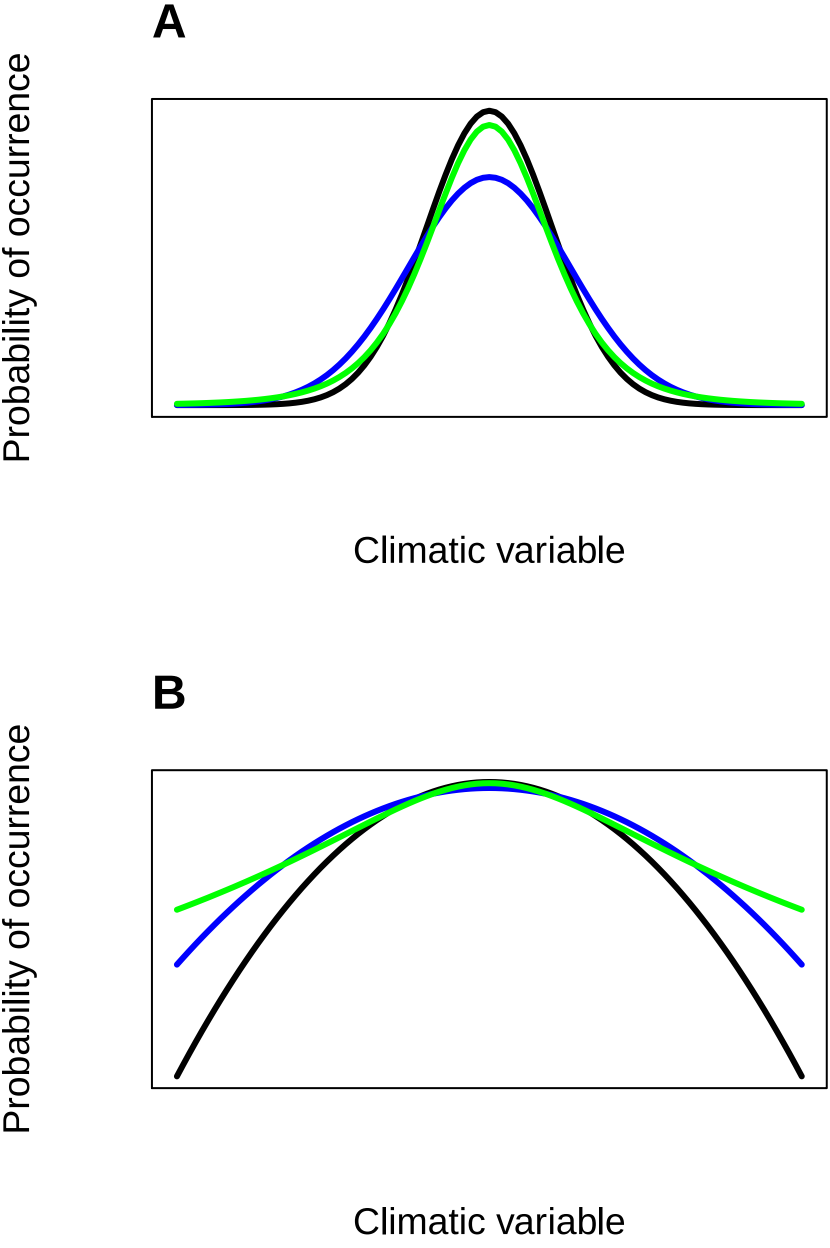
plastic response) (left column), and (*ii*) a temporal shift in environmental quality plus climatic variability (a short-term anomaly counteracting the climatic trend) (right column). (A, B) Seasonal variation in environmental quality in historical climate (black curve) *versus* climate change (red curve) scenarios. (A) Climate change = continuous trend. (B) Climate change = a shift in historical climate plus climatic variability. The level of environmental quality that acts as a cue for the initiation of the plastic response is indicated. (C, D) Reaction norms from three genotypes in the climate change scenarios depicted in A and B. Their responses to environmental cues (or lack thereof) are evidenced by a change in the slope of their reaction norms. It is assumed that the trait changes continually after the threshold is exceeded. The black genotype does not respond to the temporal shift in the appearance of the cue (C) or climatic variability (D), keeping the phenotypic trajectory corresponding to the historical climate. The red genotype has adjusted its reaction norm to the shift in the cue (C) or climatic variability (D). The purple genotype, together with adjusting its reaction norm as for the red genotype, shows increased plasticity (steeper slopes; C, D). The plateaus in the red and purple genotypes (D) arise when the environment goes back above the threshold in B. The orange dashed line indicates the occurrence of selection at the end of the season. (E, F) Adaptive landscape assuming directional selection, showing the relative position of the three genotypes in the scenarios of continuous climate change (E) and climatic variability (F), following the phenotypic trait expression observed at the time of selection (orange dashed line). (G, H) As for E and F, but this time assuming stabilizing selection when building the adaptive landscape.

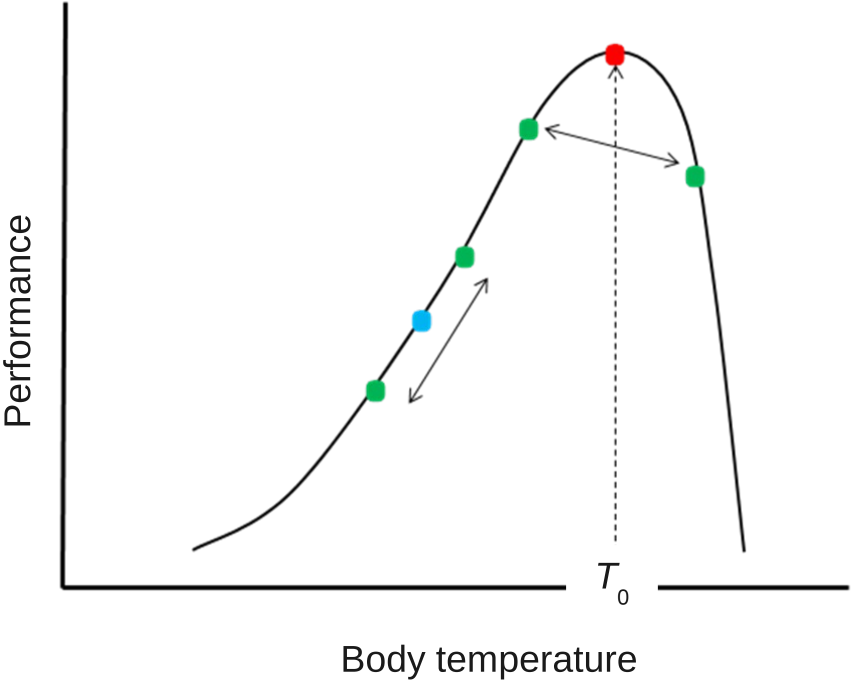
Fig. 4. A partial summary of population theory describing the effect of a change in environmental variability on the long-term stochastic population growth rate, λ_s. Abbreviations: IID, independently and identically distributed; VR, vital rate; VRV, vital rate variance. References: 1: Tuljapurkar (1990); Pfister (1998); 2: Doak *et al.* (2005); 3: Morris *et al.* (2006); 4: Gross *et al.* (1998), Caswell & Kaye (2001), Tuljapurkar *et al.* (2003), Menges & Quintana-Ascencio (2004),

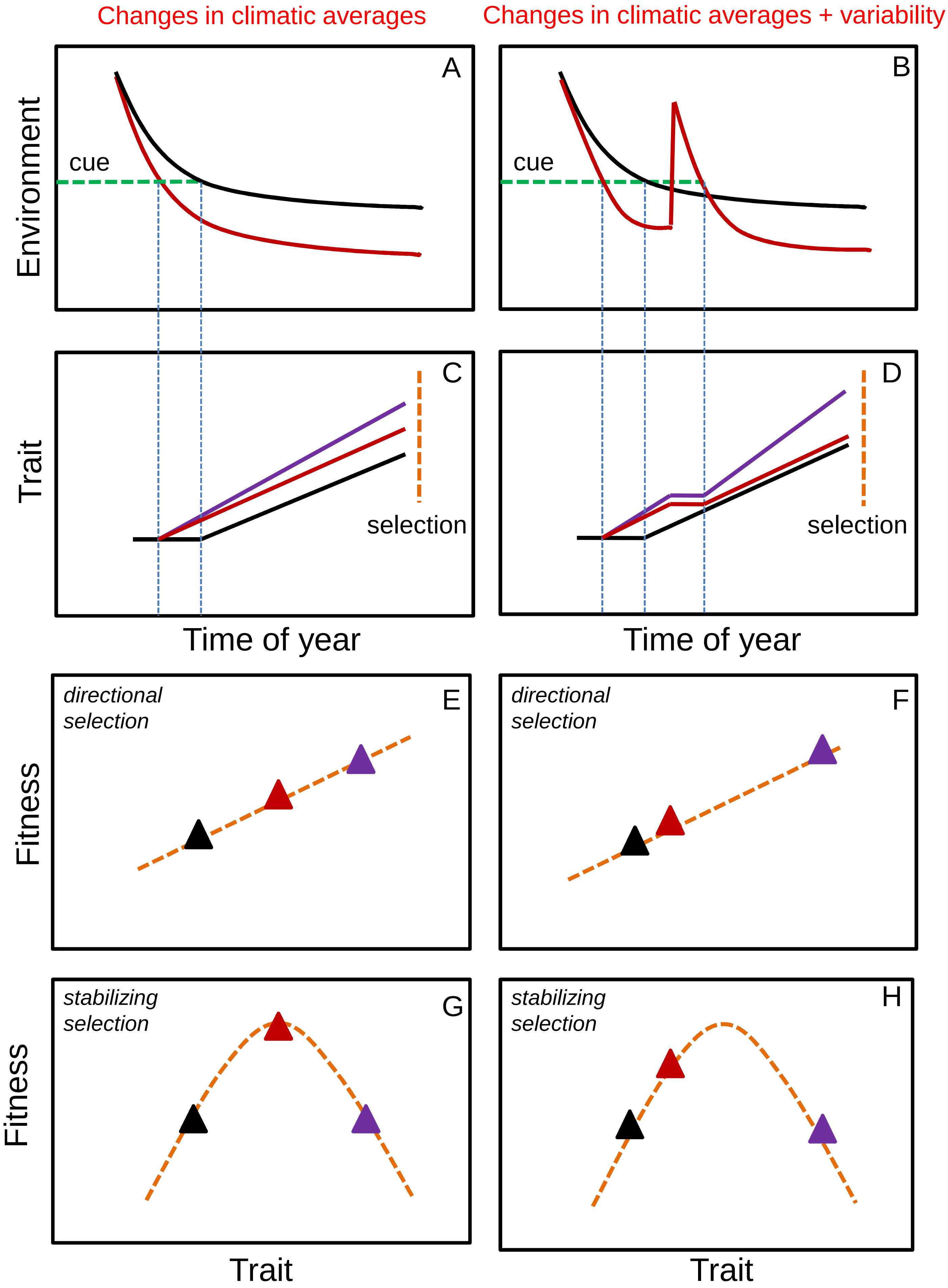
Tuljapurkar & Haridas (2006).

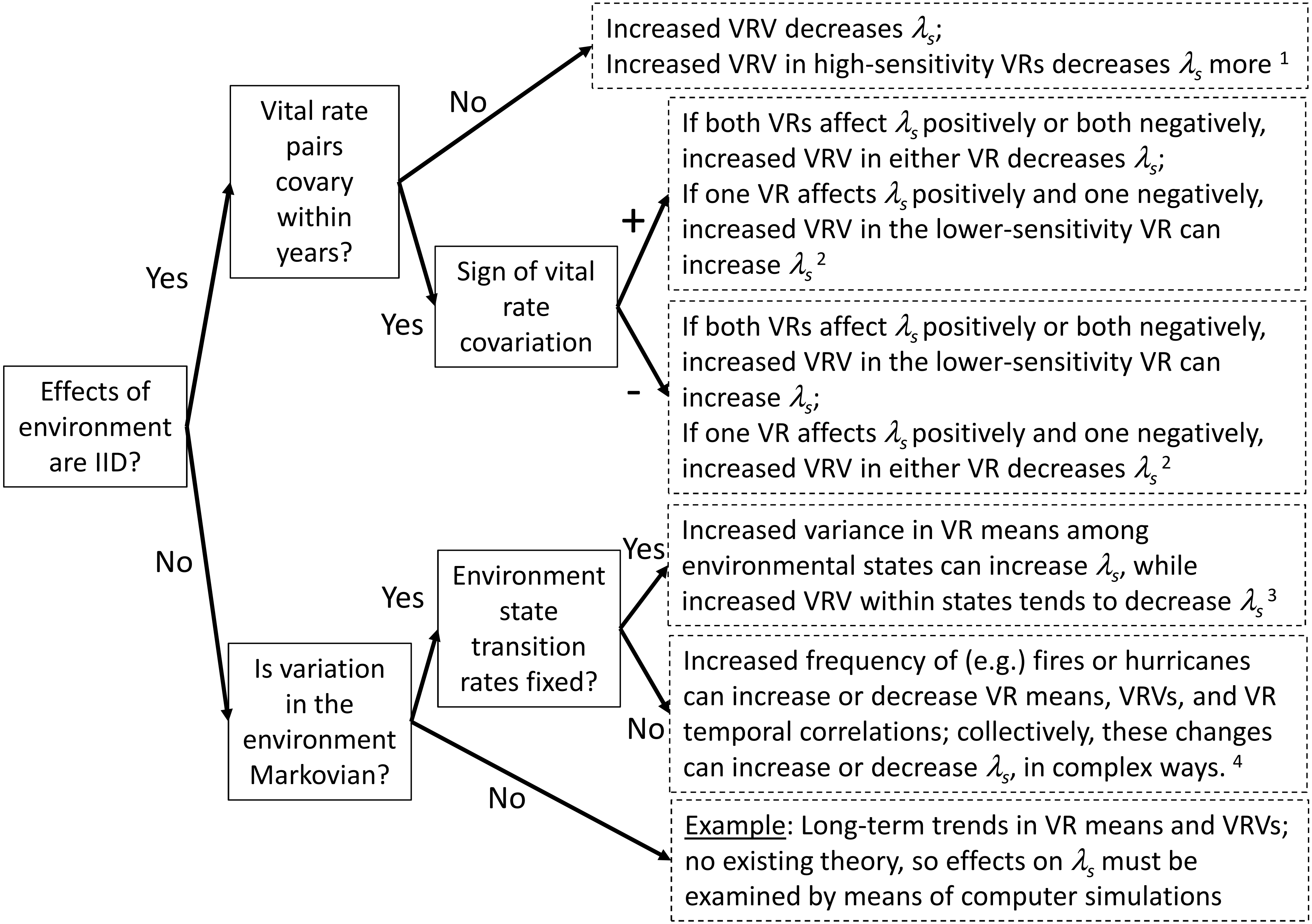
Fig. 5. In a changing climate, the mean and variance of environmental conditions may change in the same or in opposite directions, and may drive similar changes in the means and variances of vital rates.

Fig. 6. Mechanisms exacerbating phenological mismatches at geographic range limits. (A) Greater influence of harsh climatic events at range limits. In the example, the phenology of a consumer (blue) overlaps well with the average phenology of its resource (green). If the probability of occurrence of harsh climatic events that damage the resource is greater at range limits (black dotted line) than at the range center (grey dotted line), a phenological shift in the resource (red) should exacerbate the phenological mismatch at range limits. The black arrow indicates the direction of the shift in the plant phenology. (B) Decreased sampling probability of phenological tails at range limits. If the abundance of a key resource that is abundant throughout the geographic range (green) decreases towards range limits (red), statistical sampling will dictate a shorter resource phenology at range limits, with a later start and earlier end of the phenological period (dotted vertical lines). In the example, resource phenologies were generated by randomly sampling from a normal distribution, with the abundance away from range limits being five times greater than the abundance at range limits.


A
Probability of occurrence
Climatic variable
B
Probability of occurrence
Climatic variable


Performance
T_0
Body temperature


Changes in climatic averages
Changes in climatic averages + variability
A
B
Environment
cue
cue
C
D
Trait
selection
selection
Time of year
Time of year
directional selection
E
directional selection
F
Fitness
stabilizing selection
G
stabilizing selection
H
Fitness
Trait
Trait



Increased VRV decreases λ_s;
Increased VRV in high-sensitivity VRs decreases λ_s more [1]

If both VRs affect λ_s positively or both negatively, increased VRV in either VR decreases λ_s;
If one VR affects λ_s positively and one negatively, increased VRV in the lower-sensitivity VR can increase λ_s [2]

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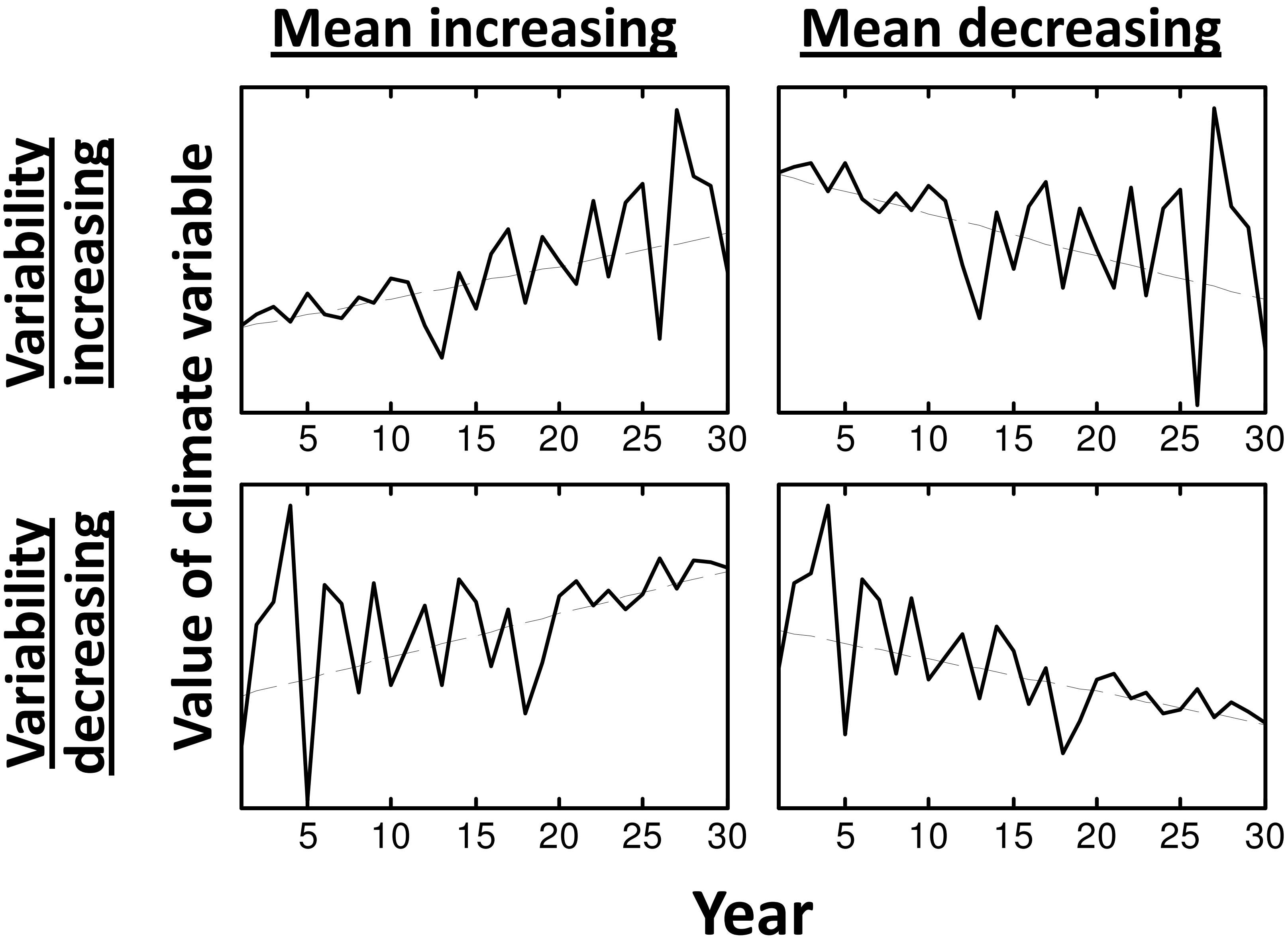
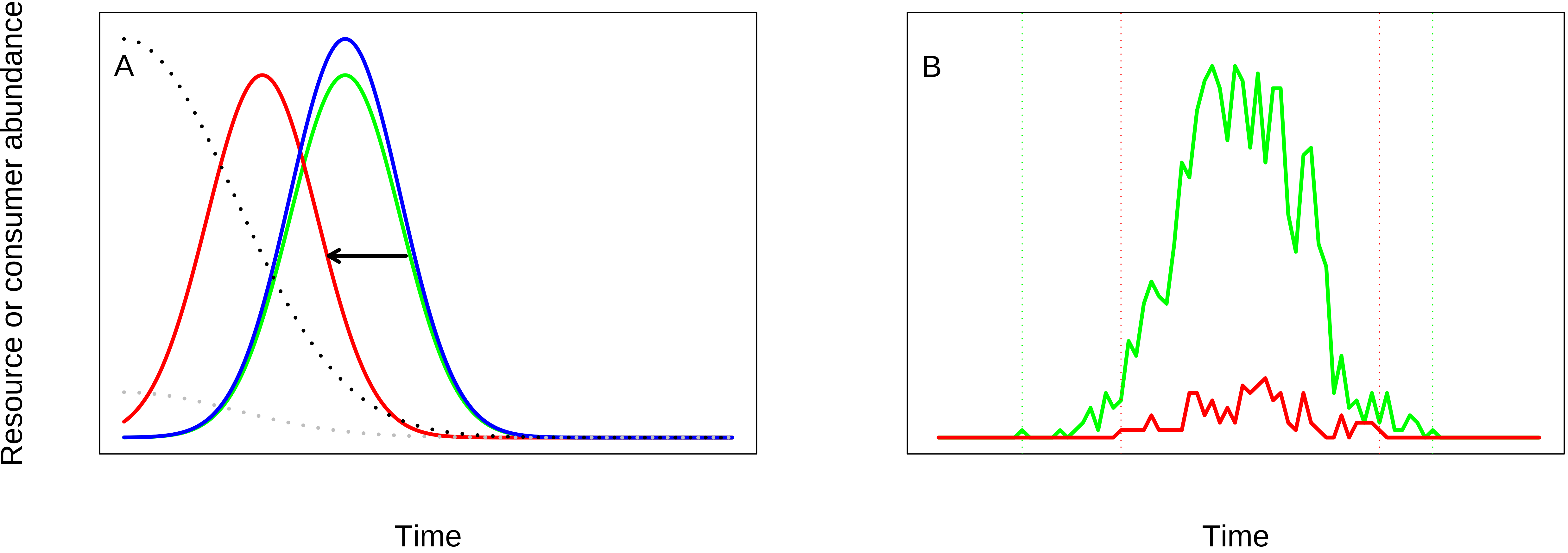
If one VR affects λ_s positively and one negatively, increased VRV in either VR decreases λ_s [2]

Increased variance in VR means among environmental states can increase λ_s, while increased VRV within states tends to decrease λ_s [3]

Increased frequency of (e.g.) fires or hurricanes can increase or decrease VR means, VRVs, and VR temporal correlations; collectively, these changes can increase or decrease λ_s, in complex ways. [4]

Example: Long-term trends in VR means and VRVs; no existing theory, so effects on λ_s must be examined by means of computer simulations


Mean increasing
Mean decreasing
Variability increasing
Variability decreasing
Value of climate variable
5
10
15
20
25
30
Year


Resource or consumer abundance
A
Time
B
Time