Adapting to climate change: a perspective from evolutionary physiology

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ABSTRACT: Much attention has been given to forecasting the likely effects of ongoing climate change on biodiversity. A large and often contentious literature has developed about how changes in species' ranges should be modelled and how additional biological mechanisms might be incorporated to improve their utility. Nonetheless, 2 areas stand out as relatively underappreciated: the importance of understanding a species' physiological capacities when forecasting its response to climate change, and the likely influence that capacities for genetic change across generations and changes in plastic responses, or the lack thereof, will have on a species' response. Although perhaps not as well developed as correlative approaches to understanding species responses to change, mechanistic approaches are advancing rapidly. In this review, we explore several of the key messages emerging from the mechanistic approach, embodied in evolutionary physiology, to understanding and forecasting species responses to climate change.

KEYWORDS: Physiological ecology · Macrophysiology · Phenotypic plasticity · Demography · Adaptation · Selection

1. INTRODUCTION

In October 2009, the International Energy Agency (IEA) announced a major opportunity to mitigate climate change presented by the downturn in carbon emissions resulting from the global financial crisis. Their forecast estimated an emissions reduction of 3%, bringing a future target of 450 ppm CO_2 apparently within reasonable reach (IEA 2009). Whilst the IEA report is optimistic about the political feasibility of a 450 ppm target (compare this with the IPCC Special Report on Emissions Scenarios; IPCC 2000), and achieving such a target would certainly reduce the extent of ongoing climate change, given the radiative forcing of CO_2 as a greenhouse gas (Archer & Rahmstorf 2010), the present course of human activities still commits the globe to substantial changes in climate. Indeed, even if radiative forcing remained at the level experienced in 2000, warming and other changes in climate would continue. Independent assessments also indicate that the trajectory of emissions has exceeded even the highest forecasts made by the IPCC (IPCC 2007). Thus the planet is now committed to anthropogenic climate change. Moreover, new evaluations suggest that dangerous environmental impacts will require smaller degrees of warming than previously thought (Smith et al. 2009).

Biologists no longer doubt that biological systems have already responded to the current global anthropogenic changes in climate. Many studies have demonstrated substantial shifts in the geographic ranges and phenologies of species from a broad array of taxa, indicating a coherent fingerprint of climate change (e.g. Walther et al. 2002, Parmesan & Yohe 2003, Genner et al. 2004, Nussey et al. 2005, Both et al. 2006, Møller et al. 2006, Parmesan 2006, Pörtner & Knust 2007, Lenoir et al. 2008, le Roux & McGeoch 2008, Chen et al. 2009, Steltzer & Post 2009). Given the substantial evidence of shifting ranges and phenologies, and of substantial range shifts in the past (Dynesius & Jansson 2000, Davis & Shaw 2001), much attention has also been given to forecasting the likely effects of ongoing climate change on species and ecosystems from these perspectives (e.g. Midgley et al. 2003, Thomas et al. 2004, Thuiller et al. 2006, Kearney et al. 2008). A large body of often contentious literature has developed about how changes in species' ranges should be modelled and how additional biological mechanisms might be incorporated to improve their utility (e.g. Pearson & Dawson 2003, Elith et al. 2006, Hijmans & Graham 2006, Brooker et al. 2007, Soberón 2007, Sutherst et al. 2007, Beale et al. 2008, Jeschke & Strayer 2008, Keith et al. 2008, Elith & Graham 2009).

Nonetheless, 2 areas stand out as relatively underappreciated: the importance of understanding a species' physiological capacities when forecasting its response to climate change (reviewed by Helmuth et al. 2005, Kearney & Porter 2009), and the likely influence that capacities for genetic change across generations and changes in plastic responses, or the lack thereof, will have on a species' response (Lande & Shannon 1996, Stillman 2003, Bradshaw & Holzapfel 2006, 2008, van Asch et al. 2007, Kearney et al. 2009a). In many ways, these 2 areas of research are inseparable. If evolutionary or plastic adjustments are impossible (or simply slower than the rate required to keep up with environmental change), the demographic effects of a mismatch between physiological capacities (in a multi-species context, see de Mazancourt et al. 2008) and environmental variation will lead to local extinction. Indeed, when the rate of environmental change is below ca. 10% of a phenotypic standard deviation per generation, mean time to extinction increases rapidly (Burger & Lynch 1995). The degree of unpredictability of an environment can also make the presence of genetic variance disadvantageous (Lande & Shannon 1996). Thus patterns of environmental noise will affect responses to environmental change (Stenseth et al. 2002, Tuljapurkar et al. 2003, Ranta et al. 2006, Pertoldi et al. 2008). If organisms can locate new areas that are better suited to their physiological capacities, a range shift might take place; however, if such sites are unavailable or inaccessible (Hill et al. 1999, Perry et al. 2005), the population is likely to go extinct. Consequently, understanding the extent to which current ranges set variation in physiological characteristics— and the extent to which such characteristics might change via either plasticity or evolution—form key elements of forecasting biological responses to global change (Chown & Terblanche 2007, Pörtner & Farrell 2008, Hoffmann 2010). Although perhaps not as well developed as correlative approaches, mechanistic approaches are advancing rapidly (e.g. Kearney & Porter 2009). Here we explore several of the messages emerging from mechanistic modelling.

2. PHYSIOLOGICAL TRAITS AND FUNDAMENTAL LIMITS

Organisms posses a wide range of systems that maintain function, restrict damage or depress metabolism under extreme conditions (such as up-regulation of heat shock proteins; Feder & Hofmann 1999, Sørensen et al. 2003). Understanding how and why these systems vary through space and time to ensure survival and reproduction lies at the very heart of evolutionary physiology (Prosser 1986, Hoffmann & Parsons 1997, Mangum & Hochachka 1998, Feder et al. 2000, Hochachka & Somero 2002, Sørensen et al. 2003, Chown et al. 2004). Thus evolutionary physiology has particular significance in the context of climate change responses.

One concept in evolutionary physiology that has proven especially fruitful from both theoretical and empirical perspectives is that of the performance curve (Fig. 1). This concept has been applied in a variety of guises (e.g. Huey & Stevenson 1979, Vannier 1994, Pörtner 2001), but in essence all performance curves represent the response of a physiological rate to a change in an environmental variable. Furthermore, one can consider how the form of this response might change under various circumstances (Levins 1968, Gilchrist 1995, Kingsolver & Huey 1998, Davis et al. 2005). Performance curves also provide a point of departure for investigations of the biochemical and cellular mechanisms underlying variation in particular physiological functions (Pörtner 2001, 2002, de Jong & van der Have 2008). Most commonly, the environmental variable of interest is temperature, but physiological and vital rates (e.g. reproduction, expected lifetime fecundity [R_o], and maximum intrinsic rate of increase [r_{max}]) also vary with other environmental variables (such as pH and humidity) (Chown & Gaston 2008). These performance curves, and their spatial and temporal variation, provide a useful means of understanding how physiological variation can influence a spe-
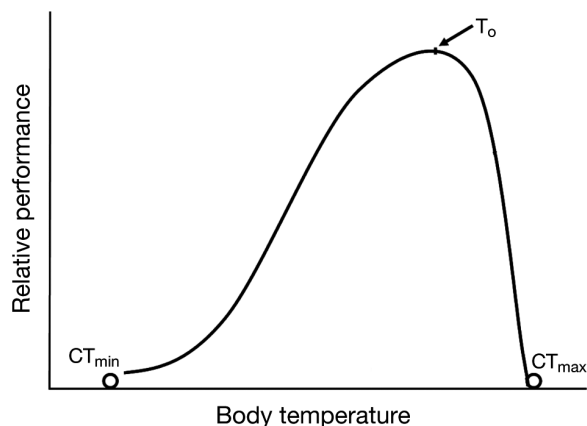
Fig. 1. A typical thermal performance curve. Parameters such as the optimal temperature (T_o), critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}) have a considerable influence on fitness (Angilletta 2009). Figure courtesy of S. Clusella-Trullas

cies' response to climate change (Buckley 2008). Such relationships also underlie physiologically based species distribution models (Crozier & Dwyer 2006, Austin 2007, Buckley 2008, Kearney & Porter 2009, Kearney et al. 2009a). Consequently, renewed attention has been given to the thermal sensitivity of performance and to thermal limits in general, as well as the application of these physiological measures in the laboratory to ecological problems in nature (e.g. Angilletta et al. 2002, 2006, Loeschcke & Hoffmann 2007, Pörtner & Knust 2007, Kristensen et al. 2008b, Chown et al. 2009, Kellermann et al. 2009).

A theoretical understanding of variation in the limits, breadth, optima and maxima of thermal performance curves is well developed. Perhaps one of the most notable conclusions of a recent review thereof (Angilletta 2009) is that empirical evidence has failed in many cases to support the predictions of current theory. This mismatch between theory and data might stem from ecological interactions among species, costs of resource acquisition and spatial structure of the environment—all of which have not been adequately captured by existing models (Davis et al. 1998, de Mazancourt et al. 2008, Angilletta 2009, Mitchell & Angilletta 2009). The mismatch might also result from fundamental limits to some aspects of thermal performance curves. For example, whilst metabolic functions of metazoans have an upper thermal limit of ca. 47°C (Pörtner 2002), heat tolerance seems to have limited capacity for genetic and plastic responses (Gilchrist & Huey 1999, Chown 2001, Mitchell & Hoffmann 2010). Likewise, thermal specialists and generalists differ substantially in the extent to which physiological limits might evolve (Hoffmann et al. 2003a, Kellermann et al. 2009). Nonetheless, theory has clarified expectations

for when and how physiological traits might significantly influence demographics, and thus geographical distributions and range limits (see e.g. Holt et al. 1997).

Biologists have empirically demonstrated that physiological traits can limit the distributions and ranges of species (reviewed in Hoffmann & Blows 1994, Gaston 2003, 2009). Moreover, the fact that species richness depends strongly on temperature provides further support for this idea (see Allen et al. 2002, Clarke & Gaston 2006, Wang et al. 2009). Nonetheless, many approaches to niche modelling assume implicitly (and sometimes incorrectly) that geographic distributions provide an adequate index of a species' environmental tolerance (e.g. Bonier et al. 2007). Not only may other factors be responsible for influencing species range limits and abundance structure, but the direction of causality may also sometimes be difficult to discern (Gaston 2003, 2009). Be that as it may, physiological traits play an important initial demographic role by influencing survival and reproduction under a given set of environmental conditions (Soberón 2007).

The significance of understanding such relationships between the phenotype and the environment has recently been highlighted by 2 studies (Deutsch et al. 2008, Huey et al. 2009). Both studies considered environmental temperatures and thermal optima in a spatially explicit context. These studies define: (1) the difference between the optimal temperature for physiological performance and the mean (or maximal) body temperature as the 'thermal safety margin', and (2) the difference between the critical thermal maximum (CT_{max}) and the mean (or maximal) body temperature as the 'warming tolerance'. By analyzing latitudinal variation in the safety margin and the warming tolerance, these studies have shown that tropical ectotherms could be at considerably greater risk from environmental warming than their temperate counterparts.

Whether tropical ectotherms are actually at greater risk than temperate organisms from environmental warming is a more difficult question to answer than some biologists have acknowledged. From a climatic perspective, both current and forecasted changes in temperature may be accompanied by increased precipitation and cloud cover in many tropical regions (Trenberth & Shea 2005, Meehl et al. 2007, Trenberth et al. 2007, Adler et al. 2008, Zhou et al. 2009), which could reduce thermal loads for ectotherms in these areas. By contrast, regions just outside the tropics not only are historically prone to the highest environmental temperatures (Bonan 2002), but also are likely to experience less precipitation and cloud cover in the future. Thus ectotherms at these latitudes, rather than those in the tropics, might be most at risk. A more recent and larger compilation of data suggests that this may well be the case for squamate reptiles (S. Clusella-

Trullas et al. unpubl data). Moreover, this study also showed that variation in preferred body temperatures and critical thermal maxima are more strongly related to the variances of precipitation and temperature, respectively, than either is to the mean temperature. Thus changes in mean environmental temperatures might have played a smaller role in the evolution of performance curves than have changes in thermal extremes and their interactions with precipitation (and likely cloud cover). In a similar vein, tropical species of *Drosophila* from eastern Australia have relatively high upper thermal limits which are no closer to thermal extremes likely to be experienced by these species in the field than are those of a non-tropical group (J. Overgaard et al. unpubl. data).

These findings highlight the significance not only of mean values for influencing the evolution of performance curves, but also variance in the parameter of interest, extreme events, the predictability of both and the time scale over which they take place relative to the duration of various stages (Angilletta et al. 2006, Chown & Terblanche 2007). Along with changes in average conditions, changes in daily and seasonal variation and in the frequency of extreme events are an integral part of current and forecast climate change (Katz & Brown 1992, Easterling et al. 2000, Jentsch & Beierkuhnlein 2008, Knapp et al. 2008). Thus understanding the likely responses of traits to these changes, and the demographic consequences of any response, is important for forecasting the impacts of change. Indeed, a limited range of examples has already demonstrated the considerable demographic and evolutionary significance of extreme events and combinations of events that increase physiological stress (Grant & Grant 1993, Brown & Brown 1998, Parmesan et al. 2000, Gutschick & BassiriRad 2003, Helmuth et al. 2006, Jentsch et al. 2007, Parker et al. 2008, Wegner et al. 2008, Welbergen et al. 2008, Pelini et al. 2009).

Many traits also show plasticity (Pigliucci 2005), which can result in the alteration of direct and indirect interactions among individuals and their environments, so affecting population and community dynamics, and aspects of community and ecosystem functioning (Pertoldi et al. 2007). Hence, to predict the biological outcome of an environmental change, understanding the magnitude and direction of phenotypic plasticity (i.e. the potential of individuals to respond over the short term) and the speed at which the population can evolve (i.e. the potential of the population to respond over the long term) is also important. Although plasticity is often viewed as a likely way that organisms can deal with climate change, the effectiveness of this strategy depends on whether organisms can predict stressful conditions. Phenotypic plasticity can be interpreted as a bet-hedging strategy in an unpredictable environment (Simons & Johnston 1997). When the magnitude of genetic variation is insufficient to create a diversity of phenotypes that can be exposed to selection, phenotypic plasticity, by producing variation within populations, will enrich the evolutionary potential. However, phenotypic plasticity can also reduce the ability for evolutionary adaptation (see van Buskirk & Steiner 2009). Moreover, the genetic constitution of a specific population might significantly affect its ability to respond to changing environmental conditions via plasticity. For example, small populations exposed to genetic drift and inbreeding may be less plastic; a phenomenon described by Fowler & Whitlock (1999) as inbreeding depression for canalisation (Fig. 2). Few experiments examine the significance of this phenomenon for traits of physiological importance in natural populations. Unpredictable thermal variation should lead not only to a broadening of performance curves, but also to a reduction in phenotypic plasticity (Kingsolver & Huey 1998, Deere & Chown 2006, Angilletta 2009). Thus, in areas where climate change involves a decline in the predictability of extremes, populations that currently show considerable plasticity may face high costs because of inappropriate responses. Moreover, these costs may differ considerably among life stages because of the variation in strategies and the significance of behavioural adjustment among them (e.g. Huey et al. 2003, Marais & Chown 2008). Understanding the significance of extreme events remains a pressing, yet under-investigated, issue (see Schwager et al. 2006, Chown & Terblanche 2007 for further discussion).

Importantly, climate change will affect several environmental parameters simultaneously. Thus populations are likely to encounter concurrent changes in
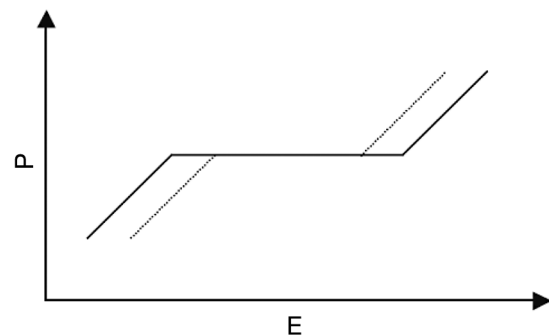

Fig. 2. Schematic illustration of canalization. For a given genotype, the phenotype (P) is a non-linear function of the environment (E), as shown by the solid line. For a 'normal' range of environments, the genotype shows no phenotypic variation, but variation exists outside this range. If canalization is reduced, e.g. by inbreeding, then this 'zone of canalization' is narrowed, as shown by the dotted line. The result is more environmental variance in the population (modified after Lewontin 1974)

temperature, water availability and resource supply. Furthermore, environmental stress may cause a pronounced reduction in effective population size and, in consequence, reduce evolutionary potential and increase inbreeding rate. Typically, laboratory investigations do not adopt a multifactorial approach, preferring to vary one parameter while holding others constant, which may constrain the ecological relevance of such studies (Gibbs 1999, Harshman & Hoffmann 2000). However, multifactor assessments will be important for understanding future responses. Not only is variation in performance curves associated with such interactions (see above), but multi-factor assessments may reveal trait–environment and genotype–environment interactions that limit responses to change. Genotype–environment interactions for a trait within a population suggest genetic variation for phenotypic plasticity, and will increase the phenotypic variance of the trait, which will depress the response to selection (Pertoldi & Bach 2007). There is ample evidence for trait interactions limiting responses to selection (Etterson & Shaw 2001, Blows et al. 2004).

Moreover, synergistic interactions among climate and other factors are expected (Brook et al. 2008). Although evidence for ecological synergies is limited at present (Darling & Côté 2008), multivariate studies are starting to emerge (e.g. Hayward et al. 2001, Juliano et al. 2002, Chown et al. 2007, Hoverman & Relyea 2007, Campero et al. 2008, Kristensen et al. 2008a, Liu et al. 2009). Ultimately, the need for replication limits the number of factors that can be examined in one experiment to no more than a few. Common garden experiments, field releases of manipulated organisms, and mesocosm trials provide useful ways of overcoming these experimental limitations, because the more natural conditions represent a multifactor change in the environment (Loeschcke & Hoffmann 2007, Kristensen et al. 2008a,b, Gaston et al. 2009, Overgaard et al. 2010). Whilst the ultimate cause of the response may not always be detectable from these approaches, this cause might be elucidated by combining experiments under natural conditions with laboratory experiments.

3. POTENTIAL AND REALIZED EVOLUTION DURING CLIMATE CHANGE

Despite the complexity of selective factors in changing environments, evolutionary responses are well documented. The earliest examples include the evolution of metal tolerance in plants and the evolution of pesticide tolerance in insects (Bishop & Cook 1981). More recently, rapid evolutionary changes during the course of biological invasions have also been observed (Strauss et al. 2006, Carroll & Fox 2007). Substantial phenotypic responses to climate change have been documented for several traits (e.g. Walther et al. 2002, Convey et al. 2003, Perry et al. 2005, Bradshaw & Holzapfel 2006, Millien et al. 2006, Babin-Fenske et al. 2008), and it has also been shown that species which appear incapable of responding are suffering adverse consequences (Møller et al. 2008, Ozgul et al. 2009). However, only a few studies have so far demonstrated a genetic basis to these responses (Nussey et al. 2005, Umina et al. 2005, Bradshaw & Holzapfel 2008), and it is not yet clear to what extent phenotypic changes reflect plasticity or evolutionary change (Gienapp et al. 2007, 2008). Indeed, recent studies of red-billed gulls and Soay sheep failed to document evidence for genetic change, despite large, climate-associated declines in body size (Teplitsky et al. 2008, Ozgul et al. 2009).

For the traits typically investigated by evolutionary physiologists, evidence of climate-induced evolution is limited (Gienapp et al. 2008). Nevertheless, a few studies have had the power to detect evolutionary adaptation to climate change (Bradshaw & Holzapfel 2001, Franks et al. 2007, Hoffmann & Daborn 2007). Where evolutionary changes have not been detected, plastic changes might have compensated for the demographic impacts of climate change, as in the case of birds shifting their nesting time in response to food availability (Teplitsky et al. 2008). Despite the relative lack of empirical evidence to date, rapid evolution of phenotypes and their plasticity is expected from theoretical models (see reviews in Ghalambor et al. 2007, Angilletta 2009). Moreover, it has also been widely documented in laboratory studies of responses to environmental temperature and water availability (e.g. Bennett et al. 1992, Cavicchi et al. 1995, Bull et al. 2000, Gibbs et al. 2003, Bubliy & Loeschcke 2005, Driessen et al. 2007, Sørensen et al. 2007, Vera et al. 2008).

Plastic changes have an underlying genetic basis and the extent of plasticity may thus also evolve (Scheiner 2002, Driessen et al. 2007). For example, Nussey et al. (2005) showed that great tits *Parus major* in the Netherlands have increased their phenotypic plasticity to cope with more unpredictable spring weather in the Netherlands over the last 32 yr. This is one example illustrating heritable genetic variation for the ability to respond in a plastic manner. However, estimates of heritability and variance components for the physiological mechanisms underlying plastic responses (Krebs et al. 1998) are scarce.

A problem in extrapolating from laboratory studies to likely field responses is that the traits characterized under laboratory conditions might not be relevant to field ecology. Two issues related to the measurement of heat tolerance illustrate this point. First, the rates of

evolution in response to heat stress will depend on how this trait is measured. Recent studies of tsetse flies, vinegar flies and Argentine ants have shown that the rate of controlled thermal change, part of the procedure for estimating critical thermal limits, affects not only the mean thermal limit but also its variance and acclimation potential (Terblanche et al. 2007, Chown et al. 2009, Mitchell & Hoffmann 2010). The latter study showed that substantial differences in phenotypic variance emerged when rates of thermal change were varied, influencing the heritability and evolvability of traits. These findings underscore the need to document rates of environmental change appropriate to the organism of interest (see also Sinclair 2001). The second issue is that measures of heat tolerance can be quite poorly correlated, underscoring the importance of measuring tolerance in a meaningful way. In *Drosophila*, intraspecific comparisons have revealed limited evidence for genetic correlations between traits such as knockdown resistance and mortality rate (Hoffmann et al. 1997, Berrigan & Hoffmann 1998), suggesting that different genetic mechanisms underlie these traits (Hoffmann et al. 2003b, Rako et al. 2007, but see Sørensen et al. 2007). Yet correlations between these traits do appear at the interspecific level (Hori & Kimura 1998, Berrigan 2000, Mitchell & Hoffmann 2010), which may reflect patterns of correlated selection rather than genetic correlations.

The potential for adaptation can also be usefully explored within a demographic framework. When population sizes fluctuate or are small, the potential for demographic extinction exists even when populations might possess genetic variation for adaptation (Burger & Lynch 1995). Moreover, if effective population size is small, the amount of heritable variation may be limited and selection could be overwhelmed by genetic drift, making all phenotypes or alleles effectively selectively neutral (Lynch 1996). Thus the population may be unable to evolve in response to selection, leaving it vulnerable to demographic and environmental stochasticity, which might, in consequence, be the dominant factor in determining the fate of small populations (Drake & Lodge 2004, Hoarau 2005).

As population size increases, evolutionary change becomes possible, but adaptation might nevertheless be opposed by gene flow and genetic drift during a population bottleneck (Holt et al. 2003, 2004), and perhaps further confounded by inbreeding depression. These different components have rarely been compared within the context of adaptation to climate change. In a recent study, Willi & Hoffmann (2009) examined the relative impacts of heat stress and demographic factors on experimental populations of *Drosophila birchii*. Demographic factors were more important in small populations (20 flies), whereas heritable

variation for dealing with heat stress became important in larger populations (100 flies) and predominated in even larger populations (1000 flies). Although most traits that have been examined in model organisms (e.g. *D. melanogaster*) vary genetically within populations, the results of Mitchell & Hoffmann (2010) suggest that this is not always the case. Moreover, the situation becomes more complicated when different species are compared. For example, tropical species of *Drosophila* that are sensitive to desiccation have little genetic variation for desiccation resistance when compared to more widespread species that were less sensitive (Kellermann et al. 2009). Similar comparative data for other taxa are urgently required.

Small population size can also lead to inbreeding, and inbreeding depression is often more severe under stressful environmental conditions (reviewed in Armbruster & Reed 2005). Thus climatic conditions that are considered benign for a large population may be highly stressful for a smaller population of the same species. Liao & Reed (2009) found that inbreeding by environment interactions affected extinction risk for a wide range of population sizes and substantially reduced the mean persistence time, compared to a situation where such interactions were not included. Thus, apart from considering synergistic interactions between environmental factors, interactions between genetic and environmental factors should be considered in future empirical and modelling studies as they are likely have strong impacts on the distribution of performance curves.

Because the effects of climate change on the environment can be complex and involve altered biotic interactions, adaptation may be slowed by the multiple genetic changes that might be required (Van Doorslaer et al. 2009). Thus not only could responses to selection be constrained by genetic correlations among traits (Blows et al. 2004) and by patterns of gene flow (Kirkpatrick & Barton 1997, Holt et al. 2003, Bridle et al. 2009), but they might also be slowed by the fact that the right combination of alleles for adapting to new conditions is not available. Moreover, even when genetic variation is present, the environment can affect the expression thereof, such that it is not expressed when phenotypic selection is most intense (Robinson et al. 2009).

4. THE BROADER CONTEXT

As indicated by the preceding discussion, the demographic context of phenotypic variation has considerable significance to the process of adaptation. Not only does dispersal among patches influence the evolution of traits and their plasticity, but the changing meta-

community also plays a role in determining how populations respond to change (reviewed in Chown & Terblanche 2007, Angilletta 2009; see also Holt & Keitt 2000, Ricklefs 2008, Tylianakis et al. 2008, Mitchell & Angilletta 2009). Given this situation, predictions at the community level seem either pointless at present or unworthy of pursuit (see Lawton 1999, Simberloff 2004, Ricklefs 2008), especially since initial conditions, instabilities and model errors should greatly affect the predicted impact of climate change on ecological communities. Nonetheless, one might still have hope for forecasting the impacts of climate change on species or populations (or more broadly at the landscape and macroecological levels).

Mahlman's (1998) pinball-machine-thought experiment provides a useful analogy for this situation. In the game, the path of the ball is unpredictable after a few collisions with the machine's bumpers, but at some point the ball will end up in the gutter. The odds of the ball ending up in the gutter can be altered dramatically by changing the slope of the playing field. In this latter scenario, the trajectory of the ball remains as unpredictable as before the change in slope. Nevertheless, one can predict that the ball will require more time to reach the gutter. Forecasting the impact of climate change on diversity can be viewed in a similar fashion: many of the details of ensuing interactions will not be especially clear, but the general trends should be reasonably comprehensible.

Currently, 2 broad approaches are available for understanding the interplay between physiology and the environment, and perhaps for forecasting responses to climate change within a broader context. The first, 'analytical' approach amounts to scaling up spatially explicit studies by adopting an $r \times c$ matrix perspective (Gaston et al. 2008, 2009). Traditionally, cells of such a matrix would comprise the presences/absences of species or their respective abundances at a series of sites (e.g. Bell 2003). However, the matrix can be populated with virtually any variable, such as critical thermal maximum of a series of populations. In a spatially explicit form, spatial variation in an environmental factor (e.g. mean temperature) might form the first matrix. With an appropriate function relating the environmental variable to survival or growth rate, these data might be translated into a matrix of predicted abundances. The function matrix could be considered invariant across space, time or taxonomy (niche conservatism; see Wiens & Graham 2005). Alternatively, spatial variation in the function matrix might reflect predicted or realized phenotypic plasticity, which in turn could be associated with a matrix containing dispersal rates among populations. Formal mathematical approaches for investigating the relationships among matrices and for identifying signifi-

cant variation in parameters are available (see Dray & Legendre 2008). Likewise, characteristics of matrices, such as nestedness, can be analyzed to assess the roles that various factors play in structuring assemblages. Clearly, such an approach is closely related to physiologically based models of species' distributions (Kearney & Porter 2009), crop performance models (e.g. Brisson et al. 1992), spatially explicit population viability modelling (e.g. Carroll 2007), landscape ecology (e.g. Werner et al. 2009) and landscape genetics (Balkenhol et al. 2009).

The second, 'simulation' approach (or general simulation modelling [GSM]), is similar to the analytical approach in the sense that it is spatially explicit and adopts a series of Cartesian layers (Gotelli et al. 2009). However, the simulation approach diverges at this point in a way that avoids problems associated with curve fitting and parameters associated with the concatenation of multiple species models. In essence, the simulation approach involves the settings of 3 'control knobs': dispersal limitation, evolutionary origins and environmental gradients. Whilst these factors are the basic settings, multiple controls are clearly required for each (e.g. Gotelli et al. 2009). The GSM makes relatively few assumptions, as do models of geometric constraints (see Currie & Kerr 2008) and, at least from a 'first order perspective', as does the metabolic theory of ecology (Brown et al. 2004). The GSM approach therefore makes a useful addition to the suite of approaches available to predict the likely impacts of climate change, although it has yet to be tested. A comparison of the outcomes of the GSM and analytical matrix approaches to the same set of data might prove especially informative (see Zurell et al. 2009 for an analogous approach).

5. CONSERVATION IMPLICATIONS

Determining the biodiversity impacts of climate change is a considerable challenge (Schwenk et al. 2009). Clearly, evolutionary physiology has much to offer in this undertaking. For example, the suggestions that tropical ectotherms might face the greatest risk of extinction from warming (and drying) and might lack the genetic variation to adapt (Hoffmann et al. 2003a, Kellermann et al. 2009) draws immediate attention to the conservation needs of these organisms, which were previously considered to be at less risk than ectotherms in other regions. A demonstration of the significance of shade to many species for physiological regulation, and patterns of habitat conversion, provide further grounds for concern (Kearney et al. 2009b).

As reviewed here, substantial shifts in the ranges and phenologies of species from an array of groups

have occurred in response to climate change (Walther et al. 2002, Parmesan & Yohe 2003, Nussey et al. 2005, Parmesan 2006, Lenoir et al. 2008, Chen et al. 2009, Steltzer & Post 2009). These observations emphasise the importance of mitigating such shifts by maintaining corridors or by securing large areas with suitable habitats for wildlife. Without such initiatives, many populations may become extinct due to combined effects of environmental stress, lack of evolutionary potential and inbreeding depression.

Evolutionary physiology can also make valuable contributions to other areas. For example, the effects of anthropogenically assisted biological invasions and climate-induced range shifts will be increasingly difficult to separate (Tolley et al. 2008, Walther et al. 2009). Physiologically based models of species' distributions coupled with investigations of the success of particular genotypes during environmental change may provide one means of separating human- and climate-induced range shifts, especially since these genotypic differences have a profound effect on the success of invasions (Keller & Taylor 2008) as well as on current ability to forecast their ranges in new areas (Mau-Crimmins et al. 2006, Fitzpatrick et al. 2007, Duncan et al. 2009). Similarly, much attention is focused on assisted translocation (Richardson et al. 2009). Whilst this strategy will be useful for only a minority of species designated of special interest, investigations of likely demographic success in new areas will have to consider the physiological capabilities of the species. Moreover, although assisted translocation of entire species may be difficult, translocation of genotypes adapted to different conditions is likely to be much more feasible and might provide an insurance policy against future change (Broadhurst et al. 2008, Hedrick & Fredrickson 2010, but see Bijlsma et al. 2010). In this regard, assessments of movements of individuals into areas perhaps already occupied by other populations of the species may have to move away from the consideration of neutral markers only (which will show differences based mostly on time of isolation) and consider genes that are likely to have significance in the context of environmental responses (Demontis et al. 2009, Pertoldi et al. 2010). Genome-based evolutionary physiology has much to offer here too. For example, genome-wide breeding strategies can be used on captive populations of endangered species before translocation into the wild to optimize genetic variability in physiologically important parts of the genome (Pertoldi et al. 2010).

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