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RESEARCH REVIEW

Toward a conceptual synthesis for climate change responses

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ABSTRACT

Aim To identify hypotheses for how climate change affects long-term population persistence that can be used as a framework for future syntheses of ecological responses to climate change.

Location Global.

Methods We surveyed ecological and evolutionary concepts related to how a changing climate might alter population persistence. We organized established concepts into a two-stage framework that relates abiotic change to population persistence via changes in the rates or outcomes of ecological and evolutionary processes. We surveyed reviews of climate change responses, and evaluated patterns in light of our conceptual framework.

Results We classified hypotheses for population responses to climate change as one of two types: (1) hypotheses that relate rates of ecological and evolutionary processes (plasticity, dispersal, population growth and evolution) to abiotic change, and (2) hypotheses that relate changes in these processes to four fundamental population-level responses (colonization, acclimatization, adaptation or extinction). We found that a disproportionate emphasis on response in the climate change literature is difficult to reconcile with ecological and evolutionary theories that emphasize processes. We discuss a set of 24 hypotheses that represent gaps in the literature that limit our ability determine whether observed climate change responses are sufficient to facilitate persistence through future climate change.

Main conclusions Though theory relates environmental change to fundamental ecological and evolutionary processes and population-level responses, clear hypotheses based on theory have not been systematically formulated and tested in the context of climate change. Stronger links between basic theory and observed impacts of climate change are required to assess which responses are common, likely or able to facilitate population persistence despite ongoing environmental change. We anticipate that a hypothesis-testing framework will reveal that indirect effects of climate change responses are more pervasive than previously thought and related to a few general processes, even though the patterns they create are incredibly diverse.

Keywords

Adaptation, climate change, dispersal, evolution, extinction, population growth, population, selection.

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INTRODUCTION

The environmental impacts of climate change are as diverse and complex as the climate system itself, and are altering the spatial distributions and phenotypes of species world-wide (Helmuth *et al.*, 2006; Parmesan, 2006). Although the fingerprint of global warming is detectable across many ecosystems (Root *et al.*, 2003), understanding how these early observations relate to the long-term effects of climate change remains one of the most important research challenges of our time. The challenge is
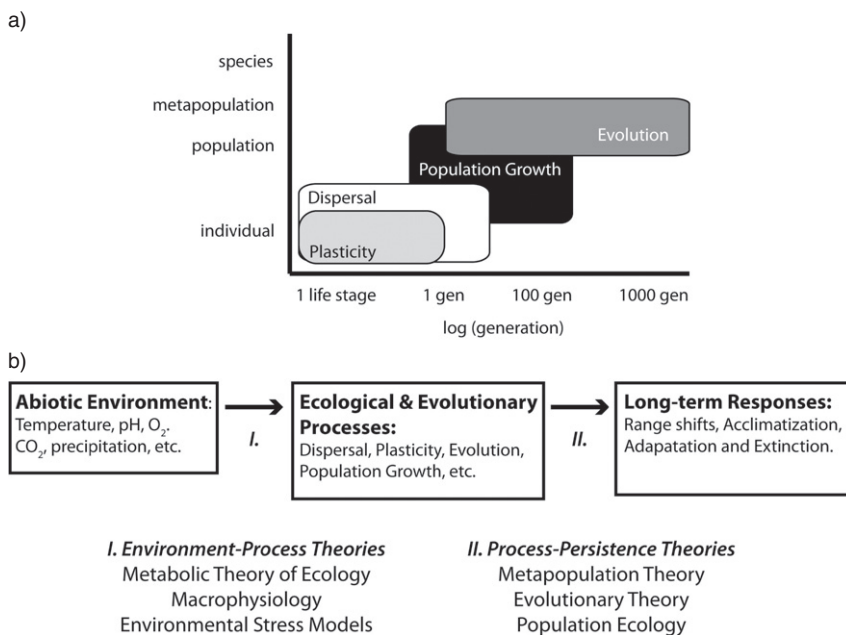
a)

b)

I. Environment-Process Theories
Metabolic Theory of Ecology
Macrophysiology
Environmental Stress Models

II. Process-Persistence Theories
Metapopulation Theory
Evolutionary Theory
Population Ecology

Figure 1 A conceptual framework relating environmental change to long-term population responses. (a) Fundamental processes mediating ecological and evolutionary responses to climate change occur across levels of ecological organization and temporal scales. Plasticity and dispersal occur within as little as one generation (gen) and are population- or individual-level processes, while population growth and evolution involve populations and longer periods of time. (b) Ecological and evolutionary theories provide models for how the abiotic environment influences fundamental processes (Table 2, 1), as well as models for how changes in these processes influence long-term species persistence (Table 2, 2).

two-fold: first, ecologists and evolutionary biologists must continue to document the nature and magnitude of ecological and evolutionary responses to climate change. This documentation is essential, but will be most helpful when observations and theory are united in a framework that can then guide future research and conservation. Thus, the second challenge now facing ecologists is to develop and test theoretically grounded hypotheses. Hypothesis-testing can robustly relate observations to their underlying mechanisms, and facilitate integration of these findings into a general theory for climate change ecology.

After nearly two decades of increasing interest in climate change, there is now a need for synthesis of the fundamental ecological and evolutionary theory that describes how we expect climate change to influence long-term species persistence (Pertoldi & Bach, 2007; Reed *et al.*, 2011). Despite over 1000 studies that document ecological impacts of climate change (McCarty, 2001; Root *et al.*, 2003; Helmuth *et al.*, 2006; Parmesan, 2006), efforts to develop general, theoretical insights have been frustrated by the emphasis on how patterns change in response to climate change and by the under-reporting of the processes that drive these changes. Recent syntheses of ecological and evolutionary theories are advancing a more general understanding of range shifts as responses to climate change (Burton *et al.*, 2010; Phillips *et al.*, 2010), but broader syntheses of the processes determining responses to climate change at the population level are still limited. Consequently, it remains difficult to answer basic questions about which hypothesized effects of climate change are most often rejected and which are most often supported. Which climate change responses are most common? Which are most enduring? We know which responses are most commonly observed and reported (Parmesan, 2006), but we do not know whether the most commonly reported responses are truly the most common in nature until we test a full, logical set of hypotheses for responses to climate change that consider the underlying processes.

Climate change studies generally have not reported results in the context of multiple, alternate hypotheses, and consequently the range of possible responses is far from evenly sampled. For example, the most frequently documented responses to climate change are acclimatization, e.g. plasticity of phenological events, and geographic range shifts, broadly defined to include range expansions and contractions (Root *et al.*, 2003; Parmesan, 2006; Gienapp *et al.*, 2008). These responses, however, are also the most intuitive and easily documented, and may be more readily observed than adaptation or extinction. The prevalence of acclimatization and range shifts in the literature may also reflect the rapid time-scale of their underlying processes (Fig. 1), rather than indicate that they are truly more common than the generally slower responses of adaptation or extinction (Gienapp *et al.*, 2008). Further, as a discipline, climate change ecology implicitly addresses whether and how long-term population persistence is possible in a changing climate. Alone, observation of one response (e.g. a pattern of colonization suggesting a range shift) does not imply that a range shift leads to long-term population persistence (Atkins & Travis, 2010; Burton *et al.*, 2010). This insight leaves us with little information on the persistence, fragility (Atkins & Travis, 2010) or frequency of ecological responses.

A prerequisite to a synthesis of the mechanisms underlying climate change responses is a framework to organize theoretical predictions for possible responses. Previous frameworks have grouped responses into ecological and evolutionary categories as a way to distinguish short- and long-term mechanisms (Parmesan, 2006; Reed *et al.*, 2011). However, a closer look at the processes that influence long-term persistence reveals that a more informative framework would ignore a distinction between the perceived time-scales of ecology and evolution and would focus more on relating the environment to long-term population responses via a small set of fundamental ecological and evolutionary processes (Ellner *et al.*, 2011). We synthesize

climate change responses and their underlying causes to generate hypotheses to generate a cross-disciplinary framework to guide future research.

A FRAMEWORK FOR ECOLOGICAL CLIMATE CHANGE RESPONSES

The effects of abiotic environmental change on population persistence can be understood primarily in terms of four fundamental processes (Fig. 1a). *Plasticity* of individual phenotypes (including behaviour, morphology or physiology) allows performance in a range of environmental conditions (Pigliucci, 2001). *Population growth*, whether positive or negative, integrates all direct and indirect effects of the environment on performance and fitness of individuals. *Dispersal* of individuals facilitates the expansion and recovery of populations, including movement into new habitats. *Evolution* describes changes in gene frequency in a population over time.

The four fundamental processes can explain the responses of populations to a changing environment. Populations may respond by becoming *extinct*, or by persisting. We can further characterize persistence by its underlying mechanism(s), and we refer to responses of *acclimatization*, *adaptation* and *colonization*. Populations may persist in a changing environment because of phenotypic acclimatization of individuals to environmental conditions, or because adaptation of populations changes gene frequency and increases or maintains fitness. Populations may also persist by moving through space, colonizing favourable habitats in previously unfavourable areas. The fundamental processes described above can also cause population extinction. Each response depends on certain conditions and constraints on the underlying processes (Table 1).

Ecological and evolutionary theories relate processes to population responses, and can be integrated to formulate hypotheses for how abiotic change might ultimately affect populations (Fig. 1b, Table 2). This approach blurs the distinction between evolutionary and ecological theories and favours an emphasis on theories that relate abiotic change to changes in the rates or outcomes of processes, and theories that relate changes in the rates of processes to long-term population responses (Fig. 1b, Table 2). Below, we use this approach to identify a range of hypotheses for the impacts of climate change on populations. While the links between processes and responses are often treated as one-to-one (e.g. evolution to adaptation, plasticity to acclimatization, dispersal to colonization, and population growth to extinction), we emphasize the interactions and non-intuitive connections between processes and responses. In addition, we focus on direct links between abiotic changes and changes in the processes outlined in Fig. 1(b), and we do not discuss in depth how the links between environment and process may be mediated by other factors like species interactions.

Classic theory has several limitations when applied to climate change scenarios. Immediate challenges include extending theories of selection that assume spatial equilibrium into a dynamic context (Phillips *et al.*, 2010), development of interdisciplinary theories (Pertoldi & Bach, 2007), and incorporation of climate variation into demographic models (Drake, 2005). Our approach (Fig. 1b) highlights two additional challenges. First, short-term population persistence does not always imply long-term persistence, and theory needs to more concretely outline conditions for long-term persistence in a changing environment. Second, climate-induced natural selection may be strongest on traits that are not directly related to climate (e.g. thermal

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Table 1 Ecological and evolutionary processes, subject to conditions and constraints, determine four main population responses to climate change.

Acclimatization: Plasticity in phenological or physiological traits, performance or behaviours
    Conditions: capacity for variation, accurate environmental cues (*e.g.* Pigliucci, 2001)
    Constraints: limited capacity for variation, trade-offs, high maintenance or production costs, unreliable environmental cues (e.g. Nussey *et al.*, 2005)

Colonization: Changes in dispersal to a new area, or in population growth in that new area that allow a new population to persist
    Conditions: dispersal; suitable habitat for dispersal or recruitment; sufficient dispersal rate in relation to rate of environmental change (Møller *et al.*, 2006); population growth in new habitat (Thomas *et al.*, 2001)
    Constraints: limited dispersal potential, geographic barriers to movement, unsustainable mortality rates during or after dispersal

Adaptation: Evolutionary change in gene frequency in a population that increases or maintains fitness under new environmental conditions
    Conditions: heritable trait directly or indirectly influenced by climate (Nussey *et al.*, 2005); variation in climate-related trait upon which selection can act; population growth rate sufficient to compensate for reduction in survival or fitness due to selection
    Constraints: critical trait unresponsive to climate or not heritable or variable (e.g. Hoffmann *et al.*, 2003); antagonistic genetic correlations that impede evolutionary change (Atkins & Travis, 2010), genetic drift in small populations that limits the effect of natural selection; generation time too long relative to the rate of environmental change; strong cost of selection that drives population abundance to zero; simultaneous changes in habitat, food and interacting species that cause overall reductions in fitness

Extinction: Population growth is negative and abundance declines to zero
    Conditions: Small geographic range, population size, insufficient genetic variation (Pounds *et al.*, 2006); other responses not possible (Pounds *et al.*, 2006); slow recovery time relative to disturbance (McLaughlin *et al.*, 2002)
    Constraints: Large geographic range or population size, connectivity to other populations

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Table 2 Summary of hypotheses for climate change responses following framework outlined in Fig. 1(b).

Hypotheses	Predicted response
1. Hypotheses for how abiotic change alters key processes	
1.1. Environmental warming has nonlinear, positive effects on population growth in ectotherms	Adaptation, colonization
1.1.a. In temperate climates, a few degrees of warming may enhance population growth, as long as resources do not limit additional growth	Adaptation, colonization
1.1.b. Population growth rate may respond positively to warming when an additional generation is added in response to longer growing seasons	Adaptation, colonization
1.2. Abiotic change can alter dispersal through plasticity	Adaptation, colonization, acclimatization
1.2.a. Abiotic change reduces dispersal distance and population connectivity through plasticity in dispersal-related traits	Adaptation, colonization, acclimatization
1.2.b. Plasticity in navigational behaviours or other habitat-related traits can drive sudden shifts in the spatial distribution of individuals in response to climate change	Adaptation, colonization, acclimatization
2. Hypotheses for how systematic change in processes determines long-term persistence	
2.1. Rapid population growth in a changing environment facilitates adaptation	Adaptation
2.1.a. Following an extreme climatic event that causes high mortality and selection, a high rate of population growth is critical for persistence that depends on adaptation	Adaptation, extinction
2.2. Effects of climate change on dispersal can influence adaptation	Adaptation
2.2.a. High dispersal will favour adaptation to climate at leading range edges when marginal populations have lower fitness in the new environment than source populations	Adaptation, colonization, extinction
2.2.b. High dispersal from range centres may impede adaptation at trailing range edges where adaptation to new climate conditions is required for persistence	Adaptation, colonization
2.3. Evolution at the leading and trailing edges of a species' range may be fundamentally different	Adaptation, colonization
2.3.a. At trailing edges, populations may persist through evolution of climate-related traits	Adaptation, colonization
2.3.b. At leading edges, non-climate traits such as species interactions or dispersal abilities will evolve more rapidly	Adaptation, colonization
2.4. Populations with moderate plasticity may have the greatest ability to adapt to climate change	Acclimatization, adaptation
2.4.a. Adaptation of phenotypes in populations with too much plasticity may lag so far behind changing climate conditions that species will be driven to extinction when climate conditions exceed the range of variation tolerated by plasticity in relevant traits	Acclimatization, adaptation
2.4.b. Populations with too little plasticity may not be able to tolerate any change, and may go extinct if they cannot colonize more favourable habitat	Acclimatization, adaptation
2.5. Changing climates may affect metapopulations differently from panmictic populations	Colonization, adaptation, extinction
2.5.a. Organisms in metapopulations may be adapted to disperse when conditions deteriorate	Colonization
2.5.b. Metapopulation structure enhances rapid range expansion at the leading (northerly, uphill) range edge, but may slow responses at the trailing range edge	Colonization
2.5.c. Individuals occurring in newly founded populations have a genetic predisposition to disperse	Colonization, adaptation
2.5.d. Panmictic populations have high dispersal rates among locations, suggesting that the rate of a geographic range shift should not be limited by dispersal	Colonization
2.5.e. Colonization and range expansion for isolated populations are likely to be dispersal limited	Colonization

These are a few hypotheses that emerge from our framework, and represent important next steps for research, but this table is not an exhaustive list of possible hypotheses. Numbers refer to cross-references in the text.

tolerance), but rather on traits that limit colonization or population growth (such as species interactions) or reproduction (generation time or timing). These two challenges emerge as themes in our overview of conceptual hypotheses for climate change responses.

Hypotheses for how abiotic change alters key processes (Table 2, 1)

Abiotic environmental changes affect the rates and outcomes of ecological and evolutionary processes. Several quantitative theo-ries relate physiological and metabolic rates to population-level processes (Brown *et al.*, 2004; Gaston *et al.*, 2009). These theories go beyond categorizing environmental conditions as stressful or not, and use basic biological principles to relate processes such as population growth rates and dispersal to environmental variables like temperature or oxygen availability (Savage *et al.*, 2004; O'Connor *et al.*, 2007; Pauly, 2007). Other theories relate environmental conditions to traits and trade-offs. Environmental conditions that increase mortality of individuals with certain trait values can cause selection and adaptation, but in a natural setting where individuals have to contend with both the physical

environment and species interactions, trade-off models that incorporate environmental change are essential (Burton *et al.*, 2010).

From this perspective, we identified fundamental insights in the recent literature that provide general links between climate and processes to illustrate how hypotheses can be formulated. In many cases, links between the abiotic environment and processes are reasonably well established, so we focus here on hypotheses that are more recent and promising in the context of climate change.

Warming accelerates demographic rates in ectotherms
(Table 2, 1.1)

Warming of a few degrees can either accelerate metabolic and demographic rates in ectotherm populations (Savage *et al.*, 2004; Gillooly *et al.*, 2006; O'Connor *et al.*, 2007), or cause sharp declines in demographic rates if warming exceeds optimal temperatures. Geographic patterns are emerging that suggest populations in temperate and polar regions may not typically live at their thermal optima, whereas in tropical regions many populations are at their thermal maximum (Deutsch *et al.*, 2008). This pattern implies that in temperate climates, a few degrees of warming may enhance population growth, as long as resources are not limiting (Table 2, 1.1.a). Projections derived from metabolic ecology are not universal, but do imply first-order relationships between abiotic (temperature) change and the rates of ecological and evolutionary processes that could cause predictable population-level responses (Fig. 1b).

Population growth rate may also respond positively to warming when an additional generation is added in response to longer growing seasons (Table 2, 1.1.b). Producing an additional generation within a year may speed up evolutionary processes. In recent years, many butterflies and moths in Central Europe have added a previously unknown generation in accordance with environmental warming (Altermatt, 2010).

Through either mechanism, small increases in environmental temperature could have nonlinear, positive effects on population growth (Table 2, 1.1). As we will explain below, these changes also increase the potential for adaptation and colonization (Table 2, 2.1).

Abiotic change can alter dispersal through plasticity
(Table 2, 1.2)

Dispersal is the process by which individuals move among habitat patches, and the rate, timing and success of dispersal is critical not only to colonization success and population persistence, but also to evolutionary processes such as gene flow and adaptation. Climate change can affect dispersal by altering the spatial distributions of origination and destination habitats, the environmental cues for dispersal or settlement, or the environment in which individuals disperse. The potential for dispersal-related phenotypes to acclimatize or adapt to these changes may often determine the impacts of climate change on population structure, adaptation and range shifts.

In many species, the timing and distance of dispersal is influenced by phenotypic traits, and a change in the environment can directly alter these phenotypes (Simmons & Thomas, 2004; Burton *et al.*, 2010). For example, most marine animals disperse as larvae in the plankton, and their potential dispersal distance and survival are influenced by their size, morphology and parental investment (Morgan, 1995). The duration of the marine larval period is temperature dependent, and there is very little variation among taxa in this effect (O'Connor *et al.*, 2007). Warming accelerates development and shortens the larval period, potentially reducing dispersal distance and population connectivity (O'Connor *et al.*, 2007; Munday *et al.*, 2009) (Table 2, 1.2.a). Temperature-induced plasticity also reduces potential dispersal distance with warming by affecting ballooning distance in spiders (Bonte *et al.*, 2008) and dispersing versus non-dispersing behaviour in lizards (Massot *et al.*, 2008).

In other cases, plasticity in dispersal-related phenotypes can increase potential dispersal to suitable habitats, accommodating climate-driven change in the spatial arrangement of critical habitat. For example, plasticity in navigational behaviours or other habitat-related traits can drive sudden shifts in the spatial distribution of individuals in response to climate change (Møller *et al.*, 2006) (Table 2, 1.2.a). Climate change has already affected the size or location of suitable breeding or settlement habitat, causing increases in dispersal for some birds and insects (Thomas *et al.*, 2001; Hughes *et al.*, 2003; Møller *et al.*, 2006). In summary, direct effects of climate change on phenotypes, navigational behaviour or habitat-finding traits may alter the rate or success of dispersal (Table 2, 1.2). Simply knowing when this occurs, and whether this effect is positive or negative for a certain taxon or in a certain environment, would represent a major advance in our ability to project possible responses to climate change.

Hypotheses for how systematic change in processes determines long-term persistence (Table 2, 2)

Ecological and evolutionary theories provide criteria and conditions for species persistence (Table 1). However, theory has focused less on how small changes in the rates of the underlying processes (adaptation, dispersal, etc.) lead to changes in long-term species persistence (Fig. 1b). In many cases, it may be possible for theoretical predictions of responses to climate change to incorporate changes in the rates of processes (e.g. dispersal) even with imperfect information on the absolute rates of processes themselves. Information on the constraints (Table 1) on the rate and magnitude of change can be combined with theories that quantitatively relate abiotic change to the rates of ecological and evolutionary processes (Fig. 1b) to provide simple directional predictions or constrain uncertainty about a climate-induced change in a critical process. Even simplified, coarse approaches that provide predictions for the directionality of change (if not precise estimates of the magnitude) would substantially enhance the quality of forecast effects of climate change (Clark *et al.*, 2001; Helmuth *et al.*, 2006). Hypotheses for how abiotic conditions alter processes then need to be paired

with hypotheses for how changes in processes affect persistence (Table 2), and we identify several such hypotheses here.

Rapid population growth in a changing environment facilitates adaptation (Table 2, 2.1)

Population growth rate is one key determinant of whether a population successfully adapts or becomes extinct in response to natural selection. When changing climate conditions cause differential survival and natural selection, maladapted individuals either die or fail to reproduce as successfully as their conspecifics. This cost of selection causes rates of population growth to decline, even as the population may be adapting to its new conditions. For example, body and bill size in Galapagos finches (*Geospiza fortis*) evolves quickly in response to drought. Measurable adaptation between different years, however, was accompanied by an 85% decline in population size and a negative population growth rate (Grant & Grant, 1995). This cost of selection can also affect long-term persistence, even when adaptation does occur, by interacting synergistically with other effects of climate change that reduce abundance, such as reduced availability of habitat, food and mutualist species. Consequently, rapid evolution interacts strongly with ecological processes, creating a race between adaptation and extinction (Stockwell *et al.*, 2003). Organisms with the capacity to evolve more quickly, such as those with short generation times, high reproductive rates or both, will suffer a reduced growth rate for less time, and will therefore be more likely to survive the costs of selection. To date, most examples of adaptation to climate change involve species with short generation times, including mosquitoes, fruit flies and small mammals (Bradshaw & Holzapfel, 2006).

For some populations, the cumulative effects of extreme events and gradual environmental change occurring with climate change may decide the race between evolution and extinction. Extreme events might cause high mortality and selection, but the potential for a population to persist through adaptation depends on whether ongoing environmental change allows rapid population growth (Table 2, 2.1).

Effects of climate change on dispersal can influence adaptation (Table 2, 2.2)

Changing climatic conditions may directly affect dispersal rates, through plasticity in dispersal traits (Table 2, 1.2) or through a change in habitat configuration or quality. A change in dispersal could interact with evolution synergistically to influence adaptation or extinction (Fig. 2), but the effects on adaptation of changes to dispersal probably depend on whether the population is at the leading or trailing edge of a species range.

Dispersal among populations can bring maladapted genes that swamp local variation and prevent adaptation, or it can bring beneficial genes that facilitate adaptation (Lenormand, 2002; Balanyà *et al.*, 2006). For example, dispersal from low-latitude populations may carry beneficial thermal tolerance genes to poleward populations (Bridle & Vines, 2007). Theoretical and empirical evidence supports both positive and negative effects of dispersal on adaptation (Thomas *et al.*, 2001; Atkins &
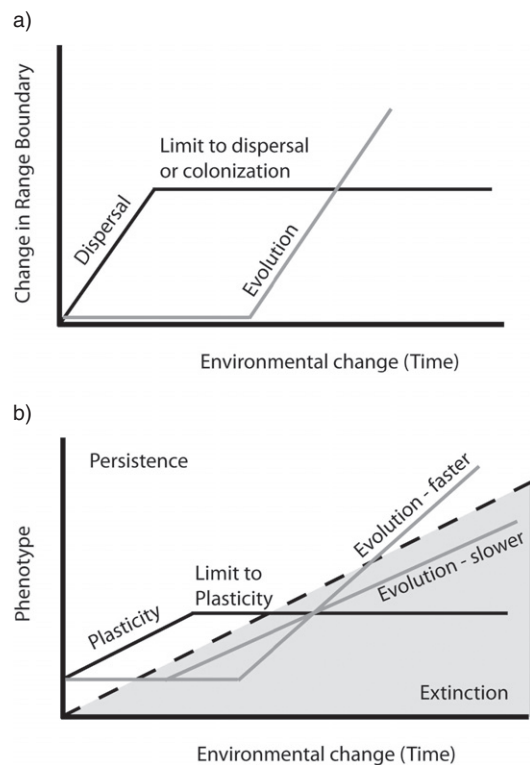
Figure 2 Ecological and evolutionary processes can act together to determine the time-scale and trajectory of ecological responses to climate change. Colonization and ultimately range expansions (a) can be mediated by dispersal in the short term, and over the longer term adaptation to range-limiting conditions (directly or indirectly related to climate conditions) can facilitate further range expansions. Extinctions at the leading edge would reverse or slow this trajectory. In a case where there is no dispersal among populations (b), the rate of phenotypic change may determine whether a population persists (dashed line) in a changing environment. Phenotypic change can reflect plasticity, evolution or an interaction of the two processes. Plasticity may occur rapidly, but will ultimately be limited by inherent constraints. Ultimately, phenotypic traits or plasticity in those traits will need to adapt a rate sufficient to maintain fitness and prevent population extinction (gray area).

Travis, 2010), and it is not yet clear whether one type of effect is more common or predictable. Several hypotheses can be articulated: In general, we expect that high dispersal will favour adaptation to climate at leading range edges when marginal populations have lower fitness in the new environment than source populations (Table 2, 2.2.a), but high dispersal from range centres may impede adaptation at trailing range edges where adaptation is occurring to climate conditions that have yet to be experienced by the species (Table 2, 2.2.b).

Rapid evolutionary processes can facilitate colonization and range shifts (Table 2, 2.3)

In regions where climatic conditions vary spatially across a heterogeneous landscape, rapid evolution can facilitate coloni-

zation and ultimately range shifts in several different ways. First, evolution of phenotypes related to dispersal and population growth can facilitate colonization and range expansions, thereby allowing persistence (Hughes *et al.*, 2003; Simmons & Thomas, 2004; Burton *et al.*, 2010; Phillips *et al.*, 2010). Rapid evolution in fruit fly wing size (Huey *et al.*, 2000), cane toad leg length (Phillips *et al.*, 2006) and lizard morphology (Losos *et al.*, 1997) has facilitated persistence and spread in new habitats. It is important to note that climate-induced changes in dispersal need not be adaptive. It is in fact difficult to justify adaptive changes in dispersal a priori in cases where the range margin has historically been determined by dispersal limitation and not habitat quality. It is not always clear how a changing climate could drive changes in dispersal that facilitate colonization and range expansion when conditions prior to climate change were insufficient to select for increased dispersal. More likely is the a priori expectation that climate directly affects dispersal-related phenotypes through plasticity, or indirectly through population structure (Burton *et al.*, 2010), and these changes in turn alter dispersal and colonization (Table 2, 1.2).

Abiotic, climate-related conditions are only one of the major constraints on species geographic ranges (Brown *et al.*, 1996). Several dimensions of a species' niche may constrain colonization of new habitat, and change in any of these limitations may allow colonization. Mobile consumers, for example, appear more able to track climatic conditions through space than foundation species like corals or trees because their dispersal abilities are greater (Kinlan & Gaines, 2003). However, if the foundation species is absent, the mobile species may not be able to colonize the new area, regardless of the climate. For example, poleward range shifts in certain butterflies appear limited by the absence of adequate host plants (Pelini *et al.*, 2009). Invasion of new habitats, therefore, may require adaptation to new foundation species (e.g. taiga species instead of boreal species), new species interactions, or new combinations of climate conditions. Changes in habitat quality because of differential species responses represent indirect effects of climate change on a mobile species. This limitation to colonization imposed by habitat may be a stronger selective agent, or habitat preference traits may adapt more readily, than traits directly related to climate like thermal tolerance.

The interplay of evolution and other mechanisms of range shifts, such as dispersal and population growth in the presence of other species, can result in a nonlinear pattern of range shifts even if environmental change is steady over time (Fig. 2) (Thomas *et al.*, 2001; Phillips *et al.*, 2010). A dispersal-mediated range shift may occur relatively quickly, only to become limited by niche-based constraints. Continued persistence may then depend on adaptation or a range expansion that may occur at a rate that could be unrelated to the previous rate of expansion.

Evolution can also modify projections of geographic distributions based on ecological mechanisms of range shifts (e.g. climate envelopes) by slowing or preventing range contraction (Phillips *et al.*, 2010). At contracting range margins where climatic conditions threaten to exclude a species from a portion of

its former range, populations may evolve sufficient tolerance to resist this change. Although examples of rapid evolution suggest that this may be possible (Stockwell *et al.*, 2003), one test of this hypothesis found that fruit flies (*Drosophila birchii*) had limited capacity to evolve further resistance to the climatic conditions that set range edges (Hoffmann *et al.*, 2003). In this species, there was little to no genetic variation in critical climate-related traits within the populations at the edge of the range.

Evolution at the leading and trailing edges of a species' range may be fundamentally different (Excoffier *et al.*, 2009) (Table 2, 2.3). At trailing edges, populations may persist through evolution of climate-related traits (Table 2, 2.3.a), while at leading edges, non-climate traits such as species interactions or dispersal abilities may evolve more rapidly (Table 2, 2.3.b) (Thomas *et al.*, 2001; Burton *et al.*, 2010; Phillips *et al.*, 2010).

Evolution and plasticity can interact in numerous ways to influence population responses (Table 2, 2.4)

Evolution and plasticity are fundamentally different processes that are subject to unique conditions and constraints (Table 1). Each can alter phenotypes to facilitate short-term persistence in response to new climates, and together they can have synergistic positive or negative consequences (Gienapp *et al.*, 2008). Alone, phenotypic plasticity allows individuals or their offspring to tolerate a change in the environment without negative fitness consequences (Pigliucci, 2001). Adaptation allows populations to persist in a changing environment through underlying genetic change caused by differential survival. To the extent that plasticity reduces mortality or fitness differences, plasticity can impede adaptation and long-term persistence (Fig. 2).

Species with moderate plasticity may have the greatest ability to adapt to climate change (Table 2, 2.4). Even when selection can lead to adaptation in response to climate change, plasticity imposes a time lag (Huey & Kingsolver, 1993; Burger & Lynch, 1995). Phenotypes with a wide range of variability due to plasticity may allow a population to persist in a changing environment as long as environmental change is within the range tolerated by plasticity in key traits, but when climate conditions exceed this range, the population may not persist. In this way, plasticity may buffer adaptation of phenotypic traits by delaying the timing of environmental change from the impact on a genotype (Fig. 2b) (Table 2, 2.4.a). Conversely, species with too little plasticity may not be able to tolerate any change, and may become extinct if they cannot immediately colonize more favourable habitat (Fig. 2b) (Table 2, 2.4.b).

Alternatively, plasticity itself may evolve and facilitate adaptation to new climates (Fig. 2b). Spring is arriving earlier in Holland, and great tits (*Parus major*) that exhibit more plasticity in their egg-laying date are better able to match hatching of their eggs with food availability (Nussey *et al.*, 2005). Greater plasticity in the timing of egg laying has been traced to higher lifetime reproductive success. This plasticity is heritable and selective pressures have increased over time (Nussey *et al.*, 2005). Evolution of greater plasticity therefore represents a mechanism for adapting to climate change that can act in addi-

tion to changes in trait means. Greater plasticity may be particularly beneficial as climates become more variable.

Changing climates may affect metapopulations differently than panmictic populations (Table 2, 2.5)

Changes in the abiotic environment related to climate change can directly affect one or several of the processes that determine population isolation, and therefore whether its persistence is determined by the dynamics of a panmictic population, metapopulation or isolated population. This distinction is important, because critical factors for anticipating persistence, such as the rate of colonization of vacant habitat, the minimum habitat area required and resilience to local extinctions, can be very different depending on where along the continuum of population structure a population falls.

Metapopulation theory explicitly relates spatial structure, dispersal, colonization and extinction to population persistence. As such, it can accommodate changes in processes and predict the outcome of multiple changes in processes for persistence. A metapopulation is an assemblage of spatially delimited local populations that are coupled by some degree of dispersal (Levins, 1970; Hanski & Gaggiotti, 2004). Long-term persistence of a species at the regional level is maintained by successful dispersal and colonization of empty habitat patches balancing local extinctions. In contrast, panmictic populations are characterized by dispersal and gene flow throughout their geographic range, while isolated populations are not connected by dispersal.

Accounting for population structure when projecting the impacts of climate change may lead to surprising predictions of ecological responses. For example, in a metapopulation, increasing local extinctions may not be detrimental to regional species persistence as long as the extinctions are balanced by colonization of new habitats. Small aquatic ecosystems in pools, ponds or treeholes are at a higher risk of desiccation in a warmer world (Bradshaw & Holzapfel, 1988; Altermatt *et al.*, 2009) and local aquatic communities may face an elevated risk of extinction. However, many aquatic organisms, and especially those inhabiting ephemeral habitats, possess drought-tolerant dispersal stages. In a long-term study with three *Daphnia* species, Altermatt *et al.* (2008) found that increased local extinction rates are compensated by increased dispersal success in warmer summers. Overall, the proportion of occupied patches remained constant (or increased for some species), but at higher rates of colonization (a combination of higher population growth, dispersal propagule production and dispersal success) and extinction. A focus on (negative) population growth as a process related to climate change independently of dispersal would have missed these interactive effects, and the overall trajectory of the metapopulation.

Population structure may also indicate whether a range shift can occur at a rate sufficient to track changing climate conditions. This may be especially true for metapopulations in which long-distance dispersal among habitat patches is common. Organisms in metapopulations may be adapted to disperse when conditions deteriorate (Southwood, 1962; Crone *et al.*,

2001) (Table 2, 2.5.a). For two species of lagomorph, metapopulation structure is predicted to enhance rapid range expansion at the leading (northerly, uphill) range edge, but may slow responses at the trailing range edge (Anderson *et al.*, 2009) (Table 2, 2.5.b). Butterflies are among the best-studied examples of animals that often occur in metapopulations (Thomas & Hanski, 2004). Many European and North American butterflies have shifted their range northwards over the last 100 years (Parmesan *et al.*, 1999; Crozier, 2003), suggesting that some of these metapopulations may be favoured to adjust their range in a changing environment due to their inherent processes of dispersal and colonization. A possible functional explanation could be that individuals occurring in newly founded populations have a genetic predisposition to disperse (Niitepõld *et al.*, 2009) (Table 2, 2.5.c) and that this genetic difference also affects population growth (Hanski & Saccheri, 2006). Thus, when climate change speeds up the turnover of habitat patches, butterflies in newly founded populations are selected for a higher propensity to disperse, which eventually may facilitate and increase the dispersal beyond current range limits and cause range shifts. Panmictic populations also have high dispersal rates among locations, suggesting that the rate of a geographic range shift should not be limited by dispersal in these populations (Table 2, 2.5.d). Species that are nearly panmictic, including many marine fish and intertidal invertebrates, appear to show some of the most rapid range shifts (Helmuth *et al.*, 2006). In contrast, range shifts for isolated populations are likely to be dispersal limited (Table 2, 2.5.e).

A CONCEPTUAL FRAMEWORK REQUIRES HYPOTHESIS TESTING

We envision that the conceptual framework outlined in Fig. 1 can be used to synthesize future studies and answer fundamental questions, including which processes are most likely to lead to persistence over the long-term, which are common and which are rapid. We have highlighted several hypotheses that need to be tested in a variety of natural conditions (Table 2), and we also note that the framework (Fig. 1b) can accommodate many more hypotheses. This goal of synthesis can only be achieved if studies test and reject specific hypotheses and report all tests. Studies of population responses that test alternative hypotheses for underlying processes (Thomas *et al.*, 2001) and studies that report 'null' results (i.e. no change) (Parmesan & Yohe, 2003) are essential for determining which responses are likely or important. Additional advantages of testing hypotheses in a conceptual framework are that hypotheses can clearly test direct and indirect effects of climate change, incorporate the time-scale over which responses are expected to occur, allow for comparison of effect sizes, and test whether traits related to species interactions, reproduction or climate adapt faster or more commonly.

A complete set of alternative hypotheses for the impacts of climate change necessarily integrates physiological, ecological and evolutionary processes, direct and indirect effects of climate change, and can facilitate the development of new theory and empirical tests. This integration goes beyond the combination of

potential impacts of climate change based on one conceptual framework (e.g. causes of range shifts) or a single climate factor (e.g. temperature), and synthesizes ideas from traditionally more distinct intellectual disciplines. It is through this integration that we can advance general theory.

CONCLUSIONS

Climate change is altering ecological patterns and processes at every level of biological organization. Interpretations of ecological responses as 'species dependent' ignore the importance of general ecological and evolutionary processes that determine dynamic population- and species-level consequences of climate change. Basic ecological and evolutionary theories can be applied to the general problem of population persistence in a changing climate in two ways. One way is to relate abiotic changes to changes in the rate, strength or outcome of fundamental ecological and evolutionary processes. The second way is to relate changes in the rates, strength or outcomes of processes to the likelihood of long-term population persistence. Within this framework, hypotheses drawn from basic theories should be tested in the context of climate change, and the results (both rejected and retained hypotheses) need to be synthesized to gain a broader understanding of how environmental change affects species persistence generally. Application of this framework for hypothesis testing may reveal that climate change responses are more pervasive than previously thought and related to a few general mechanisms, even though the patterns they create are incredibly diverse.

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REFERENCES

Altermatt, F. (2010) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1281–1287.

Altermatt, F., Pajunen, V.I. & Ebert, D. (2008) Climate change affects colonization dynamics in a metacommunity of three *Daphnia* species. *Global Change Biology*, **14**, 1209–1220.

Altermatt, F., Pajunen, I. & Ebert, D. (2009) Desiccation of rock pool habitats and its influence on population persistence in a *Daphnia* metacommunity. *PLoS ONE*, **4**, e4703.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.

Atkins, K.E. & Travis, J.M.J. (2010) Local adaptation and the evolution of species' ranges under climate change. *Journal of Theoretical Biology*, **266**, 449–457.

Balanyà, J., Oller, J.M., Huey, R.B., Gilchrist, G.W. & Serra, L. (2006) Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science*, **313**, 1773–1775.

Bonte, D., Travis, J.M.J., De Clercq, N., Zwertvaegher, I. & Lens, L. (2008) Thermal conditions during juvenile development affect adult dispersal in a spider. *Proceedings of the National Academy of Sciences USA*, **105**, 17000–17005.

Bradshaw, W.E. & Holzapfel, C.M. (1988) Drought and the organization of tree-hole mosquito communities. *Oecologia*, **74**, 507–514.

Bradshaw, W.E. & Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.

Bridle, J.R. & Vines, T.H. (2007) Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology and Evolution*, **22**, 140–147.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Burger, R. & Lynch, M. (1995) Evolution and extinction in a changing environment – a quantitative genetic analysis. *Evolution*, **49**, 151–163.

Burton, O.J., Phillips, B.L. & Travis, J.M.J. (2010) Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters*, **13**, 1210–1220.

Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke, R. Jr, Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O., Schlesinger, W.H., Wall, D.H. & Wear, D. (2001) Ecological forecasts: an emerging imperative. *Science*, **293**, 657–660.

Crone, E.E., Doak, K. & Pokki, J. (2001) Ecological influences on the dynamics of a field vole metapopulation. *Ecology*, **82**, 831–843.

Crozier, L. (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, **135**, 648–656.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, **105**, 6668–6672.

Drake, J.M. (2005) Population effects of increased climate variation. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1823–1827.

Ellner, S.P., Geber, M.A. & Hairston, N.G. (2011) Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*, **14**, 603–614.

Excoffier, L., Foll, M. & Petit, R.J. (2009) Genetic consequences of range expansions. *Annual Review of Ecology, Evolution and Systematics*, **40**, 481–501.

Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S., Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L.,

Schulte, P.M., Spicer, J.I., Stillman, J.H., Terblanche, J.S. & Van Kleunen, M. (2009) Macrophysiology: a conceptual reunification. *The American Naturalist*, **174**, 595–612.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. & Merilä, J. (2008) Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167–178.

Gillooly, J.F., Allen, A.P., Savage, V.M., Charnov, E.L., West, G.B. & Brown, J.H. (2006) Response to Clarke and Fraser: effects of temperature on metabolic rate. *Functional Ecology*, **20**, 400–404.

Grant, P.R. & Grant, B.R. (1995) Predicting microevolutionary responses to directional selection on heritable variation. *Evolution*, **49**, 241–251.

Hanski, I. & Gaggiotti, O.E. (2004) *Ecology, genetics and evolution of metapopulations*. Elsevier Academic Press, Amsterdam.

Hanski, I. & Saccheri, I.J. (2006) Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biology*, **4**, 719–726.

Helmuth, B., Mieszkowska, N., Moore, P. & Hawkins, S.J. (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 373–404.

Hoffmann, A.A., Hallas, R.J., Dean, J.A. & Schiffer, M. (2003) Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science*, **301**, 100–102.

Huey, R.B. & Kingsolver, J.G. (1993) Evolution of resistance to high-temperature in ectotherms. *The American Naturalist*, **142**, S21–S46.

Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D. & Serra, L. (2000) Rapid evolution of a geographic cline in size in an introduced fly. *Science*, **287**, 308–309.

Hughes, C.L., Hill, J.K. & Dytham, C. (2003) Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceeding of the Royal Society B: Biological Sciences*, **270**, S147–S150.

Kinlan, B.P. & Gaines, S.D. (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**, 2007–2020.

Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*, **17**, 183–189.

Levins, R. (1970) Extinction. *Lecture Notes in Mathematics*, **2**, 75–107.

Losos, J.B., Warheit, K.I. & Schoener, T.W. (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, **387**, 70–73.

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320–331.

McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences USA*, **99**, 6070–6074.

Massot, M., Clobert, J. & Ferrière, R. (2008) Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, **14**, 461–469.

Møller, A.P., Flendsted-Jensen, E. & Mardal, W. (2006) Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. *Global Change Biology*, **12**, 2005–2013.

Morgan, S.G. (1995) Life and death in the plankton: larval mortality and adaptation. *Ecology of marine invertebrate larvae* (ed. by L.R. McEdward), pp. 279–322. CRC Press, Boca Raton, FL.

Munday, P.L., Leis, J.M., Lough, J.M., Paris, C.B., Kingsford, M.J., Berumen, M.L. & Lambrechts, J. (2009) Climate change and coral reef connectivity. *Coral Reefs*, **28**, 379–395.

Niitepõld, K., Smith, A.D., Osborne, J.L., Reynolds, D.R., Carreck, N.L., Martin, A.P., Marden, J.H., Ovaskainen, O. & Hanski, I. (2009) Flight metabolic rate and Pgi genotype influence butterfly dispersal rate in the field. *Ecology*, **90**, 2223–2232.

Nussey, D.H., Postma, E., Gienapp, P. & Visser, M.E. (2005) Selection on heritable phenotypic plasticity in a wild bird population. *Science*, **310**, 304–306.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Lester, S.E., Halpern, B.S., Kinlan, B.P. & Weiss, J.M. (2007) Temperature control of larval dispersal and implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 1266–1271.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637–639.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pauly, D. (2007) *Gasping fish and panting squids: oxygen, temperature and the growth of water-breathing animals*. International Ecology Institute, Oldendorf/Luhe.

Pelini, S.L., Dzurisin, J.D.K., Prior, K.M., Williams, C.M., Marsico, T.D., Sinclair, B.J. & Hellmann, J.J. (2009) Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 11160–11165.

Pertoldi, C. & Bach, L.A. (2007) Evolutionary aspects of climate-induced changes and the need for multidisciplinary. *Journal of Thermal Biology*, **32**, 118–124.

Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803–803.

Phillips, B.L., Brown, G.P. & Shine, R. (2010) Life-history evolution in range-shifting populations. *Ecology*, **91**, 1617–1627.

Pigliucci, M. (2001) *Phenotypic plasticity: beyond nature and nurture*, 1st edn The Johns Hopkins University Press, Baltimore, MD.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Cosuegra, J.A., Fogden, P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-

Viteri, A., Puschendorf, R., Santiago, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.

Reed, T.E., Schindler, D.E. & Waples, R.S. (2011) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology*, **25**, 56–63.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J. (2003) Fingerprints of global warming in wild plants and animals. *Nature*, **421**, 57–60.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004) Effects of body size and temperature on population growth. *The American Naturalist*, **163**, E429–E441.

Simmons, A.D. & Thomas, C.D. (2004) Changes in dispersal during species' range expansions. *The American Naturalist*, **164**, 378–395.

Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews*, **37**, 171–211.

Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94–101.

Thomas, C.D. & Hanski, I. (2004) Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. *Ecology, genetics and evolution of metapopulations* (ed. by I. Hanski and O.E. Gaggiotti), pp. 489–514. Elsevier Academic Press, Amsterdam.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.D., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

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M.I.O. and E.R.S. conceived the research. M.I.O. and E.R.S. led the writing, M.L.P. contributed concepts and text on evolutionary processes and F.A. contributed concepts and text on metapopulation dynamics.

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