Toward a conceptual synthesis for climate change responses

Mary I. O’Connor1*, Elizabeth R. Selig2, Malin L. Pinsky3 and Florian Altermatt4

RESEARCH REVIEW

1Department of Zoology and Biodiversity Research Centre, University of British Columbia, 2370-6270 University Blvd, Vancouver, BC Canada, V6T 1Z4, 2Science and Knowledge Division, Conservation International, 2011 Crystal Drive, Suite 500, Arlington, VA 22202, USA, 3Hopkins Marine Station, Department of Biology, Stanford University, 120 Oceanview Blvd, Pacific Grove, CA 93950, USA, 4Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Ueberlandstrasse 133, CH-8600 Dübendorf, Switzerland

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 to 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.

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 (Helmut 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...
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 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 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).

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

<table>
<thead>
<tr>
<th><strong>Acclimatization</strong></th>
<th>Plasticity in phenological or physiological traits, performance or behaviours</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Conditions</strong></td>
<td>capacity for variation, accurate environmental cues (e.g. Pigliucci, 2001)</td>
</tr>
<tr>
<td><strong>Constraints</strong></td>
<td>limited capacity for variation, trade-offs, high maintenance or production costs, unreliable environmental cues (e.g. Nussey et al., 2005)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Colonization</strong></th>
<th>Changes in dispersal to a new area, or in population growth in that new area that allow a new population to persist</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Conditions</strong></td>
<td>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)</td>
</tr>
<tr>
<td><strong>Constraints</strong></td>
<td>limited dispersal potential, geographic barriers to movement, unsustainable mortality rates during or after dispersal</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Adaptation</strong></th>
<th>Evolutionary change in gene frequency in a population that increases or maintains fitness under new environmental conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Conditions</strong></td>
<td>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</td>
</tr>
<tr>
<td><strong>Constraints</strong></td>
<td>critical trait unresponsive to climate or not heritable or variable (e.g. Hoffmann et al., 2003); antagonistic genetic correlations that impede evolutionary change (Atkins &amp; 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</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Extinction</strong></th>
<th>Population growth is negative and abundance declines to zero</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Conditions</strong></td>
<td>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)</td>
</tr>
<tr>
<td><strong>Constraints</strong></td>
<td>Large geographic range or population size, connectivity to other populations</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Predicted response</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Hypotheses for how abiotic change alters key processes</td>
<td></td>
</tr>
<tr>
<td>1.1. Environmental warming has nonlinear, positive effects on population growth in ectotherms</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>1.1.a. In temperate climates, a few degrees of warming may enhance population growth, as long as resources do not limit additional growth</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>1.1.b. Population growth rate may respond positively to warming when an additional generation is added in response to longer growing seasons</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>1.2. Abiotic change can alter dispersal through plasticity</td>
<td></td>
</tr>
<tr>
<td>1.2.a. Abiotic change reduces dispersal distance and population connectivity through plasticity in dispersal-related traits</td>
<td>Adaptation, colonization, acclimatization</td>
</tr>
<tr>
<td>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</td>
<td>Adaptation, colonization, acclimatization</td>
</tr>
<tr>
<td>2. Hypotheses for how systematic change in processes determines long-term persistence</td>
<td></td>
</tr>
<tr>
<td>2.1. Rapid population growth in a changing environment facilitates adaptation</td>
<td>Adaptation</td>
</tr>
<tr>
<td>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</td>
<td>Adaptation, extinction</td>
</tr>
<tr>
<td>2.2. Effects of climate change on dispersal can influence adaptation</td>
<td></td>
</tr>
<tr>
<td>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</td>
<td>Adaptation, colonization, extinction</td>
</tr>
<tr>
<td>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</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>2.3. Evolution at the leading and trailing edges of a species’ range may be fundamentally different</td>
<td></td>
</tr>
<tr>
<td>2.3.a. At trailing edges, populations may persist through evolution of climate-related traits</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>2.3.b. At leading edges, non-climate traits such as species interactions or dispersal abilities will evolve more rapidly</td>
<td>Adaptation, colonization</td>
</tr>
<tr>
<td>2.4. Populations with moderate plasticity may have the greatest ability to adapt to climate change</td>
<td>Acclimatization, adaptation</td>
</tr>
<tr>
<td>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</td>
<td>Acclimatization, adaptation</td>
</tr>
<tr>
<td>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</td>
<td>Acclimatization, adaptation</td>
</tr>
<tr>
<td>2.5. Changing climates may affect metapopulations differently from panmictic populations</td>
<td>Colonization, adaptation, extinction</td>
</tr>
<tr>
<td>2.5.a. Organisms in metapopulations may be adapted to disperse when conditions deteriorate</td>
<td>Colonization</td>
</tr>
<tr>
<td>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</td>
<td>Colonization</td>
</tr>
<tr>
<td>2.5.c. Individuals occurring in newly founded populations have a genetic predisposition to disperse</td>
<td>Colonization, adaptation</td>
</tr>
<tr>
<td>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</td>
<td>Colonization</td>
</tr>
<tr>
<td>2.5.e. Colonization and range expansion for isolated populations are likely to be dispersal limited</td>
<td>Colonization</td>
</tr>
</tbody>
</table>

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.
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 & 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.

ACKNOWLEDGEMENTS

We are grateful to Jennifer Balch, Lauren Buckley, Jason Fridley and Jennifer Williams for thoughtful discussion and feedback on earlier drafts. F.A. was supported by the Swiss National Science Foundation (grant NPBBSP3-124435). M.L.P. was supported by a NSF Graduate Research Fellowship.

REFERENCES


**BIOSKETCHES**

Mary I. O’Connor studies how abiotic factors affect the rates and outcomes of ecological processes. Specifically, recent work has included the use of general models of how ecological rates scale with temperature to affect community-level processes, including dispersal and herbivory in marine ecosystems.

Elizabeth R. Selig’s research focuses on analysing how climate change and other human impacts will affect ecosystem services and human well-being in marine ecosystems and where conservation efforts should be prioritized.

Malin Pinsky studies spatial ecology, dispersal and population genetics in marine species and Florian Altermatt studies metapopulation dynamics and their role in mediating climate change impacts in aquatic crustaceans and terrestrial insects.

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.

Editor: Martin Sykes