



Assessing the components of adaptive capacity to improve conservation and management efforts under global change

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Abstract: *Natural-resource managers and other conservation practitioners are under unprecedented pressure to categorize and quantify the vulnerability of natural systems based on assessment of the exposure, sensitivity, and adaptive capacity of species to climate change. Despite the urgent need for these assessments, neither the theoretical basis of adaptive capacity nor the practical issues underlying its quantification has been articulated in a manner that is directly applicable to natural-resource management. Both are critical for researchers, managers, and other conservation practitioners to develop reliable strategies for assessing adaptive capacity. Drawing from principles of classical and contemporary research and examples from terrestrial, marine, plant, and animal systems, we examined broadly the theory behind the concept of adaptive capacity. We then considered how interdisciplinary, trait- and triage-based approaches encompassing the oft-overlooked interactions among components of adaptive capacity can be used to identify species and populations likely to have higher (or lower) adaptive capacity. We identified the challenges and value of such endeavors and argue for a concerted interdisciplinary research approach that combines ecology, ecological genetics, and eco-physiology to reflect the interacting components of adaptive capacity. We aimed to provide a basis for constructive discussion between natural-resource managers and researchers, discussions urgently needed to identify research directions that will deliver answers to real-world questions facing resource managers, other conservation practitioners, and policy makers. Directing research to both seek general patterns and identify ways to facilitate adaptive capacity of key species and populations within species, will enable conservation ecologists and resource managers to maximize returns on research and management investment and arrive at novel and dynamic management and policy decisions.*

Keywords: climate change, extinction risk, genetic variation, phenotypic plasticity, resilience, vulnerability assessment

Evaluación de los Componentes de la Capacidad Adaptativa para Mejorar la Conservación y los Esfuerzos de Manejo bajo el Cambio Global

Resumen: *Quienes manejan los recursos naturales y otros practicantes de la conservación se encuentran bajo una presión sin precedentes para categorizar y cuantificar la vulnerabilidad de los sistemas naturales con base en la evaluación de la exposición, la sensibilidad y la capacidad adaptativa de las especies ante el cambio climático. A pesar de la urgente necesidad por estas evaluaciones, no se han articulado ni las bases teóricas de la capacidad adaptativa ni los asuntos prácticos que subyacen su cuantificación de una manera que*

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sea directamente aplicable al manejo de los recursos naturales. Ambos son críticos para los investigadores, los administradores y otros practicantes de la conservación para desarrollar estrategias confiables para evaluar la capacidad adaptativa. Examinamos de manera general la teoría detrás de la capacidad adaptativa tomando principios de la investigación clásica y contemporánea y ejemplos de los sistemas terrestres, marinos, de plantas y de animales. Después consideramos cómo pueden usarse las estrategias interdisciplinarias de rasgo y priorización, que engloban las interacciones de los componentes frecuentemente ignorados de la capacidad adaptativa, para identificar especies y poblaciones con la probabilidad de tener una capacidad adaptativa más alta (o más baja). Identificamos los obstáculos y el valor de dichos esfuerzos y abogamos por una estrategia coordinada de investigación interdisciplinaria que combine la ecología, la genética ecológica y la eco-fisiología para así reflejar los componentes relacionados de la capacidad adaptativa. Buscamos proporcionar una base para la discusión constructiva entre quienes manejan los recursos naturales y los investigadores. Esta discusión se necesita urgentemente para identificar las direcciones de la investigación que entregarán respuestas a las preguntas del mundo real hechas que enfrentan quienes manejan los recursos, otros practicantes de la conservación y quienes hacen las políticas. Dirigir esta investigación para que busque patrones generales e identifique formas que faciliten la capacidad adaptativa de especies clave y poblaciones dentro de especies permitirá que los ecólogos de la conservación y quienes manejan los recursos maximicen las devoluciones de inversión en la investigación y el manejo y que lleguen a decisiones políticas y de manejo que sean novedosas y dinámicas.

Palabras Clave: cambio climático, evaluación de la vulnerabilidad, plasticidad fenotípica, resiliencia, riesgo de extinción, variación genética

Introduction

In the context of rapid climate change, making informed decisions about where and how to allocate funds for conservation and management of species is crucial. There is general agreement that decisions should be based on vulnerability assessments incorporating exposure and sensitivity and reflecting the adaptive capacity of species (Williams et al. 2008; Dawson et al. 2011). Despite urgent need for such assessments, the definition and theoretical basis of adaptive capacity, as well as practical issues underlying its quantification, remain uncertain for researchers and practitioners. We incorporated principles of classical and contemporary research to provide a broadly accessible discussion of the theory behind the concept of adaptive capacity. We identified interdisciplinary trait- and triage-based research approaches that can be applied to identify species and populations likely to have higher (or lower) adaptive capacity and discuss the challenges inherent in these endeavors. We argue for a concerted interdisciplinary research approach that combines ecology, ecological genetics, and eco-physiology to reflect the interacting components of adaptive capacity.

The ecological niche can serve as a theoretical framework for discussions about adaptive capacity. The term *niche* connotes a species' role, position, behavior, and distribution in its environment; has a long history (e.g., Liebig 1840; Shelford 1913; Grinnell 1917); and was the subject of foundational theoretical and experimental work (Elton 1927; Allee et al. 1949; Hutchinson 1957; Odum 1959). Fisher's (1930, 1958) work on the niche has particular relevance for understanding adaptive capacity.

Fisher (1930) noted that no organism is "perfectly adapted" and proposed that an organism's realized level of adaptation could theoretically be evaluated if one could simultaneously assess evolutionary pressures on that organism in infinite dimensions. It is because there are many different selective forces acting on an organism (e.g., environmental conditions and interactions with predators, prey, and competitors) that species can rarely be optimally adapted to any climatic regime (Villen-Perez et al. 2013). Consequently, species constantly adapt and change over time, tracking changes in the environment. The process of adaptive evolution generally leads to slow and gradual changes in the organismal traits that define species' niches (Peterson et al. 1999; Wiens et al. 2010; but see Schluter 2000). The less-predictable or larger the climatic change, the less likely an organism will effectively accommodate the changes (Fig. 1a) (Fisher 1930, 1958). Theory predicts that individuals with narrow tolerance limits (specialists) will decline more in overall performance or contribution to subsequent generations (fitness) than generalists for a given magnitude of change in the environment away from the historical baseline (Fisher 1958). Thus, the fit of organisms to their environment reflects several factors, including phenotypic plasticity, adaptive evolution, and ecological-sorting processes (e.g., migration, community assembly, and habitat selection [Ackerly 2003]), all of which can constrain niche evolution.

The term *adaptive capacity* can be defined so as to encompass early ecologists' ideas of environmental tracking: the capacity of a species or its populations to cope with or respond to a given change (e.g., climate change) by persisting in situ or shifting to more suitable ranges or microhabitats (Dawson et al. 2011). Adaptive capacity

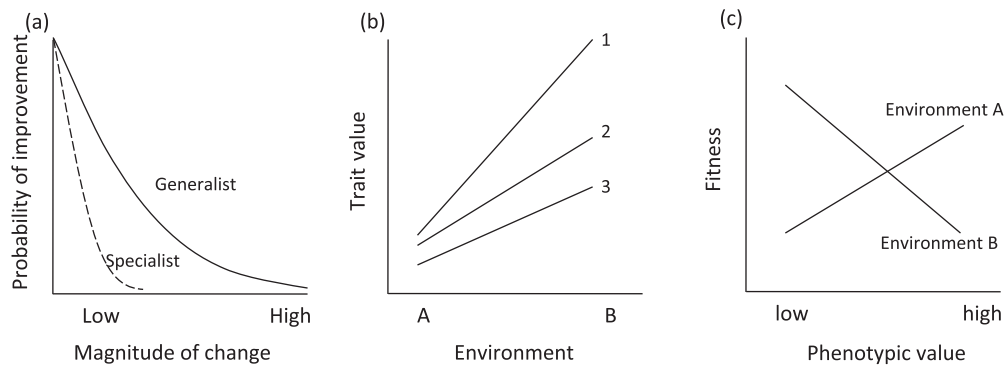


Figure 1. (a) Heuristic illustration of the hypothesis that the larger the change effected by a mutation, the lower its likelihood of being beneficial for the organism and of the truism that change is less likely to benefit an ecological-specialist than ecological-generalist species (adapted from Fisher 1958). (b) Examples of reaction-norm plots used to illustrate phenotypic plasticity (1–3, genotypes that could be independent clonal genotypes, recombinant inbred lines, varieties, or populations or species; A and B, different environments). The plot illustrates the effect of genotype, environment, and the interaction between these effects. Genotype 1 has the greatest phenotypic plasticity, whereas genotype 3 has the least. (c) General example of the adaptive value of phenotypic plasticity in a genetic sense.

can likewise be deconstructed into three main components (not necessarily mutually exclusive) that exhibit some alignment with Fisher's concepts: demographic or life-history traits, including dispersal and colonization abilities; genetic diversity and potential for evolutionary adaptation by natural selection; and phenotypic plasticity, including physiological acclimation. Although each of these contributors can be assessed with a combination of empirical, observational, and modeling approaches, integrated quantification remains a nontrivial exercise, and as Fisher's multidimensional analogy instructs, the components interact in important ways.

We dissected the components of adaptive capacity and considered the challenges researchers and practitioners face in quantifying these components in the context of species-level vulnerability assessments. In so doing, we hope to stimulate discussion among natural-resource managers, other conservation practitioners, and researchers to facilitate focused research and enable sound, cost-effective, efficient progress toward management in a changing climate.

Components of Adaptive Capacity and Challenges They Pose

Life-History Traits

Life-history characteristics may lead some species to have higher adaptive capacity. Species with shorter generation times are potentially more likely to rapidly accumulate mutations and genetic diversity—the basis of genetic adaptation—in response to selective environments such as altered climate (Wright et al. 2006; but see, Morris et al. 2008). Species with a greater ability to learn may be

more able to track changing environments (Fisher 1958; Galef & Laland 2005). Because dispersal allows organisms to follow conditions to which they are adapted, species with greater dispersal capacity should have greater ability to adapt to climate change (Thomas et al. 2004; Foden et al. 2013).

Although many studies attempt to classify adaptive capacity based on life-history traits, the challenge is in developing such proxies. Foden et al. (2013) use expert opinion to develop proxies of sensitivity and adaptive capacity for approximately 17,000 species. Their proxies are based on expert opinion and measurable life-history traits because actual measures of genetic variability and plasticity are lacking at this scale. Likewise, Angert et al. (2011) used proxies of dispersal and reproductive capacities and found species-level traits only weakly and inconsistently predict magnitudes of range shifts. These authors conclude that to be effective in predicting adaptive capacity, trait-based predictions must incorporate multiple components (e.g., population structure, evolutionary, and climatic history) and must consider patterns of genetic diversity and phenotypic plasticity.

Genetic Variation and Evolvability

Evolution can happen on sufficiently small time scales that adaptation by natural selection may serve as a mechanism of demographic resilience to environmental change (Bell & Gonzalez 2009; Hoffmann & Sgrò 2011; but see, Chevin et al. 2010). Thus, genetic variation and evolvability (i.e., potential for evolution to occur) comprise key components of adaptive capacity. Studies that examine evolvability and adaptation in a climate-change context indicate this emerging approach has promise (Etterson

& Shaw 2001; Walters et al. 2012; Foden et al. 2013; Pespeni et al. 2013). In such studies, assessing current levels of genetic variation (adaptive and neutral) within species or populations is a priority because evolutionary responses depend on the extent of that variation (Sgro et al. 2011). Genetic variation differs among populations within and across species. Recent technological advances raise hopes of identifying genetic markers for traits that confer tolerance to climate change within species. These markers could be used to forecast responses of species to environmental change (Pennings & Richards 1998; Villen-Perez et al. 2013; Sunday et al. 2014). However, in many cases, climate-change response is likely mediated by many genes that each have small effects rather than by a few genes that have large effects, which makes identification of adaptive markers challenging (Rockman 2012; Shaw & Etterson 2012). The extent of genetic variation may correlate with aspects of a species' life history (e.g., genome size, dispersal distance, generation time) (Siol et al. 2010) and reflect evolutionary history such as past climatic events and biogeographic processes. Consequently, patterns of genetic variation or evolvability cannot be inferred from life history alone.

Calls for the assessment of genetic variation in management decision-making contexts have emerged (Hendry et al. 2011; Hoffmann & Sgrò 2011; Sgro et al. 2011; Villen-Perez et al. 2013). For example, studies focused on impacts of ocean warming and acidification on calcifying marine organisms highlight the role of adaptive evolution as a response to global change (Kelly et al. 2013; Pespeni et al. 2013; Sunday et al. 2014). However, such data have yet to be applied widely to conservation and management. Ideally, integrated investigations of genetic variation in traits that confer resilience and assessments of the extent to which these traits are passed between generations (heritability) could be used to identify the level of adaptive capacity of taxa or populations within taxa. Techniques to predict additive genetic variation from genomic approaches are being developed.

Management practices can also affect genetic variation. Fragmentation and barriers to movement of genes among populations (gene flow) can reduce genetic variation. In contrast, genetic variation can be enhanced by maintaining corridors and connectivity among habitat patches and identifying and protecting populations with high genetic diversity or areas that have been historical refuges from climate change. Managed relocation can also be a way to introduce characteristics (specific genotypes or alleles) of individuals typical of warmer climates into a population (Sgro et al. 2011; Weeks et al. 2011). Other approaches, including quantitative genetic and selection experiments, may help estimate evolutionary potential and untangle links between life-history traits, plasticity (see below), and evolvability (Shaw & Etterson 2012; Sunday et al. 2014).

Phenotypic Plasticity

The final, and perhaps most elusive, component of adaptive capacity is phenotypic plasticity, which remains poorly understood (Nicotra et al. 2010; Moritz & Agudo 2013). Plasticity is defined as the range of phenotypes (physical expression of genetic potential; e.g., height, wing length) that a given genetic individual (genotype) can express as a function of environment (Fig. 1b) (Bradshaw 1965; Schlichting 1986). For example, plants can express plasticity in flowering-time and insects in larval-emergence dates in response to temperature (e.g., Anderson et al. 2012). Plasticity thus encompasses variation in phenotype from the scale of seconds or days (e.g., acclimation of metabolic rates) to longer-term changes in labile traits. Labile traits can include behaviors or alterations to developmental processes. Examples of plastic changes include shifts in allocation of resources from leaves to stems and facultative resorption of developing litters in times of environmental harshness. Irreversible developmental modifications (e.g., leaf anatomy and morphology, color morph in insects) reflect plastic changes at a longer time scale. At each temporal scale, there are likely to be plastic traits that influence an organism's capacity to respond to climate change. The relative importance of these traits differs among organisms and environmental contexts.

Phenotypic plasticity can contribute to adaptive capacity by conferring resilience to perturbation in current environments and by increasing ability to establish and persist in novel environments. Plasticity may also contribute to adaptive evolution via genetic assimilation (see references in Nicotra et al. [2010]). By virtue of exposing new, or previously hidden, elements of the phenotype in novel environments, plasticity may buy time for adaptive evolution (Schlichting 2008; Chevin et al. 2010; Palumbi et al. 2014). Alternatively, plasticity may buffer the impact of climate (Reusch 2014). For example, plasticity in laying date in response to temperature in great tits (*Parus major*) reduces likelihood of extinction by approximately 500 times, even in the absence of genetic adaptation (Vedder et al. 2013).

There are several misconceptions about plasticity that warrant clarification. First, phenotypic plasticity is not an emergent characteristic of a system (e.g., an ecosystem); rather, it is an attribute of particular traits in component organisms of that system. As such, plasticity itself can vary between individuals and among populations of a species. Phenotypic plasticity is also not necessarily a characteristic of a species; rather, it may be a characteristic of the traits expressed by individuals of that species (e.g., Nicotra et al. 2010). Theory predicts that an organism may lose genetic variation and plasticity over evolutionary time in some traits (canalization), while others remain plastic (Dejong 1995; Van Buskirk & Steiner 2009).

Thus, plasticity should not be considered an alternative to genetic variation. Instead, species, populations, or lineages will vary in both trait means and trait plasticity because both are ultimately under genetic control. Plasticity in a trait can be heritable and subject to selection (Nicotra et al. 2010), but not all plasticity is adaptive; some is neutral or even maladaptive (van Kleunen & Fischer 2005).

For plasticity to be adaptive in the evolutionary sense, it must be associated with increased fitness (Fig. 1c), and the adaptive value of the response may vary depending on the conditions under which it is assessed (Davidson & Nicotra 2012). Thus, it is important to understand the shape of the response and the environments that the organism is likely to encounter (current and future). Plasticity that is currently evolutionarily adaptive may not be in the future. Conversely, future conditions may expose new phenotypes to selection (Schlichting 2008). Finally, changing community structure and species interactions can affect both the magnitude and adaptive value of plastic responses (McGuire & Agrawal 2005).

Epigenetic variation—stable alterations in gene expression triggered by environment—can result in novel phenotypes that may add to evolutionary potential (Robertson & Wolf 2012). Thus, epigenetic changes have been identified as a potential mechanism underlying expression of plastic phenotypes within and across generations (Bossdorf et al. 2008; Jablonka & Raz 2009). Epigenetic changes typically occur at faster time scales than genetic ones and thus may constitute an important mechanism for response to rapid environmental change. Most epigenetic variation is not passed to offspring, but in some instances environmental cues in one generation can cause heritable epigenetic changes (Richards 2006) and lead to adaptive evolution in the absence of genetic change (Beldade et al. 2011). Even in the absence of inheritance, epigenetically induced plasticity may allow individuals to persist in stressful situations long enough for genetic adaptation (genetic assimilation) to occur (Pigliucci et al. 2006). Such a model applies in a range of species including yeasts (Sollars et al. 2003) and *Arabidopsis* (True et al. 2004), though it remains unclear how common or significant epigenetic influences on adaptive capacity will prove to be.

Theory predicts that adaptive plasticity should evolve in heterogeneous environments where signals of environmental conditions are reliable (van Kleunen & Fischer 2005). There is little consensus about which traits, or species, will possess adaptive or maladaptive plasticity relevant to improving adaptive capacity in response to climate change (Nicotra et al. 2010; Shaw & Etterson 2012; Vedder et al. 2013). The potential of plasticity to buy time for adaptation will vary depending on the pattern of genetic (or epigenetic) variation for plasticity, the mechanisms by which plasticity arises, gene flow among populations, generation time, and life-history characteristics.

American pikas (*Ochotona princeps*) provide an interesting example of the impact of behavioral plasticity (Fig. 2). They have declined markedly in distribution and density in recent decades (as well as over paleontological records) in parts of their range, such as across the Great Basin. In contrast, Columbia River Gorge pikas exhibit dietary and behavioral plasticity uncharacteristic of the species elsewhere. They now specialize on mosses found commonly on low-elevation Gorge taluses, despite the mosses' low nutritional value (Varner & Dearing 2014), whereas elsewhere the species is a dietary generalist. Furthermore, despite the species' reputation for being obligately tied to talus, individuals in the Gorge spend much of their time during high daytime temperatures under the shade of forest canopy rather than remaining in unshaded talus. In contrast to Gorge pikas, the less-plastic Basin pikas appear to be declining at or have been extirpated from many sites, due to combinations of chronic-heat stress, acute-cold stress, low growing-season precipitation, and less-nutritious vegetation. (For additional details, see Beever et al. [2010], Beever et al. [2011] and Beever et al. [2013].)

Variation in Adaptive Capacity among and within Species

Species with broad niche widths with respect to diet, space use, activity budgets, and physiological tolerances should have a higher adaptive capacity than species with more specialized requirements. Thus, one might expect that species such as coyotes (*Canis latrans*), deer mice (*Peromyscus maniculatus*), and dandelions (*Taraxacum officinale*), which have flexible resource requirements and occur in many ecosystem types, will have greater genetic variation or phenotypic plasticity and therefore greater adaptive capacity than plant or animal species that are more limited by soil moisture, temperature, or other environmental constraints (e.g., Engelmann spruce [*Picea engelmannii*]).

Niche breadth is likely to best translate to higher adaptive capacity where connectivity of habitat across the species' range is maintained. Even widespread species will have limited potential for adaptive evolution if habitat is fragmented and species are consequently prevented from accessing their full range of habitat types. Conversely, even low levels of gene flow among populations can have substantial impact on genetic variation (Sgro et al. 2011). The role of historical habitat refugia (important pockets of genetic diversity) and connections among populations in maintaining species over periods of environmental fluctuation is receiving increased attention (Moritz & Agudo 2013). Researchers have advocated conservation of areas demonstrated to be historical refugia for species during previous periods of climatic change. Hendriks et al. (2014) illustrate how conserving

refugia dominated by marine macrophytes may buffer against coastal acidification. By conserving refugia and ensuring connections among them (or between refugia and the remainder of the range) one can provide stages on which climate change can shift the actors (species) around (Beier & Brost 2010; Brost & Beier 2012). Such actions seek to maximize (or minimize reductions in) the theoretical niche space of the species (i.e., the Hutchinsonian [1957] “*n*-dimensional hypervolume”) amidst numerous selective forces such as no-analog climate conditions to which species have not been exposed previously. The relationship between historical occupation of refugia and current patterns of adaptive capacity deserves further investigation.

Adaptive capacity may also vary meaningfully among populations within species (e.g., between refugial or core populations and marginal ones) (Valladares et al. 2014). One might expect adaptive capacity to be greater in populations from climatic and environmental contexts where changes are of intermediate magnitude (i.e., enough to constitute selective pressure yet remain sub-lethal) and have a high probability of occurring within an organism’s lifetime. Additionally, higher capacity should evolve in climate contexts where physiological, biomechanical, and other biophysical limits have not been exceeded. Such variation in adaptive capacity would reflect local adaptation in life-history and phenotypic traits and underlying genetic differentiation among populations.

Conflicting evidence surrounds prediction of whether adaptive capacity is higher at the edge versus the center of species’ geographic ranges. The abundant-center hypothesis predicts that population densities are higher and less variable at the center versus the edge of the range (Hengeveld & Haeck 1982; Thomas 1993). Alternatively, range-edge populations could be expected to have evolved a greater potential to cope with environmental changes via phenotypic plasticity as a result of a long history of selection under marginal and varied climatic conditions (Bridle & Vines 2007; Beever et al. 2008; Sexton et al. 2009). A related question is: Whether population losses within a species’ geographic range due to climatic influences occur most frequently at locations where biologically relevant aspects of the climate have changed most in contemporary time or instead in places that were already climatically marginal before contemporary climate change ensued (Beever et al. 2010)? Each scenario is plausible, depending on extent of gene flow and genetic drift among populations and the history of selection for plasticity, which in turn are driven by geography and population structure. Although uncertainty surrounding this issue remains, and context-specific outcomes will vary, “trailing-edge” declines seem more pervasive than losses from species’ range centers (Moritz et al. 2008; Wilson & Gutierrez 2011).

Guidelines for Assessing Components of Adaptive Capacity in Management and Conservation Contexts

Calls for empirical determination of the components of adaptive capacity for a range of species (e.g., Dawson et al. 2011; Sgro et al. 2011; Moritz & Agudo 2013; Valladares et al. 2014) and for greater effort to model the role of plasticity and evolvability in particular (Chevin et al. 2010) are increasingly common. Given the challenges and the reality of limited resources for both research and management, how does one maximize the ability to distinguish vulnerable from resilient species (or populations) and account for the anthropogenic context to best design conservation strategies? To maximize returns, research must focus on particular species, traits, and conditions.

Based on ecological theory, managers need be particularly aware of specialist species, communities where there is increasing variability in climate, species near their range margins, and species that have limited distribution or have already survived a bottleneck. In addition, certain life-history traits (e.g., long generation times, limited dispersal) should be seen as indicators of potentially low adaptive capacity.

We propose that decisions regarding how to assess adaptive capacity are most efficiently addressed with a two-pronged approach based on the scale at which decisions are made. On the one hand, one might ask whether there are generalities in patterns of evolvability and adaptive phenotypic plasticity that are predictable by easily quantifiable life-history or functional traits (Foden et al. 2013). Such predictors, albeit elusive as yet, would provide a powerful tool for broad-scale decisions about conservation at the landscape or community level. On the other hand, when focusing on decisions relevant to a particular community, managers need to determine on a system-by-system basis those species that are of critical importance for ecosystem function (e.g., keystone or foundation species). For these species, one can endeavor to assess potential for evolutionary response and adaptive phenotypic plasticity in key traits in response to environment, and then design appropriate targeted conservation and management strategies. These two approaches are perhaps best described as trait and triage approaches.

Trait-Based Approach

Ecological theory provides ample basis for hypotheses about adaptive capacity based on life-history traits. Analogously, functional traits (i.e., morphological, physiological, and phenological traits that affect fitness) have great power to describe the ecology of diverse species (e.g., Wright et al. 2004) and may be useful for predicting patterns of plasticity. One approach to linking evolvability

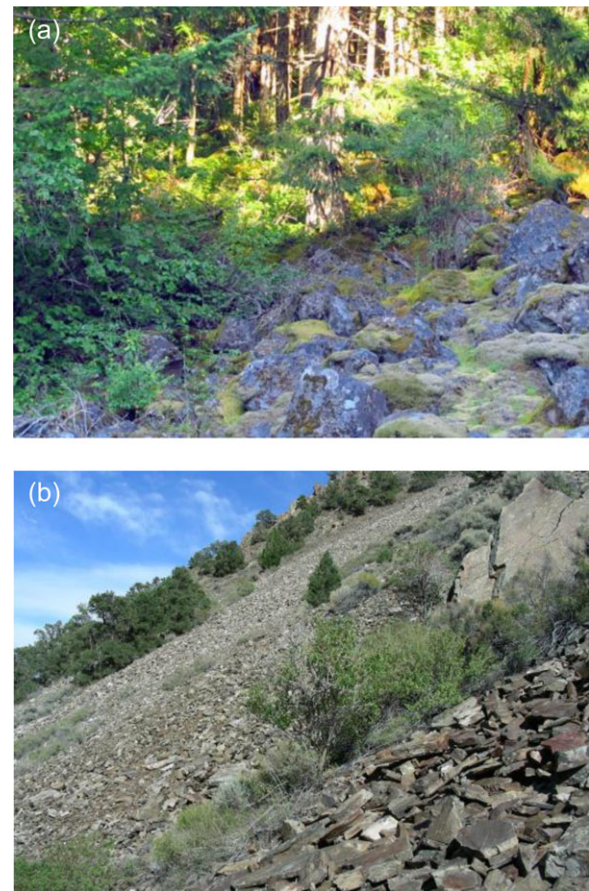
and adaptive phenotypic plasticity to adaptive capacity involves designing comparative experiments across taxa and ecosystems to identify whether the mean values of certain functional traits may be predictors or proxies of evolvability and adaptive plasticity. Adaptive plasticity in particular functional traits may be indicative of a general potential to show adaptive plasticity in a wide range of traits or across a range of environmental conditions (Davidson et al. 2011; Foden et al. 2013).

Such experiments could either be new empirical studies of correlates between functional and plasticity therein and life-history traits or could take meta-analytic approaches. Questions to be addressed include: Do particular species, lineages, or populations differ in adaptive phenotypic plasticity in functional traits? Does this depend on the sort of environmental perturbation (e.g., rapid changes in temperature, CO₂, water availability)? Do particular sets of traits consistently show adaptive phenotypic plasticity within or across taxa? A further question relevant to efficient on-the-ground management is whether the extent and adaptive value of phenotypic variation can be assessed in the natural environment instead of under controlled simulations of current or novel conditions. Assessments of the adaptive value of plasticity in nature are few for logistical reasons. They are increasing in number as analytical techniques improve; however, these assessments generally require extensive sample sizes and well-defined pedigrees (Brommer 2013). Finally, a trait-based approach in which phenotype and patterns of genetic variation and gene expression are assessed could illuminate the genetic architecture of plastic responses, thereby linking the phenotypic and genetic elements of adaptive capacity. Neill and Puettmann (2013) took a first step toward demonstrating how a trait-based approach could be used to manage for adaptive capacity in a forest system.

Such experiments are costly and time-consuming, and to have best potential to reveal general patterns, they must be highly focused. We advocate interdisciplinary discussions aimed at broad-scale synthesis of existing comparative data on components of adaptive capacity and comparative experiments to develop trait-based predictors of adaptive capacity that could have application across ecosystems. These discussions need to explicitly consider all three components of adaptive capacity so that the interactive effects among them can be captured. By assessing the life-history characteristics, genetic structure, and phenotypic plasticity of key traits, one increases the likelihood of identifying robust predictors of adaptive capacity that could be applied to conservation and management decisions and policy at landscape and community levels.

Triage-Based Approach

In many systems, long-term data or accumulated experience could be used to identify species that already show



*Figure 2. Biophysical context in which American pikas (*Ochotona princeps*) occur in the (a) Columbia River Gorge, between Washington and Oregon (U.S.A.) (photo by J. Varner), and (b) the hydrographic Great Basin, between the Sierra Nevada and Rocky Mountains of the western United States (photo taken at Wisconsin Creek, Toiyabe Range, Nevada, by E. A. Beever).*

impacts of climate change or ability to withstand changes. Practitioners typically agree that not all vulnerable species demand equivalent research or conservation investment; however, decisions regarding where to focus resources are difficult. Adaptive capacity of a species or population is one criterion that may be used for selecting conservation targets or surrogate species. We propose that working with natural-resource managers, research teams could triage the existing biota of a given community (at least among better-researched clades and for those species amenable to research) to identify where species lie along two axes, sensitivity and ecological importance, and then focus adaptive capacity research accordingly.

Conservation triage is the process of prioritizing resource allocation to maximize conservation returns relative to goals (Bottrill et al. 2008). In a census of climate sensitivity and exposure of at-risk birds in California, Gardali et al. (2012) demonstrated how

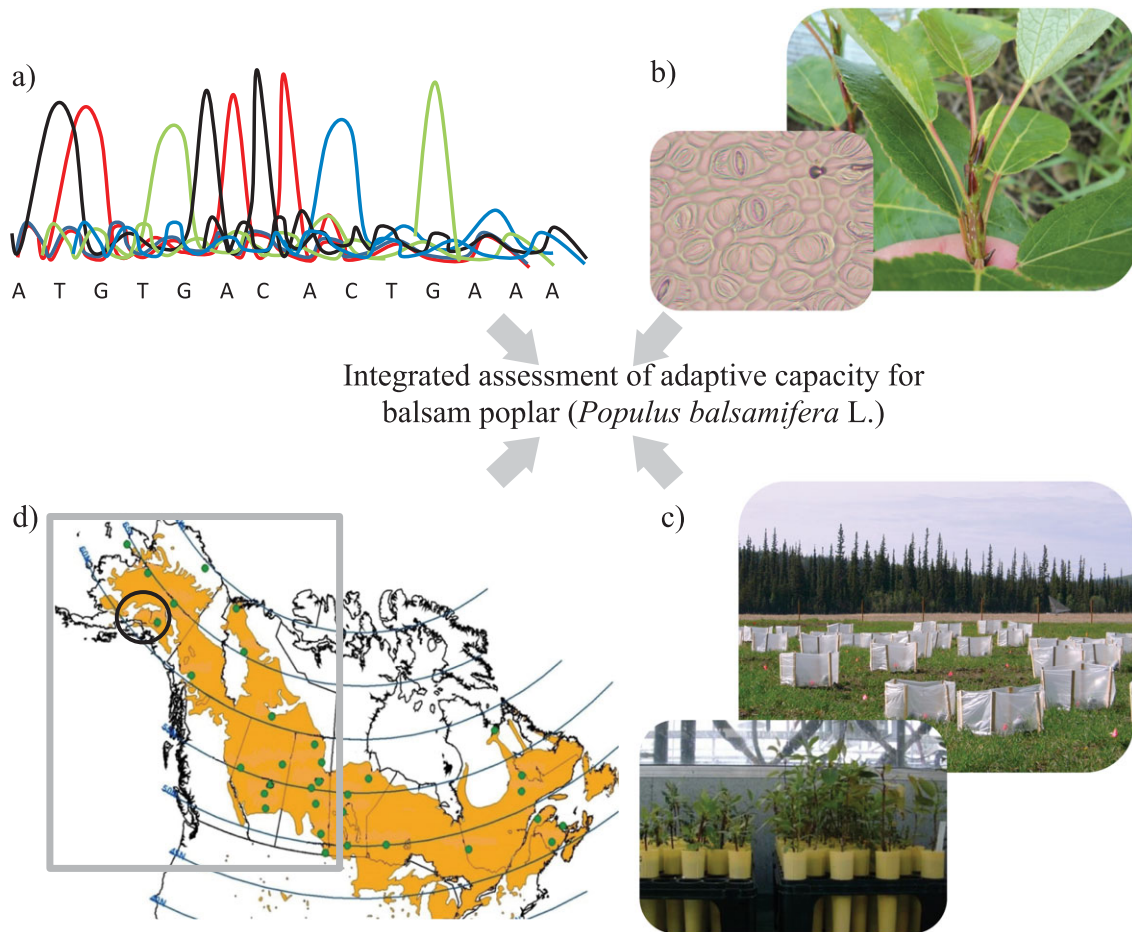


Figure 3. Quantification of variation in adaptive capacity among populations of balsam poplar was based on assessment of (a) range-wide genetic diversity and gene flow; (b) acclimation to experimentally increased temperatures (including phenotype, physiology, phenology, and cold tolerance); and (c) successful growth near its northern boundary of (d) samples from across the species' geographic distribution (shaded) (dots, populations sampled for genetic analyses; rectangle, populations included in warming experiments; circle, location of common-garden experiment).

measures and proxies of sensitivity (including elements of adaptive capacity) can be used to rank vulnerability of species. In a triage operation, sensitive species that only slightly affect community or ecosystem function could be given lower priority for research and management. Conversely, species that play a disproportionately large role in community composition (e.g., keystone or foundation species) and show evidence of sensitivity (e.g., falling population sizes, mortality events, increased susceptibility to disease) would be the focus of adaptive-capacity research. For these latter species, the goal would be to determine whether the environmental threshold of sensitivity can be identified and, if so, whether there is potential to manage the threshold and whether there is variation in adaptive capacity among individuals or populations of the species that could be harnessed for management (e.g., via managed translocation or via restoring or maintaining connectivity) (Weeks et al. 2011).

Once patterns of genetic variation and phenotypic plasticity are understood, informed decisions regarding managing for adaptive capacity can be made. For example, Balsam poplar (*Populus balsamifera*) occurs over a broad latitudinal range in North America and exhibits a locally adapted pattern of declining growing-season lengths as latitude increases (Howe et al. 2003). Integrated research on the adaptive capacity shows that northern populations have limited capacity to adapt to climate change relative to southern populations as a result of lower physiological plasticity (Robertson 2012) and lower genetic variation (Olson et al. 2010, 2013). Together these factors may limit potential for rapid evolutionary responses to climate change within the northern populations, but there is potentially sufficient plasticity for southern trees to establish in northern environments (Fig. 3). Sourcing seeds from a range of latitudes for carefully planned translocations may be the best way to

introduce genetic variation and adaptive plasticity for widely distributed species (Broadhurst et al. 2008; Thomas et al. 2013). For example, genetic rescue with small numbers of individuals can introduce genetic variation into small or threatened populations, and restoration based on genetic adaptation can be achieved through the movement of a large number of individuals so as to initiate shifts in trait characteristics in target populations (Weeks et al. 2011).

Ultimately, triage exercises are used because resources available for conservation are limited and are intended to prioritize efforts to conserve species having high ecological importance by maximizing their adaptive capacity. The efficacy of this approach will depend on effective networking among practitioners, functional ecologists, and ecological geneticists, and others.

Conclusions

To manage and conserve species in a rapidly changing climate and under growing human pressure, it is critically important to be able to assess adaptive capacity of species and populations. Understanding how evolvability and phenotypic plasticity vary among and within species will improve the ability to assess how these factors interact to confer resilience to climate change (Reale et al. 2003; Moritz & Agudo 2013) and adaptive capacity and will help buy time for species to adapt. Research can make meaningful progress and efficiently inform management if it is grounded in ecological theory and reflects an understanding of the distribution of genetic variation, evolvability, and phenotypic plasticity. However, gaining this information is costly and time-consuming. Thus, efforts to quantify adaptive capacity must be carefully focused, should use appropriate pre-existing genetic and evolutionary information, and must assess appropriate traits in relevant species and relate to realistic projections of future climates. Given Fisher's predictions (Fig. 1a), increasingly unpredictable and extreme climatic events will likely be of particular conservation concern. Thus, exploration of performance outside species' current climatic niches—across projected novel environments—is increasingly important.

Focused discussions between managers and researchers are urgently needed to identify research directions that will most effectively deliver answers that reflect the real-world needs of resource managers and other conservation practitioners and policy makers and result in for novel and dynamic management and policy decisions (Williams et al. 2008). By directing research to both seek general patterns and identify ways to facilitate adaptive capacity of key species and populations within species, conservation ecologists and resource managers will maximize returns on research and management investment.

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Literature Cited

- Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164:S165–S184.
- Allee WC, Emerson AE, Park O, Park T, Schmidt KP. 1949. *Principles of animal ecology*. Saunders, Philadelphia.
- Anderson JT, Inouye DW, McKinney AM, Colautti RI Mitchell-Olds T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences* 279:3843–3852.
- Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecology Letters* 14:677–689.
- Beever EA, Dobrowski SZ, Long J, Mynsberge AR, Piekielek NB. 2013. Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology* 94:1563–1571.
- Beever EA, Ray C, Mote PW, Wilkening JL. 2010. Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164–178.
- Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW. 2011. Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054–2070.
- Beever EA, Wilkening JL, McIvor DE, Weber SS, Brussard PE. 2008. American pikas (*Ochotona princeps*) in northwestern Nevada: a newly discovered population at a low-elevation site. *Western North American Naturalist* 68:8–14.
- Beier P, Brost B. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology* 24:701–710.
- Beldade P, Mateus ARA, Keller RA. 2011. Evolution and molecular mechanisms of adaptive developmental plasticity. *Molecular Ecology* 20:1347–1363.
- Bell G, Gonzalez A. 2009. Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters* 12:942–948.
- Bossdorf O, Richards CL, Pigliucci M. 2008. Epigenetics for ecologists. *Ecology Letters* 11:106–115.
- Bottrill MC, et al. 2008. Is conservation triage just smart decision making? *Trends in Ecology & Evolution* 23:649–654.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13:115–155.
- Bridle JR, Vines TH. 2007. Limits to evolution at range margins: When and why does adaptation fail? *Trends in Ecology & Evolution* 22:140–147.
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1:587–597.
- Brommer JE. 2013. Phenotypic plasticity of labile traits in the wild. *Current Zoology* 59:485–505.
- Brost BM, Beier P. 2012. Comparing linkage designs based on land facets to linkage designs based on focal species. *PLOS ONE* 7(e48965) DOI: 10.1371/journal.pone.0048965.

- Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* **8**(e1000357) DOI: 10.1371/journal.pbio.1000357.
- Davidson AM, Jennions M, Nicotra AB. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* **14**:419–431.
- Davidson AM, Nicotra AB. 2012. Beware: alien invasion. Where to next for an understanding of weed ecology? *New Phytologist* **194**:602–605.
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**:53–58.
- Dejong G. 1995. Phenotypic plasticity as a product of selection in a variable environment. *American Naturalist* **145**:493–512.
- Elton CS. 1927. *Animal ecology*. Sidgwick and Jackson, London.
- Etterson JR, Shaw RG. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**:151–154.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford, United Kingdom.
- Fisher RA. 1958. *The genetical theory of natural selection*. Dover, New York City.
- Foden WB, et al. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLOS ONE* **8**(e65427) DOI: 10.1371/journal.pone.0065427.
- Galef BG, Laland KN. 2005. Social learning in animals: empirical studies and theoretical models. *BioScience* **55**:489–499.
- Gardali T, Seavy NE, DiGaudio RT, Comrack LA. 2012. A climate change vulnerability assessment of California's at-risk birds. *PLOS ONE* **7**(e0029507) DOI: 10.1371/journal.pone.0029507.
- Grinnell J. 1917. The niche-relationships of the California thrasher. *The Auk* **34**:427–433.
- Hendriks IE, Olsen YS, Ramajo L, Basso L, Steckbauer A, Moore TS, Howard J, Duarte CM. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences* **11**:333–346.
- Hendry AP, Hudson K, Walker JA, Rasanen K, Chapman IJ. 2011. Genetic divergence in morphology-performance mapping between Misty Lake and inlet stickleback. *Journal of Evolutionary Biology* **24**:23–35.
- Hengeveld R, Haeck J. 1982. The distribution of abundance: I. Measurements. *Journal of Biogeography* **9**:303–316.
- Hoffmann AA, Sgrò CM. 2011. Climate change and evolutionary adaptation. *Nature* **470**:479–485.
- Howe GT, Aitken SN, Neale DB, Jermstad KD, Wheeler NC, Chen THH. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany: Revue Canadienne De Botanique* **81**:1247–1266.
- Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* **22**:415–427.
- Jablonka E, Raz G. 2009. Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *Quarterly Review of Biology* **84**:131–176.
- Kelly MW, Padilla-Gamino JL, Hofmann GE. 2013. Natural variation, and the capacity to adapt to ocean acidification in the sea urchin *Strongylocentrotus purpuratus*. *Integrative and Comparative Biology* **53**:E108–E108.
- Liebig J. 1840. *Chemistry in its application to agriculture and physiology*. Taylor and Walton, London.
- McGuire R, Agrawal AA. 2005. Trade-offs between the shade-avoidance response and plant resistance to herbivores? Tests with mutant *Cucumis sativus*. *Functional Ecology* **19**:1025–1031.
- Moritz C, Agudo R. 2013. The future of species under climate change: Resilience or decline? *Science* **341**:504–508.
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park. *Science* **322**:261–264.
- Morris WF, et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**:19–25.
- Neill AR, Puettmann KJ. 2013. Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions. *Canadian Journal of Forest Research: Revue Canadienne De Recherche Forestiere* **43**:428–440.
- Nicotra AB, et al. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**:684–692.
- Odum EP. 1959. *Fundamentals of ecology*. Saunders, Philadelphia.
- Olson MS, Levens N, Soolanayakanahally RY, Guy RD, Schroeder WR, Keller SR, Tiffin P. 2013. The adaptive potential of *Populus balsamifera* L. to phenology requirements in a warmer global climate. *Molecular Ecology* **22**:1214–1230.
- Olson MS, Robertson AL, Takebayashi N, Silim S, Schroeder WR, Tiffin P. 2010. Nucleotide diversity and linkage disequilibrium in balsam poplar (*Populus balsamifera*). *New Phytologist* **186**:526–536.
- Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA. 2014. Mechanisms of reef coral resistance to future climate change. *Science* **344**:895–898.
- Pennings SC, Richards CL. 1998. Effects of wrack burial in salt-stressed habitats: *Batis maritima* in a southwest Atlantic salt marsh. *Ecography* **21**:630–638.
- Pespeni MH, et al. 2013. Evolutionary change during experimental ocean acidification. *Proceedings of the National Academy of Sciences of the United States of America* **110**:6937–6942.
- Peterson AT, Soberon J, Sanchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. *Science* **285**:1265–1267.
- Pigliucci M, Murren CJ, Schlichting CD. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* **209**:2362–2367.
- Reale D, McAdam AG, Boutin S, Berteaux D. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**:591–596.
- Reusch TH. 2014. Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evolutionary Applications* **7**:104–122.
- Richards EJ. 2006. Opinion – inherited epigenetic variation – revisiting soft inheritance. *Nature Reviews Genetics* **7**:395–U2.
- Robertson AL. 2012. Acclimation and migration potential of a boreal forest tree, balsam poplar (*Populus balsamifera*), in a changing climate. PhD thesis, University of Alaska Fairbanks.
- Robertson AL, Wolf DE. 2012. The role of epigenetics in plant adaptation. *Trends in Evolutionary Biology* **4**:19–25.
- Rockman MV. 2012. The QTN program and the alleles that matter for evolution: all that's gold does not glitter. *Evolution* **66**:1–17.
- Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* **17**:667–693.
- Schlichting CD. 2008. Hidden reaction norms, cryptic genetic variation, and evolvability. *Year in Evolutionary Biology 2008* **1133**:187–203.
- Schluter D. 2000. *The ecology of adaptive radiations*. Oxford University Press, Oxford, United Kingdom.
- Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics* **40**:415–436.
- Sgro CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* **4**:326–337.
- Shaw RG, Etterson JR. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist* **195**:752–765.
- Shelford VE. 1913. The reactions of certain animals to gradients of evaporating power and air. A study in environmental ecology. *Biological Bulletin* **25**:79–120.
- Siol M, Wright SI, Barrett SC H. 2010. The population genomics of plant adaptation. *New Phytologist* **188**:313–332.

- Sollars V, Lu XY, Xiao L, Wang XY, Garfinkel MD, Ruden DM. 2003. Evidence for an epigenetic mechanism by which Hsp90 acts as a capacitor for morphological evolution. *Nature Genetics* **33**:70–74.
- Sunday JM, Calosi P, Dupont S, Munday PL, Stillman JH, Reusch TBH. 2014. Evolution in an acidifying ocean. *Trends in Ecology & Evolution* **29**:117–125.
- Thomas CD, et al. 2004. Extinction risk from climate change. *Nature* **427**:145–148.
- Thomas JA. 1993. Holocene climate changes and warm man-made refugia may explain why a sixth of British butterflies possess unnatural early-successional habitats. *Ecography* **16**:278–284.
- Thomas MA, Roemer GW, Donlan J, Kickson BG, Matocq M, Malaney J. 2013. Gene tweaking for conservation. *Nature* **501**:485–486.
- True HL, Berlin I, Lindquist SL. 2004. Epigenetic regulation of translation reveals hidden genetic variation to produce complex traits. *Nature* **431**:184–187.
- Valladares F, et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* **17**:1351–1364.
- Van Buskirk J, Steiner UK. 2009. The fitness costs of developmental canalization and plasticity. *Journal of Evolutionary Biology* **22**:852–860.
- van Kleunen M, Fischer M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166**:49–60.
- Varner J, Dearing MD. 2014. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal of Mammalogy* **95**:72–81.
- Vedder O, Bouwhuis S, Sheldon BC. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biology* **11**(e1001605) DOI: 10.1371/journal.pbio.1001605.
- Villen-Perez S, Carrascal LM, Seoane J. 2013. Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit. *PLOS ONE* **8**(e68448) DOI: 10.1371/journal.pone.0068448.
- Walters RJ, Blanckenhorn WU, Berger D. 2012. Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective. *Functional Ecology* **26**:1324–1338.
- Weeks AR, et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* **4**:709–725.
- Wiens JJ, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**:1310–1324.
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6**:2621–2626. e325 DOI: 10.1371/journal.pbio.0060325.
- Wilson RJ, Gutiérrez D. 2011. Effects of climate change on the elevational limits of species ranges. Pages 107–131 in EA Beever, J Belant, editors. *Ecological consequences of climate change: mechanisms, conservation, and management*. CRC Press, Boca Raton.
- Wright IJ, et al. 2004. The worldwide leaf economics spectrum. *Nature* **428**:821–827.
- Wright S, Keeling J, Gillman L. 2006. The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences of the United States of America* **103**:7718–7722.