POLICY PERSPECTIVE

Improving Conservation Outcomes with a New Paradigm for Understanding Species' Fundamental and Realized Adaptive Capacity

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Abstract

Worldwide, many species are responding to ongoing climate change with shifts in distribution, abundance, phenology, or behavior. Consequently, natural-resource managers face increasingly urgent conservation questions related to biodiversity loss, expansion of invasive species, and deteriorating ecosystem services. We argue that our ability to address these questions is hampered by the lack of explicit consideration of species' *adaptive capacity* (AC). AC is the ability of a species or population to cope with climatic changes and is characterized by three fundamental components: phenotypic plasticity, dispersal ability, and genetic diversity. However, few studies simultaneously address all elements; often, AC is confused with sensitivity or omitted altogether from climate-change vulnerability assessments. Improved understanding, consistent definition, and comprehensive evaluations of AC are needed. Using classic ecological-niche theory as an analogy, we propose a new paradigm that considers fundamental and realized AC: the former reflects aspects inherent to species, whereas the latter denotes how extrinsic factors constrain AC to what is actually expressed or observed. Through this conceptualization, we identify ecological attributes contributing to AC, outline areas of research necessary to advance understanding of AC, and provide examples demonstrating how the inclusion of AC can better inform conservation and natural-resource management.

Introduction

Many species are responding to contemporary climate change through shifts in distribution, abundance, morphology, behavior, or phenology (e.g., Dawson *et al.* 2011; Staudinger *et al.* 2013). Future climate disruptions are expected, leading to widespread concerns about species' abilities to keep pace, interactive effects with other stressors, and thresholds that will result in increased extinction rates (e.g., Quintero & Wiens 2013). To address these concerns, climate-change vulnerability assessments have emerged to evaluate factors contributing to species and habitat declines versus resilience to climate change (Glick *et al.* 2011). Vulnerability is defined by the IPCC (2014) as the propensity to be adversely affected. In the context of natural resources, vulnerability is a function of a species' or habitat's *exposure* to climate change, its *sensitivity* to that exposure, and its ability to cope with those changes through its intrinsic *adaptive capacity*. Exposure denotes the magnitude of exogenous disturbance likely to be experienced, sensitivity refers to how dependent or tightly linked a species is to current conditions, and adaptive capacity is the capacity of a species to cope with and persist under new conditions (Dawson *et al.* 2011, Glick *et al.* 2011).

Adaptive capacity (AC), as defined here and in the context of vulnerability assessment, includes evolutionary adaptive capacity (i.e., the ability to evolve), dispersal ability (which may vary from local movements to more suitable microclimates, to substantial movements beyond the historic range of species), and phenotypic plasticity (e.g., behavioral adjustments), or a combination of these (Dawson *et al.* 2011; Glick *et al.* 2011, Nicotra *et al.* in press). AC thus encompasses genetic, epigenetic, and acclimation processes and reflects genetic diversity, behavioral adaptation, dispersal ability, life-history traits, phenotypic plasticity, and evolutionary adaptation, among other factors.

Because vulnerability assessments frequently serve as the basis for the formulation of adaptation strategies and priorities, improved understanding and greater consistency in the definition of AC could lead to the design of more-strategic climate-adaptation plans. As such, planning efforts would no longer be based solely on life-history traits or on generalized bioclimatic-niche models, but also become informed by target-species' physiology, genetics, and their likelihood to persist under projected climatic changes. However, the IPCC-outlined vulnerability framework, and in particular AC, have not yet been implemented consistently. In a recent review of 403 climate-related vulnerability assessments of U.S. ecological resources, exposure was assessed as part of vulnerability in 87.9% of assessments, and sensitivity in 68.5%; however, AC was evaluated in only 33.1% of the projects (Thompson, *et al.* 2015), and **only** when both other components were also evaluated. Although comprehensive assessments of vulnerability ideally should include all three components simultaneously, AC is often excluded, incorrectly framed as the inverse of sensitivity, combined with sensitivity as a single criterion for evaluation, or considered through only one constituent component (e.g., evolutionary adaptive potential) (Thompson *et al.* 2015).

Given the high stakes associated with species extinctions, the legal implications of endangered-species listings, and costs of reduction or loss of ecosystem services that sustain human communities, we urge an increased, strategic, and cross-disciplinary research effort focused on improving understanding of AC. The scientific community needs to develop a consistent understanding and application of the term "adaptive capacity," followed by experimental designs and sampling protocols that indeed test for species' AC and not just a species' sensitivity to climatic changes. For example, some specialist species that are considered to have lower AC, in reality, may exhibit a more-generalist strategy under novel climatic conditions. The pinyon mouse (*Peromyscus truei* Shufeldt) is a good example. Although long considered a habitat specialist, it has expanded its geographic and elevational range into new habitat types in the Sierra Nevada Mountains near Yosemite National Park (USA), apparently in response to newly suitable climatic conditions created by a century of climate change (Yang *et al.* 2011).

Similarly, although niche modeling has many uses, it can under-predict species distribution because it poorly incorporates biologically relevant microclimatic refugia that permit species persistence in apparently unsuitable macroclimates (e.g., Keppel *et al.* 2012; Varner & Dearing 2014). Conversely, Heads (2015) argues that niche models typically over-predict species' actual distribution, because they do not incorporate the multitude of factors other than climate that constrain species' niches. Furthermore, although niche modeling typically uses the same climatic factors and functional relationships (e.g., linear, quadratic) across species' entire geographic ranges, 18 populations of threatened juvenile salmon (*Oncorhynchus tshawytscha* Walbaum) illustrated that survival can be determined by markedly different climatic factors (e.g., summer temperature, minimum fall stream flow) within the same river basin at both yearly and decadal time scales (Crozier & Zabel 2006). Because species and populations have different AC, we expect relative winners and losers in the face of contemporary climate change (O'Brien & Leichenko 2003). Box 1 provides an example of populations of the same species separated by as

little as 370 km exhibiting different ACs and experiencing dramatically different trends.

Paleoecological evidence demonstrates species persistence through climatic changes without large range contractions, indicating that high AC, although poorly understood, must be present (e.g., Moritz & Agudo 2013). Nevertheless, the relative importance of species': tracking of their climate niches, phenotypic plasticity, differential responses to changing climate (Jackson & Overpeck 2000), and novel mutations in their persistence (e.g., Vedder *et al.* 2013)—is rarely, if ever, known. Human-induced habitat fragmentation and other obstacles to movement that were not present in the past add to the problem of using paleoecological patterns alone to accurately predict which species will persist, where, and how, under continuing climate change.

Identifying which species or populations are likely to have limited AC, and thus may require active intervention, is critical, given managers' limited resources and the societal imperative for maintaining biological diversity. Alternatively, in some situations, conservation and particularly restoration could shift focus to species with higher AC and a greater chance of long-term viability. Nicotra *et al.* (in press) suggest dual trait- and triage-based approaches to start the process of quantification of AC and identification of priorities. To conceptually illustrate the task at hand: a manager would benefit from knowledge of multiple species' AC when deciding, for example, whether to use limited funds to acquire and conserve land, pursue a conservation easement, plant trees whose geographic range was previously farther south, or use managed relocation for an endangered forest-dwelling animal species.

Fundamental and realized adaptive capacity

To enhance decision-making and conservation actions, we introduce a novel conceptualization of species-level AC that draws on Hutchinson's (1957) concept of realized and fundamental ecological niches. Using this classic niche theory as an analogy, we propose a new paradigm that frames AC in terms of a fundamental and realized state: the former reflects aspects inherent to species, and the latter denotes how extrinsic factors constrain AC to what is actually expressed or observed. Such a conceptualization would allow us to ask what adaptation actions might be capable of enhancing AC by reducing constraints and shifting the "realized" AC closer to the "fundamental" AC. We propose that consideration of realized and fundamental AC could inform policy and aid conservation practitioners because it: (1)

facilitates explicit delineation of all the categories that determine species' intrinsic (fundamental) AC, and (2) identifies tangible management actions that may be considered to maximize realized AC (Figure 1, Supporting Information). Although there is general agreement that species-level AC can depend on a variety of intrinsic factors, there is no consensus yet on how to assess the relative importance of those factors or how to incorporate them into conservation strategies.

Using this framework of realized versus fundamental AC, we explore how managing attributes of ecological systems can enhance AC, identify critical research areas needed to advance understanding of AC, and provide examples of management strategies that would benefit from the inclusion of AC in the decision-making process. Moreover, better understanding of how species assemblages may re-sort as species respond to changes, some species more successfully than others (as a function of species' differing AC), will help inform management efforts related to species' and ecosystem functions. We encourage those in the research community to use their findings on how climate variability and change affect species to contribute to the understanding of species' AC and the factors that may limit its full expression. This new information is critical for natural-resource managers responsible for conservation of species and ecosystem services in a changing climate.

Within this conceptualization of species-level AC, the **fundamental AC** reflects a species' intrinsic ability to accommodate climate change without significant genetic losses, large range contractions or extinction, or intensive management intervention. This ability depends on its phenotypic plasticity, dispersal and colonization abilities, life-history traits, evolutionary rates, and genetic diversity (Figure 1; Dawson *et al.* 2011). For example, Great Tits (*Parus major* L.) in the Netherlands exhibited a heritable increase in plasticity in their breeding date over a recent 32-year period (Nussey *et al.* 2005). Shifts in the timing of emergence of caterpillars (the bird species' main food source) that were correlated to recent climate changes created strong selection for increased plasticity in *P. major* breeding to avoid phenological mismatches (Nussey *et al.* 2005). The evolutionary potential of a species to adapt in place, as *P. major* has, is influenced by generation time, population structure and the extent of local adaptation (O'Neil *et al.* 2014), and genetic and epigenetic diversity, which in turn are mediated by factors such as genetic drift and the introduction of novel alleles via mutation or gene flow. Regional migration potential also contributes to fundamental AC, and is influenced by dispersal and colonization abilities, which depend in part on phenotypic plasticity.
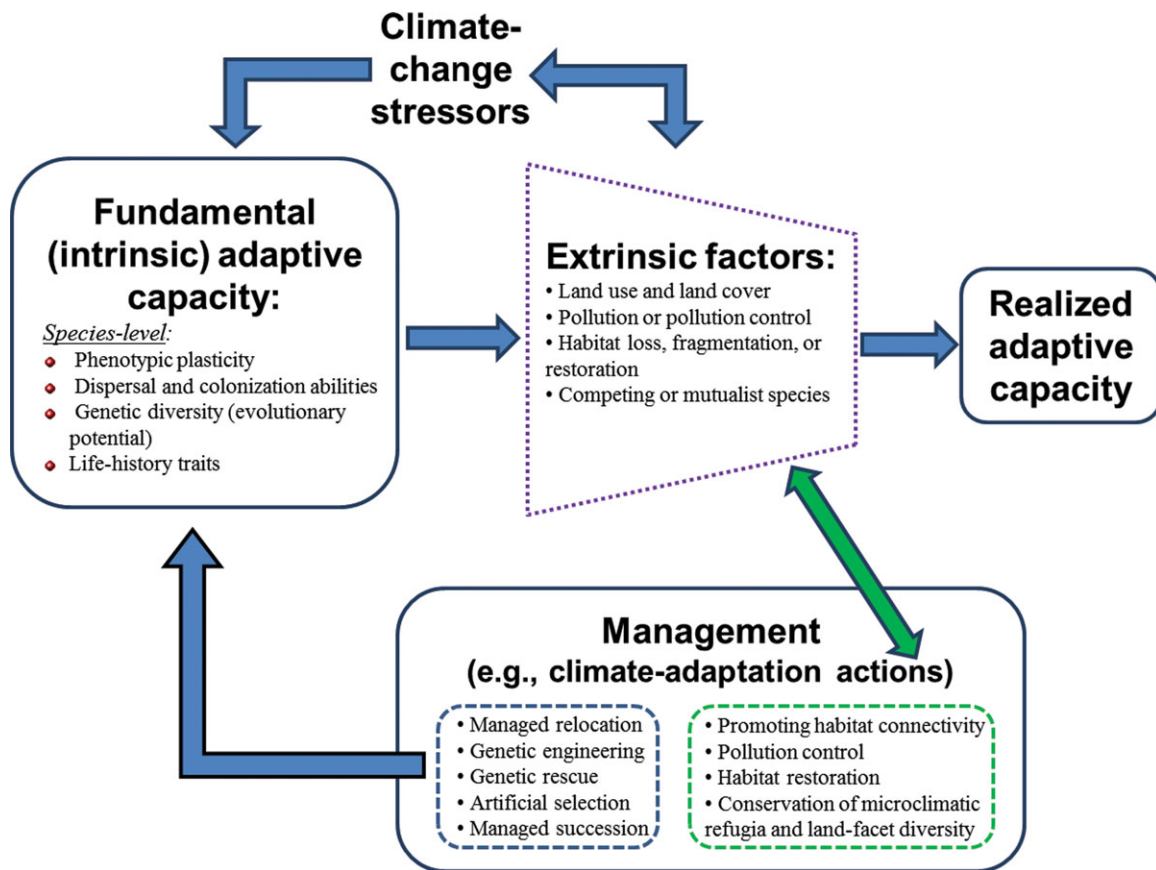
Figure 1 A new heuristic conceptualization of adaptive capacity (AC): Conceptual model of fundamental (intrinsic) and realized (extrinsically constrained) AC of a species, analogous to the fundamental and realized ecological niches of a species (*sensu* Hutchinson 1957). Climate adaptation would be achieved most effectively by minimizing the difference between realized AC and fundamental AC. Realized AC can be influenced by a range of extrinsic influences acting in the context of climate-change stressors; we primarily focus on human influences. Phenotypic plasticity is a result of the environmental influence on individual phenotypes (form and function) through developmental mechanisms. It can take the form of morphological, physiological, and behavioral responses to environmental stimuli, at time scales ranging from seconds to weeks and months. In this framework, to enhance realized AC and thus reduce the climate-related vulnerability of the target species, climate-adaptation strategies and management actions could aim to either (a) expand the fundamental AC directly (lower-left arrow; e.g., Thomas et al. 2013), as listed in the left column of climate-adaptation actions, or (b) influence realized AC indirectly by ameliorating extrinsic factors and stressors that act as a filter (as depicted by the purple "filter") from fundamental to the diminished state of realized AC, as exemplified by the green-encircled actions and arrow. Just as Hutchison's (1957) fundamental niche is constrained by any number of natural and anthropogenic factors to a species' realized niche, societal actions can influence species distributions by determining the magnitude of constraint from a species' fundamental to realized adaptive capacity. The analogy is further reinforced by understanding that the magnitude of a species' adaptive capacity will strongly affect the magnitude of change in a species' realized niche under contemporary climate change.

The individual plastic (short-term) and population-level genetic (longer-term) components of the fundamental AC operate on different timescales and the implications of these divergent timescales for overall AC are not yet understood. Furthermore, both phenotypic plasticity and evolutionary adaptation can contribute synergistically to trait shifts. Rapid climatic changes are likely to exert increasingly strong directional selection on species traits (e.g., Anderson *et al.* 2012). However, currently, basic information about the interplay between

evolutionary potential and phenotypic plasticity is lacking for most species (e.g., Foden *et al.* 2013, Charmantier & Gienapp 2014). Nonetheless, recent research (Quintero & Wiens 2013) suggests that, at least among amphibians, squamate reptiles, birds, crocodilians, mammals, and turtles, the rate of niche evolution observed across millions of years in the paleorecord was 10,000–100,000 times slower than the predicted rate of climate change from 2000 to 2100. The apparent inability of most species to keep up with the pace of 21st-century climate changes

further underscores the pressing need to investigate and quantify fundamental AC (e.g., Hoffmann & Sgrò 2011; Vedder *et al.* 2013).

The **realized AC** of a species—as observed *in situ*—reflects extrinsic factors that affect or constrain the species' fundamental AC. Although numerous "natural" extrinsic factors exist (e.g., competing species, naturally occurring barriers to movement), we focus on anthropogenic factors because they are both increasingly pervasive and, more importantly, some can be ameliorated through policy and management actions. These anthropogenic stressors seem more likely to limit the full expression of the fundamental AC than enhance it. Thus, it is feasible that a species' realized AC may be increased—within the bounds defined by its fundamental AC—through management actions that reduce anthropogenic stressors (Figure 1).

Stressors such as land-use change, harvest, eutrophication, and pollution can constrain a species' realized AC by creating barriers to dispersal and gene flow, for example. Furthermore, these stressors can exert strong selection pressure, whether stabilizing or directional, that reduces genetic diversity. Reduction in genetic diversity could potentially lower the realized AC. For example, chronic stressors such as pollution or eutrophication may reduce the ability of corals to tolerate, acclimate, or recover in the face of temperature-related bleaching events (Palumbi *et al.* 2014); alleviation of the pollution would thus be predicted to enhance realized AC. Additionally, the moss "blanket" that insulates talus interstices from ambient temperature by up to 31.5 C° (diel temperature flux in interstices was < 1 °C; Varner & Dearing 2014) is part of the unique context in the Columbia River Gorge that allows American pikas to exist >1,100 m below pikas' predicted low-elevation limit of occupancy there, given the Gorge's latitude and longitude (Simpson 2009). Anthropogenic disturbance that compromises moss cover thus could potentially reduce pikas' AC to accommodate high summer temperatures through behaviorally plastic use of microrefugia. Conversely, marine fisheries often selectively harvest the largest-bodied fish, leading to populations that are truncated in size and age structure and potentially lowering their realized AC (Hsieh *et al.* 2010).

Management actions may help counteract such negative extrinsic stressors in relation to realized AC. Currently, we have insufficient understanding of the likely success of management actions aimed at altering species-level realized AC; however, a range of actions can be envisioned (Figure 1, Box 2). Potential actions might include maintaining dispersal capacity through enhancing or restoring landscape connectivity, and evaluating the adequacy of current protected areas, given species' migration potential and fundamental AC (Hamann &

Aitken 2013). Alternatively, more-risky or -intensive actions might include increasing genetic diversity of plants via targeted ecological restoration efforts (e.g., via seed selection; see Broadhurst *et al.* 2008), genetic engineering to pre-emptively increase species' climate-hardiness (Thomas *et al.* 2013), genetic (evolutionary) rescue, or managed relocation. Application of AC in the design of management strategies can therefore serve as an important framework for linking possible conservation actions to potential climate impacts, whether those actions reflect a continuation of existing strategies (e.g., reducing current stressors: Dawson *et al.* 2011; Moritz & Agudo 2013; Thomas *et al.* 2013; Palumbi *et al.* 2014), or involve the use of novel techniques and responses.

Managing for species' adaptive capacity in an ecosystem context

The paradigm can be expanded to improve conservation at the ecosystem level. Ecological transformation, also known as a regime shift or state change, poses substantial management challenges in the context of species conservation. Managers will need to integrate the reality of transformations and the possibility of actively shaping future ecological trajectories into management plans for single and multiple species. Managing a mosaic of resilient and transforming regions will require that management actions are strategically coordinated to ensure that species-level AC is not compromised (Magness *et al.* 2011). For example, understanding how the evolutionary potential of a species is distributed geographically will help illustrate both what is being lost as conditions change, as well as how to craft a strategy to connect stable and transitioning areas. Stable macro- and micro-climatic refugia have been important facilitators and sources of biodiversity across past climate shifts (Petit *et al.* 2008; Moritz & Agudo 2013). Examples of microclimatic refugia include shade from steep or slot canyons, north-facing aspects of trees or mountains, riparian corridors, and microtopographic areas of cold-air pooling (Figure 1). Areas with high geomorphic diversity (also known as high diversity of land facets [Brost and Beier 2012] or enduring features) may provide more opportunities for species to redistribute locally or persist in microclimatic refugia and therefore, enhance species-level realized AC. Conserving refugia (Brost & Beier 2012) yet allowing other areas to be dynamic, while minimizing global extinctions, may constitute a feasible hedging strategy (Magness *et al.* 2011) for optimizing AC. Likewise, understanding how AC varies among populations within a species (e.g., see Box 1) will better enable managers to maintain genetic diversity (Alberto *et al.* 2013) and to identify and possibly

enhance, within ecosystems, populations that have highest potential to adapt to changing conditions (Hamann & Aitken 2013). However, before the implications of variation in species-level AC can be considered and applied at habitat or ecosystem scales, many basic research questions need to be answered (e.g., see Box 2).

A path forward

The need for improved and consistent understanding of AC is increasingly evident for resource managers, conservation practitioners, evolutionary biologists, and ecologists. Many research gaps remain (Nicotra *et al.* in press; Box 2); here we have indicated several potential directions for carefully designed research on management options in order to catalyze progress (Figure 1). Climate-adaptation science can unite diverse disciplines and bring together scientists and practitioners through collaborative "co-production" approaches to knowledge development, but the inter-disciplinary nature of these endeavors means that collaborators often arrive with different vocabularies and even different understandings of the same terms (Moss *et al.* 2013). Research in disparate subdisciplines has begun to assess components of AC at the species level but often not in an explicit management context; this limits the accessibility and utility of this knowledge to natural-resource managers. Consequently, an interdisciplinary synthesis effort (e.g., across genetics, ecophysiology, and evolutionary biology) could illuminate well-understood aspects of AC and highlight key research gaps. Translation from highly technical and field-specific research may be needed to integrate multiple sources of information and make it directly useful to applied-ecology researchers, conservation practitioners, and resource managers. Additionally, cooperative interdisciplinary and cross-institutional work is needed to articulate the critical on-the-ground management, research, and policy questions that, if addressed, would inform pressing resource-management challenges related to AC (*sensu* Box 2). Ideally, further questions could be identified through collaborative, stakeholder-driven processes.

Although policy and management options abound regarding where and how to direct conservation efforts under future climatic conditions, the full potential of these options to be effective under climate change is severely hampered unless we recognize the importance of, and the factors that may limit, a species' realized AC. Merely projecting species' range shifts without considering the variation in species' potential to behaviorally respond *in situ*, move, or physiologically cope with climate change ignores much of what is known about species' phenotypic plasticity, physiological tolerances, and evolutionary history (e.g., Foden *et al.* 2013; Hamann & Aitken 2013; Vedder *et al.* 2013). This bias may lead models to either overestimate climate-driven extinction risk (Schwartz 2012), or underestimate risk for species that have: particularly poor dispersal capacity, very low gene flow, highly fragmented populations, high levels of ecological specialization, or low fecundity. Lack of clear understanding of AC in the decision-making and policy contexts noted above can have ecological, economic, and social implications of great consequence. Conservation strategies will likely become more effective when the various components of AC, and factors limiting its full expression, are considered in management alternatives and climate-adaptation policies.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supporting Online Information

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