Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change

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Assessing the vulnerability of species to climate change serves as the basis for climate-adaptation planning and climate-smart conservation, and typically involves an evaluation of exposure, sensitivity, and adaptive capacity (AC). AC is a species' ability to cope with or adjust to changing climatic conditions, and is the least understood and most inconsistently applied of these three factors. We propose an attribute-based framework for evaluating the AC of species, identifying two general classes of adaptive responses: "persist in place" and "shift in space". Persist-in-place attributes enable species to survive in situ, whereas the shift-in-space response emphasizes attributes that facilitate tracking of suitable bioclimatic conditions. We provide guidance for assessing AC attributes and demonstrate the framework's application for species with disparate life histories. Results illustrate the broad utility of this generalized framework for informing adaptation planning and guiding species conservation in a rapidly changing climate.

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Rapid climate change is a defining issue of our time, and anthropogenic warming of the atmosphere is resulting in an array of impacts on species, ecosystems, and human communities. Contemporary climate-change effects range from shifts in the physical environment, including means and extremes in weather patterns, sea-level rise, ocean acidification, and drought, to disruptions in biological processes, such as species' phenologies, interactions, and distributions. Adaptive capacity (AC) is broadly defined as the ability of a species, ecosystem, or human system to cope with or adjust to changing climatic conditions (IPCC 2014). Early use of this concept largely emphasized socioeconomic systems and human institutions, but acknowledged its applicability to natural systems (Engle 2011). Application of AC to biological systems has primarily occurred in the context of climate change vulnerability assessments (CCVAs). CCVAs are the most widely used framework for assessing climate-related vulnerability and consist of three distinct components: exposure, sensitivity, and AC (Foden *et al.* 2019). Exposure reflects the type and magnitude of climatic changes that a species (or population) has experienced or is projected to experience. Sensitivity refers to the degree to which a species is affected by or susceptible to a climate-related change (IPCC 2014). In contrast, AC refers to the ability of a species to cope with, adjust to, and persist in the face of current and future climate change. This process can be further defined with respect to intrinsic capacities versus extrinsic constraints on AC (Beever *et al.* 2016). We focus here on species' intrinsic AC and acknowledge that many extrinsic factors, climatic or otherwise, can act as barriers or constraints to the innate ability of species to cope with or adjust to changes.

In a nutshell:

- Adaptive capacity (AC) – the ability of species to cope with or adjust to climatic changes – is a key component of vulnerability, yet is difficult to evaluate and apply in practice
- We describe an attribute-based framework for evaluating the AC of species or populations, which applies broadly to animals and plants
- We identified "persist in place" and "shift in space" as two classes of responses that reflect the type and level of AC in a species or population
- Operationalizing the concept of AC facilitates not only the development of adaptation strategies but also the identification of effective management actions under climate change

Because climate adaptation generally focuses on reducing climate-related vulnerabilities and risks (Stein *et al.* 2013), strategies to enhance a species' AC can be important for achieving adaptation and conservation outcomes (Prober *et al.* 2019). However, incorporation of AC information into CCVAs, climate-adaptation planning, and conservation decision

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making is fraught with challenges, which frequently include a failure to address AC either explicitly or implicitly, difficulties in distinguishing AC from sensitivity, and the use of definitions and evaluation criteria that are highly variable and often case-specific (Thompson *et al.* 2015). Ongoing setbacks in operationalizing the concept of AC have hindered its application in practice.

The increasing demand among resource managers for methods of evaluating AC has triggered the development of a growing number of trait-based assessment approaches (eg Young *et al.* 2012; Foden *et al.* 2013; Ofori *et al.* 2017). Most approaches to date have used a restricted subset of broadly defined traits (Foden *et al.* 2013) or traits applicable only to specific taxa (Cabrelli *et al.* 2014; Butt and Gallagher 2018). Even for traits that are routinely specified (eg dispersal capacity), variation in evaluation criteria hinders consistent and comparable application across taxa and systems. In a survey sent to participants of vulnerability-assessment training programs offered by the US Fish and Wildlife Service, over half (58%) of 81 respondents identified the lack of tools and methods as a primary challenge to incorporating AC into vulnerability assessments (unpublished data). When queried about priorities for helping conservation agencies apply AC in their work, 82% of participants responded that the development of improved AC assessment tools would be “useful” or “very useful”. These results indicate the need for a synthesis of AC concepts and better guidance on how to assess AC according to a robust and generalizable framework.

Building on prior work that advanced the conceptual basis for AC (Nicotra *et al.* 2015; Beever *et al.* 2016), here we offer an attribute-based framework for evaluating and communicating AC. This framework embraces an expansive view of AC that encompasses the ability to both cope with and adjust to changes, and is designed to help researchers and conservation practitioners incorporate AC into forward-looking adaptation and management practices.

Persist in place or shift in space: dual pathways for AC responses

Past research on AC has predominantly focused on the ability of species to physically move to track suitable bioclimatic conditions. Climate-driven range shifts are the subject of numerous empirical studies (eg see Rumpf *et al.* [2018]) and provide the foundation of many vulnerability assessments based on correlative models of species distributions. However, the ability of species to accommodate climatic changes in situ is not as easily documented and is therefore often underappreciated. To highlight the two general pathways in which organisms may respond to climate change through AC, we classify 36 attributes that enable a species or population to “persist in place” or “shift in space” (or both).

A species’ AC is often a reflection of its niche, characterized by the local ecological conditions that influence where an organism can occur. Changes in climatic or other physical conditions can involve shifts in the environment’s mean state, variance (ie frequency of extremes), or both (Jackson *et al.* 2009). In turn, the breadth and trend of these variables describe the historical, current, and potential future climatic conditions to which a species is exposed. Coping with new (previously unexperienced) climatic conditions occurs when a species’ existing tolerances (ie thresholds for survival and reproduction) fall within the range of variability of those conditions (Smit and Wandel 2006). In contrast, adjustments are necessary when bioclimatic changes exceed a species’ existing tolerances.

The “shift-in-space” pathway is a principal avenue for species to track suitable bioclimatic conditions. Such adjustments in location generally occur in response to changes in limiting environmental variables. Documented shifts that track temperature change, for instance, often entail poleward or upslope movements (Parmesan 2006). Range shifts tracking other bioclimatic variables (eg moisture) can lead to contrasting spatial patterns, however, with downslope shifts in elevation being as common as upslope shifts across several taxa (Rapacciuolo *et al.* 2014).

Alternatively, the “persist-in-place” pathway can occur through the availability of broad tolerances or existing flexibility (eg phenotypic plasticity), or through the acquisition of new traits or expanded tolerances. Broad tolerances, including those achieved through behavioral flexibility (Beever *et al.* 2017), can buffer a species or population from changing conditions, at least in the near term (Comte and Olden 2017). A persist-in-place response is illustrated by bird species in California’s Sierra Nevada mountains, for which nesting has on average advanced by about a week over the past century (Socolar *et al.* 2017). Although birds are highly mobile organisms, this study found the overall response to temperature increases in this avian community to be an adjustment in time (phenology) rather than a shift in space. In-situ adjustments can also result from an alteration or expansion of a species niche, including broadened tolerance or acclimatization to new conditions through microevolution (Hoffmann and Sgrò 2011; Bay *et al.* 2018). Over the past 50 years, for example, certain Hawaiian corals have exhibited evidence of thermal acclimatization to elevated ocean temperatures via increased survivorship and bleaching tolerance (Coles *et al.* 2018).

Attributes characterizing species’ AC

We identified 36 attributes for use in assessing AC (graphically depicted as an AC wheel in Figure 1), with individual attributes grouped into the following seven complexes of related characteristics: distribution, movement, evolutionary potential, ecological role, abiotic niche, life history, and demography. These attributes are based on evidence from the scholarly literature, a review of criteria used in other assessment frameworks, and the authors’ collective experience in diverse fields of ecology, conservation biology, climate science, and climate adaptation. The distribution and movement complexes broadly encapsulate the extent and capacity of an organism to move through a landscape (shift in space), whereas attributes relating to the life history and demography complexes reflect the capacity for an organism to accommodate changing climates in situ (persist in place). Attributes belonging to the three remaining complexes – namely the evolutionary potential and ecological role of organisms, along with their abiotic limits – can be used to inform both ends of this spectrum. We also highlight 12 "core" attributes, which collectively span the seven complexes and provide a comprehensive means of assessing AC when information for other attributes is unavailable. More detailed information about the core attributes, including their description, relevance to AC, and methods of evaluation, is presented in WebTable 1.

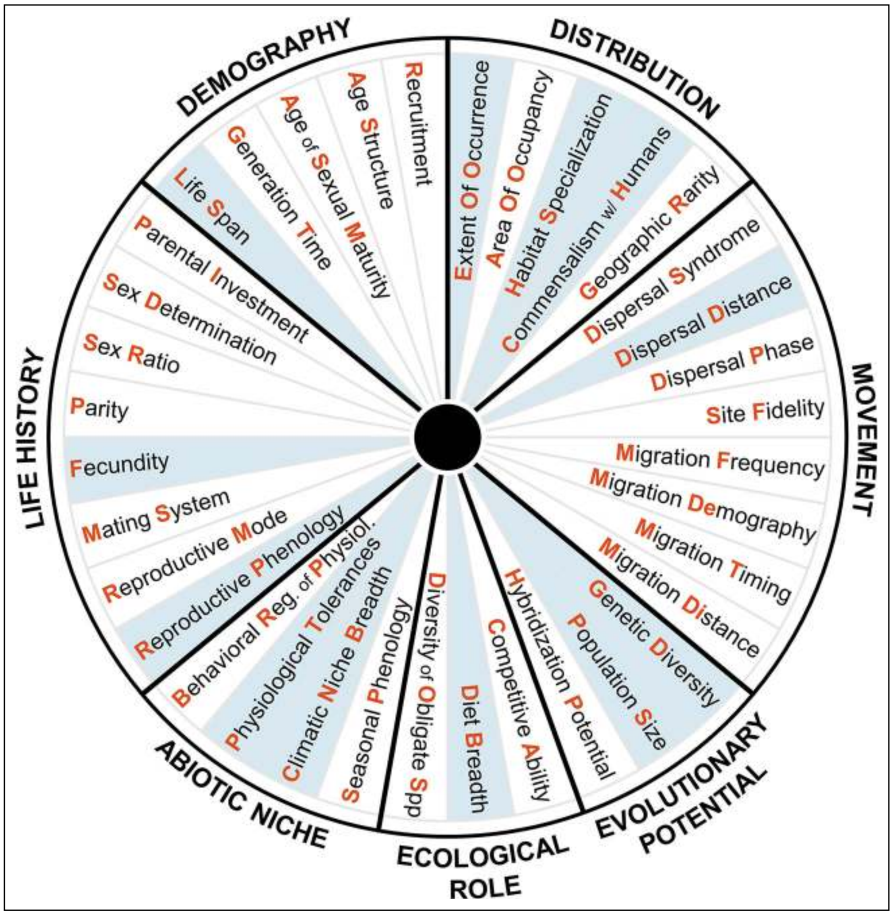

Figure 1. The adaptive capacity (AC) "wheel", depicting 36 individual attributes organized by ecological complexes (or themes). Twelve core attributes, representing attributes of particular importance and for which data are widely available, are highlighted in light blue. Letters used in attribute abbreviations (which appear in Figures 4 and 5) are shown here in red font.

Conservation prioritization relies on the development of standardized and consistent frameworks (Wade *et al.* 2017). Notably, our AC framework expands on prior efforts, and is applicable across taxa and geographies rather than being limited to specific organisms or regions. Recognizing the importance of intraspecific variation for estimating both species persistence and climatic vulnerabilities, our framework includes attributes that may be measured at both population and species levels. This flexibility allows the framework to inform climate-adaptation planning and management decisions across spatial scales.

For each attribute, species can be evaluated on a simple "low–moderate–high" scale, with criteria designed to accommodate either quantitative or qualitative assessments and accept either numerical or categorical values. Data availability will vary widely and may be largely lacking for many understudied species, and therefore for most attributes we provide multiple evaluation criteria for each level of AC to accommodate potential information gaps. In addition, attributes within a given complex can be used as surrogates (or proxies) when information for core attributes is otherwise unavailable. Suggested thresholds are based on well-established vulnerability assessment or extinction risk criteria (eg IUCN 2012; Young *et al.* 2012) or are derived from previous findings about the relationship of the attribute to AC. We summarized the resulting AC as the proportion of attributes within each of the criteria bins (ranging from low to high). We purposely do not propose a composite or overall metric, but instead encourage examining connections among attributes leading to potential cascading impacts or evaluating attributes that, by themselves, are so important that they may overwhelm other considerations (ie "deal makers" or "deal breakers").

To document the supporting evidence for an AC assessment, we also include a method that is based on the availability (amount), quality, and consistency of input information sources, as well as on expert knowledge. For each attribute, evidence is assessed independently on a "none–low–moderate–high" scale. Details about the entire framework, including attribute definitions, relevance of attributes to AC, relation of attributes to persist-in-place and shift-in-space pathways, scales of assessment, and evaluation and evidence criteria, are provided in WebTable 2.

Testing the applicability of the framework

We demonstrate the broad applicability of the AC framework by testing it on four groups of organisms with disparate life-history characteristics that offer distinct challenges for evaluating AC: (1) migratory species, (2) species with complex life cycles, (3) ectothermic vertebrate species, and (4) sessile species. To illustrate the diversity of AC assessment

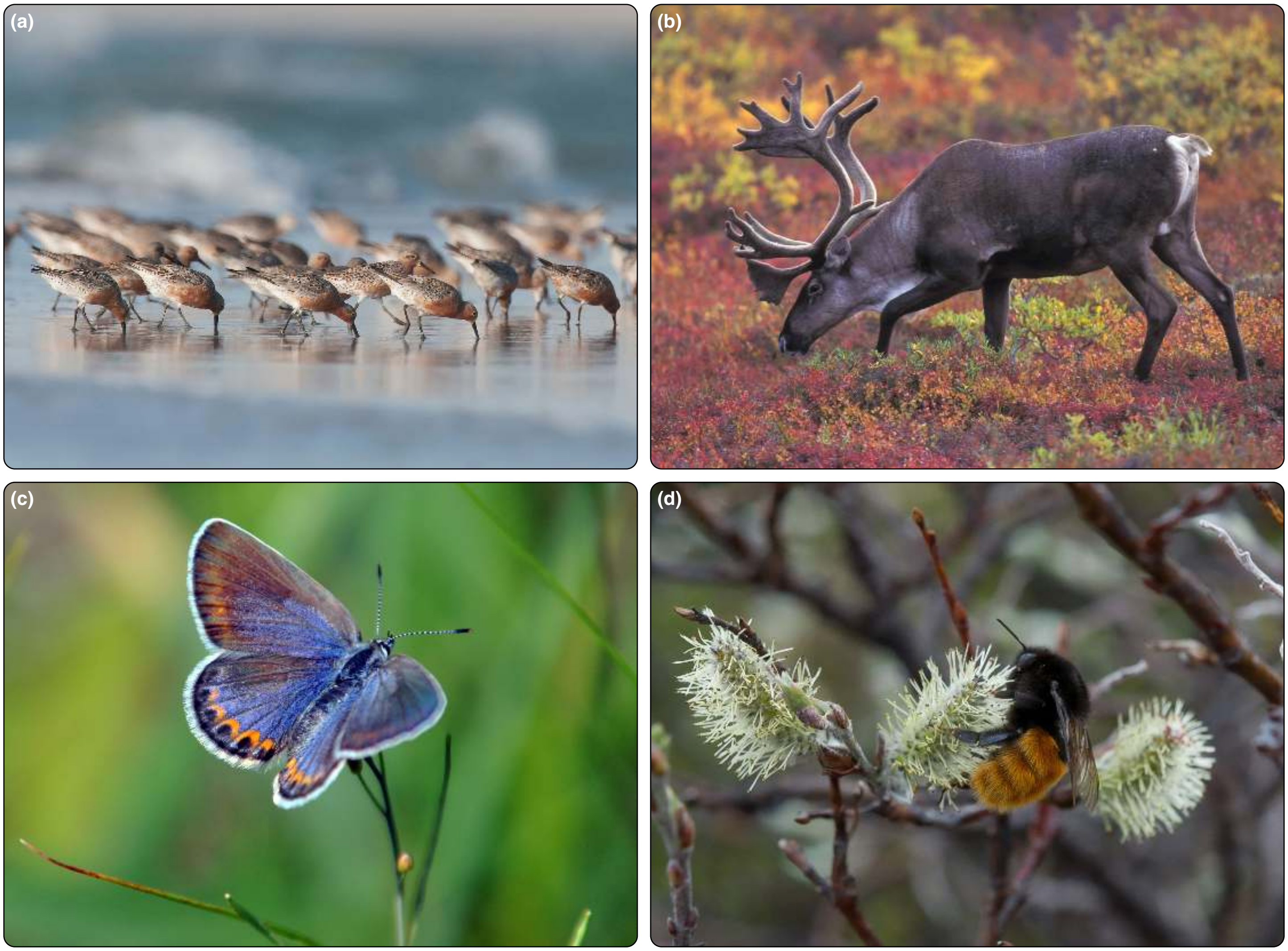

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Figure 2. Migratory species used in case-study assessments of AC: (a) rufa red knot (*Calidris canutus rufa*) and (b) Dolphin and Union barren-ground caribou (*Rangifer tarandus groenlandicus*). Species with complex life cycles used in case-study assessments of AC: (c) Karner blue butterfly (*Plebejus melissa samuelis*) and (d) alpine bumblebee (*Bombus alpinus*).

outcomes across each of these "functional" groups, we provide corresponding case studies.

Migratory species, such as the rufa red knot (*Calidris canutus rufa*) and Dolphin and Union barren-ground caribou (*Rangifer tarandus groenlandicus*), perform cyclical and predictable movements between separate areas, usually triggered by changes in local climate, resource availability, and seasonality, or for mating reasons (Figure 2). Species with complex life cycles, such as the Karner blue butterfly (*Plebejus melissa samuelis*) and alpine bumblebee (*Bombus alpinus*), have life histories that involve an abrupt ontogenetic (developmental) change in an individual's morphology, physiology, and/or behavior, usually associated with a change in habitat use. Species that undergo metamorphosis fall within in this group; examples include most insects, amphibians, and fishes. Ectothermic vertebrate species, such as the European eel (*Anguilla anguilla*) and red-eyed leaf frog (*Agalychnis callidryas*), do not rely on internal physiological sources of heat (ie metabolic processes) to control body temperature, which instead varies with external ambient temperature (Figure 3). To maintain internal body temperatures when conditions change, these organisms must move or behaviorally thermoregulate. Examples include reptiles, amphibians, and most fishes. Sessile species, such as the quiver tree (*Aloidendron dichotomum*) and ivory tree coral (*Oculina varicosa*), are organisms that are unable to move actively or spontaneously (are typically permanently attached) during the adult phase and can only move in response to outside forces, such as water or wind currents; commensal organisms would also qualify as sessile. Examples include aquatic and terrestrial plants, certain marine invertebrates (eg corals, anemones, barnacles, sponges), and freshwater organisms (eg mussels, hydra, certain crustaceans).

To demonstrate application of the framework, we evaluated the AC of two illustrative species from each of the four functional groups of organisms (species described in WebPanel 1). Visual depictions of the resulting AC assessments are

P Walker

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Figure 3. Ectothermic vertebrate species used in case-study assessments of AC: (a) European eel (*Anguilla anguilla*) and (b) red-eyed leaf frog (*Agalychnis callidryas*). Sessile species used in case-study assessments of AC: (c) quiver tree (*Aloidendron dichotomum*) and (d) ivory tree coral (*Oculina varicosa*).

presented in Figures 4 and 5, and the AC of each of the eight species is summarized in WebFigure 1. These examples span a broad range of geographies, taxonomic classifications, conservation statuses, and management contexts. Each of these assessments was independently reviewed by one or more external experts. Details of each assessment, including expert reviewer contributions, are provided in WebTable 3. We showcase a diversity of species with a range of AC, as well as situations in which species may have deal-breaker versus deal-maker attributes, and examples in which practitioners may be faced with limited data availability.

Species with a majority of attributes indicating higher levels of AC, such as the red-eyed leaf frog and quiver tree, can be considered to have greater AC overall. Conversely, species with more attributes exhibiting lower levels of AC, like the Dolphin and Union barren-ground caribou, can be regarded as possessing lower AC overall. However, numerous factors can influence the contribution of attributes to the overall AC of a species. Indeed, one or more attributes may exert exceptional influence on overall AC (positively or negatively) and be regarded as deal makers or, perhaps more commonly, deal breakers. The alpine bumblebee, for example, has a flexible diet, disperses well, and has high fecundity – all characteristics of high AC – but its intolerance of prolonged hot spells greatly reduces its overall AC. Because of this single limitation (or deal-breaker attribute), it will be difficult for the bee to sustain populations under either the persist-in-place or shift-in-space response pathway, and the species therefore may be considered to have low overall AC.

Similarly, for organisms that operate at physiological extremes, such as the rufa red knot, high-energy or high-volume food resources are critical. The rufa population's reliance on eggs of the horseshoe crab (*Limulus polyphemus*) for food at a key stopover during its long-distance migration demonstrates a narrow trophic niche (both spatiotemporally and with respect to the target resource) and may indicate niche conservatism, even under the evolutionary pressure of climate change. In contrast, the European eel has a broad diet,

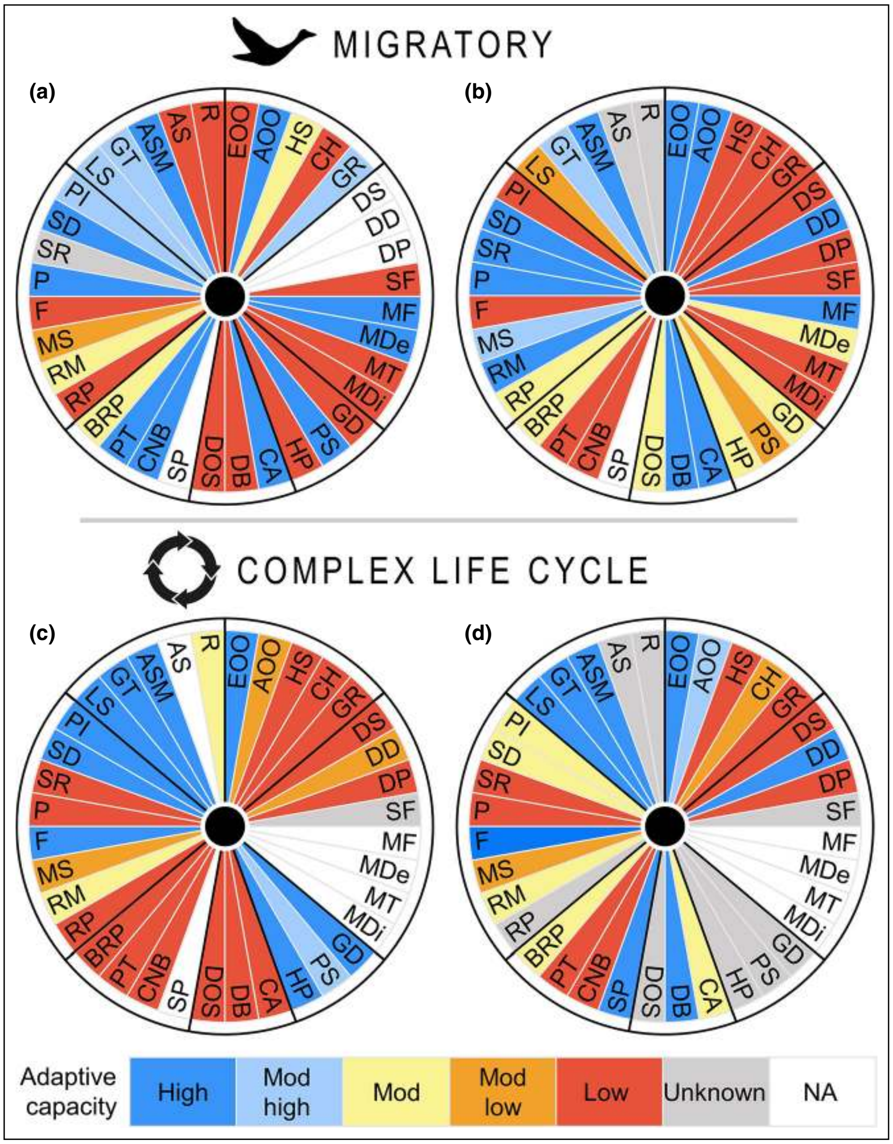

Figure 4. Assessments of AC for four species, illustrating each of two functional groups. Migratory species: (a) rufa red knot and (b) Dolphin and Union barren-ground caribou. Species with complex life cycles: (c) Karner blue butterfly and (d) alpine bumblebee. Colors of wheel "spokes" reflect the relative level of AC: low AC = red, moderate = yellow (with two subcategories: moderately low = orange, moderately high = light blue), high = dark blue. Spokes in gray indicate attributes for which AC is unknown, while spokes in white indicate attributes not applicable (NA) to a particular species. Attributes are defined in WebTable 2; abbreviations of attributes are spelled out in Figure 1.

consuming both invertebrates and vertebrates, including terrestrial fauna. This wide trophic niche provides greater options for tracking or shifting food resources under climate change, increasing the AC of the species or population (ie a deal maker).

The availability, quality, and consistency of input information (ie evidence) should also be considered when evaluating the resulting assessment of AC. For example, there is little information available about the natural history and ecology of ivory tree coral outside of the Oculina Bank region, a strip of coral reefs off the east coast of Florida. Moreover, values for some AC attributes had to be inferred from empirical studies on a related species, *Oculina arbuscula*. These informational limitations should therefore be considered in the interpretation of this assessment, but can also be used to inform and target future research needs. Conversely, the Karner blue butterfly has been well-studied due to its listing under the US Endangered Species Act and widespread population recovery and monitoring efforts. Given this extensive evidence base, we have relatively high confidence in the resulting AC assessment, which indicates low overall AC for this species.

Using AC to improve conservation outcomes

A detailed understanding of AC, as provided through this new framework, directly supports effective climate-adaptation planning and climate-smart conservation. For example, AC assessments can help establish management and policy priorities by differentiating those species presently capable of autonomously coping with or adjusting to projected changes from those that may require targeted attention or active intervention. Beyond helping to set priorities, the attribute-based framework provides a methodology for developing appropriate and relevant adaptation strategies. Because climate adaptation generally is defined as a means to reduce climate-related vulnerabilities and risks (or capitalize on potential benefits), explicitly linking strategies and actions to projected climate impacts is an overarching principle of climate-smart conservation (Stein *et al.* 2014). One approach for making such an explicit link is to use the components of vulnerability in considering actions capable of reducing exposure, reducing sensitivity, or enhancing AC. Indeed, "building adaptive capacity" figures prominently in a recently proposed typology of adaptation options (Prober *et al.* 2019).

In practice, identifying strategies to enhance the AC of species is challenging. By distinguishing relative AC levels for different attributes and across attribute complexes (Figure 1), our framework helps to match a species' AC profile with meaningful adaptation strategies and actions. For example, although improving habitat connectivity is a popular and widely invoked adaptation strategy, this may not be so relevant for species with low capacity in the "movement" attribute complex. In instances where the existing locales for such species are projected to become climatically unsuitable, managers may need to consider more intensive interventions, such as managed relocations (Lawler and Olden 2011). Likewise, if a species has low capacity in the "evolutionary potential" attribute complex, relevant responses may involve genetic or population augmentation, or other mechanisms designed to increase genetic diversity to facilitate evolutionary processes. Furthermore, certain AC attributes may be particularly relevant for tailoring interventions to buffer populations from losses during extreme events, such as heat waves, droughts, or floods. For example, Ameca y Juárez *et al.* (2014) identified four traits of herbivorous mammals that increase AC to extreme events, which reflect similar AC attributes in this framework that optimize population size, geographic extent, and competitive and movement abilities. The graphic depiction of relative AC across the full array of attributes (Figures 4 and 5), including identification of deal breakers, offers managers a powerful tool for tailoring strategies to the specific AC profile or climate-change exposure of a given species, and identifying strategies with the greatest potential to reduce vulnerabilities by enhancing AC.

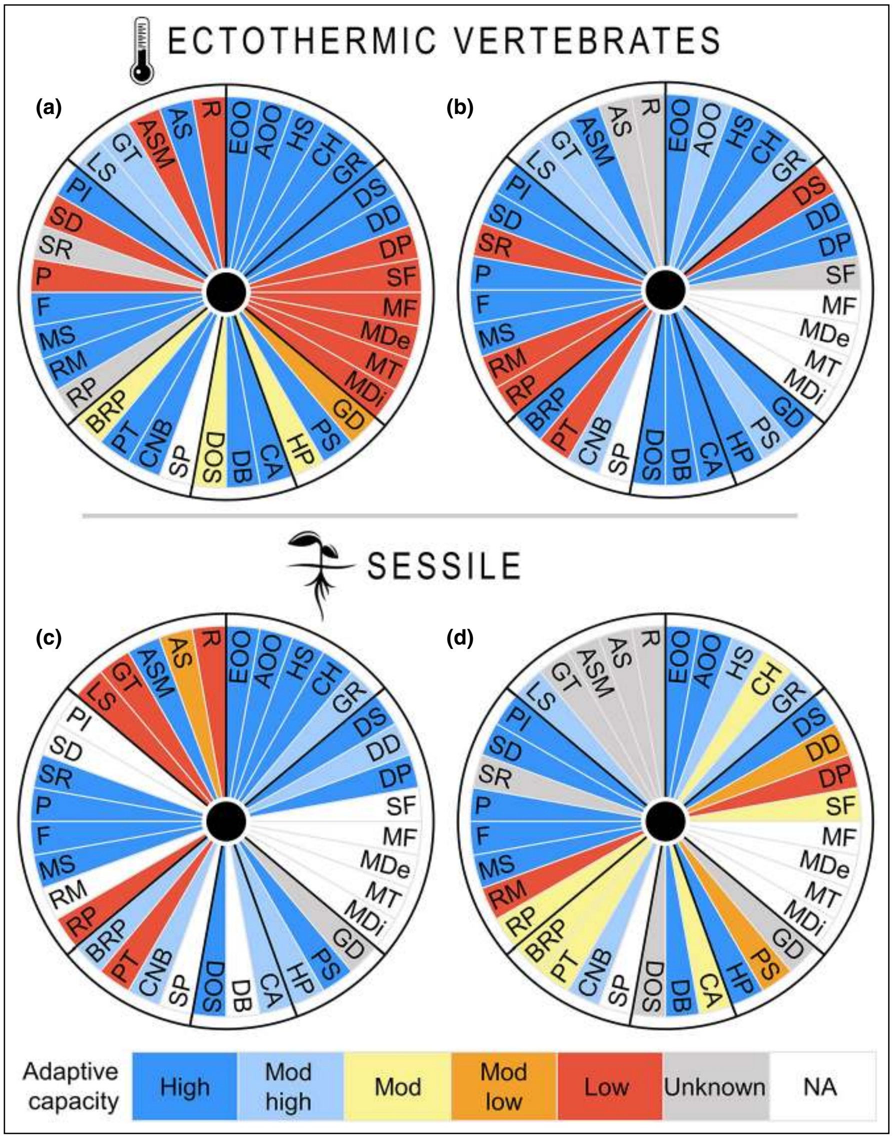

Figure 5. Assessments of AC for four species, illustrating each of two functional groups. Ectothermic vertebrate species: (a) European eel and (b) red-eyed leaf frog. Sessile species: (c) quiver tree and (d) ivory tree coral. Colors of wheel "spokes" match those described in Figure 4. Attributes are defined in WebTable 2; abbreviations of attributes are spelled out in Figure 1.

This new AC framework can also assist planners in setting climate-informed conservation goals, and specifically to determine when persistence-oriented goals continue to be appropriate, or when to set goals that accept or even facilitate ecological transformation (ie systems that deviate markedly from prior ecosystem composition, structure, or function). For example, an evaluation of AC may suggest that tree species in a given forest are capable of persisting in the face of climate-related disturbances, such as increased drought and high-severity wildfires. In this case, forest managers might emphasize the use of existing species and locally derived seed sources in restoration efforts. In cases where contemporary and projected disturbances are likely to exceed the AC of existing tree species, it may be worth intentionally transitioning the system to species or genotypes better capable of surviving under future climatic conditions. The detailed understanding of AC that derives from this new framework can help planners prepare for what has been termed "achievable future conditions" (Golladay *et al.* 2016) and craft climate-informed conservation goals. This in turn can inform decisions regarding when, where, and for how long persistence-oriented strategies may be appropriate to employ, and when a shift in focus to change-oriented goals and strategies is necessary (Stein *et al.* 2014).

Caveats for use of the framework

After testing and application, our generalized framework for operationalizing the concept of AC was robust across disparate groups of organisms and systems. However, there are several caveats and limitations not only to the use of the framework but also more generally to the concept of AC itself. These include existing knowledge gaps for certain species, challenges in recognizing the relative contribution of different attributes, issues in summarizing overall AC, and lingering ambiguity in the relationship between AC and species sensitivity.

Lack of information

The framework was designed to accommodate varying levels of input data. Nonetheless, available scientific information that can serve as an input to AC assessments can vary markedly across groups of organisms and geographic regions. This problem is not unique to this AC framework, and many other assessment protocols (eg IUCN Red List of Threatened Species) specifically recognize the issue of data-deficient species (IUCN 2012). As noted previously, we identify 12 "core" attributes that cover the full range of attribute complexes, and represent attributes for which information is often available either directly or through inference even for poorly known species. To provide transparency in the evaluation process regarding availability and quality of information, however, the framework includes a system for evaluating and scoring the strength of evidence for each assessment.

Relative contribution of attributes

Various attributes and attribute complexes will contribute differentially to the AC of different species, and possibly even the same species in different ecological or geographic settings. For example, dispersal-related attributes may be more important to AC in populations at the leading edge versus trailing edge of the range boundary of a species. The framework does not, however, attempt to weight the relative contribution of different attributes; rather, it implicitly assumes an equal contribution from each attribute. In addition, although we highlight the importance of identifying possible deal-breaker or deal-maker attributes, in practice recognizing these may prove challenging. Much also remains to be learned about how AC manifests itself in different taxonomic groups and ecological contexts, whether it is phylogenetically conserved, and if it changes over time.

Conveying overall AC

Although we recognize the desire by some for a single overall metric of AC, either quantitative or categorical, no satisfactory algorithm for calculating such a metric has yet emerged. Indeed, the broader utility of this framework is to provide practitioners with a deeper understanding of and appreciation for the factors underlying a species' AC (or lack thereof) rather than through production of a simple numeric or categorical rating. The value in assessing AC (and climate vulnerability more broadly) is not just in determining which species have high or low AC or are climate vulnerable, but also in understanding why they do. Insights revealed by understanding the underlying basis for a species' AC are the key to designing effective adaptation strategies and actions.

Relationship to sensitivity

As noted previously, most vulnerability assessments for ecological resources rely on the three-component CCVA framework of exposure, sensitivity, and AC. There has been long-standing confusion between the concepts of AC and sensitivity; the terms are frequently used interchangeably, and decisions on when to use one or the other term are often made arbitrarily. For example, Gardali *et al.* (2012) explicitly omitted AC in their CCVA "because of the inherent difficulties in scoring adaptive capacity", and therefore relied on several components of sensitivity as indirect measures of AC. Similarly, Williams *et al.* (2008) defined vulnerability as a function of sensitivity (mediated by AC and resiliency) and exposure to climate change. There are also concerns that the three-part vulnerability framework may actually constrain understanding and use of the concept of AC (Fortini and Schubert 2017). Indeed, although numerous attempts have been made to disentangle the definitions of AC and sensitivity (reviewed in WebTable 4), these have not resulted in clear and broadly accepted boundaries.

Our focus here is on AC as a stand-alone concept, and rather than attempt to delineate an artificial boundary between the two concepts, we take an expansive view of AC as the capacity of a species to persist by coping with or adjusting to changing climatic conditions. More narrowly drawn definitions of AC sometimes focus on adjustment aspects, whereas many definitions of sensitivity emphasize coping abilities (or lack thereof) based on existing tolerances and thresholds. Core attributes of AC, as defined here (Figure 1), that are often associated with sensitivity include habitat specialization, physiological tolerances, and diet breadth, while those linked to narrowly drawn definitions of AC include dispersal distance, genetic diversity, population size, and fecundity. The detailed attribute descriptions, methods of evaluation, and suggested thresholds offered in WebTable 2 should prove useful even in vulnerability assessments where a given attribute is treated as an element of sensitivity.

Rising to the adaptation challenge

Climate change is emerging as the conservation and natural-resource–use challenge of our time, yet many managers remain apprehensive about how to address climate considerations in species and ecosystem management. To overcome that challenge, we believe that the science underlying effective climate adaptation must be advanced, and that actionable tools and techniques must be provided to practitioners to realize climate-smart conservation. Understanding the ability of a species to cope with or adjust to changing climatic conditions – its "adaptive capacity" – is key to the design and implementation of effective adaptation strategies, but to date the concept has been difficult to operationalize. Although much remains to be learned about how different species may respond to changing conditions, the attribute-based framework we offer represents a tangible way for conservation and natural-resource practitioners to more consistently apply the concept of AC as they prepare for and adapt to a changing climate.

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Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2253/suppinfo