Received: 10 September 2020 | Accepted: 16 February 2021

DOI: 10.1111/gcb.15579

Global Change Biology WILEY

RESEARCH REVIEW

Building a bridge between adaptive capacity and adaptive potential to understand responses to environmental change

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Funding information
National Science Foundation, Grant/Award Number: OIA-1757324

Abstract

Adaptive capacity is a topic at the forefront of environmental change research with roots in both social, ecological, and evolutionary science. It is closely related to the evolutionary biology concept of adaptive potential. In this systematic literature review, we: (1) summarize the history of these topics and related fields; (2) assess relationship(s) between the concepts among disciplines and the use of the terms in climate change research, and evaluate methodologies, metrics, taxa biases, and the geographic scale of studies; and (3) provide a synthetic conceptual framework to clarify concepts. Bibliometric analyses revealed the terms have been used most frequently in conservation and evolutionary biology journals, respectively. There has been a greater growth in studies of adaptive potential than adaptive capacity since 2001, but a greater geographical extent of adaptive capacity studies. Few studies include both, and use is often superficial. Our synthesis considers adaptive potential as one process contributing to adaptive capacity of complex systems, notes "sociological" adaptive capacity definitions include actions aimed at desired outcome (i.e., policies) as a system driver whereas "biological" definitions exclude such drivers, and suggests models of adaptive capacity require integration of evolutionary and social–ecological system components.

KEYWORDS
adaptive capacity, adaptive potential, climate change, conservation, ecological systems, environmental change, social, systematic review

1 | INTRODUCTION

Adaptive capacity is currently a topic at the forefront of biological research due to current, rapid, and anthropogenically derived environmental change. As defined by the IPCC, adaptive capacity is the "ability of systems, institutions, humans, and other organisms to adjust to potential damage, take advantage of opportunities, or to respond to consequences." This definition draws heavily from social–ecological systems (SES) research (Fazey et al., 2007; Walker et al., 2004), which includes coupling of human and ecological systems and can include a teleological component (i.e., relating to actions of the human mind or to a purposeful outcome; Mayr, 1998). In contrast, the term is also often applied to biological systems, including ecosystems (Angeler et al., 2019), where a role for teleological processes has been generally rejected. The IPCC definition also draws heavily from the ecological concepts of resistance and resilience (Holling, 1973; Peterson et al., 1998). Notably, adaptive capacity is often excluded from climate change vulnerability assessments due to logistic constraints, even though its inclusion may affect estimates of vulnerability (Ofori et al., 2017). Adaptive capacity definitions across the literature variously include ecological components of dispersal, phenotypic plasticity, and adaptation (Nicotra et al., 2015; Thurman et al., 2020) and invoke niche concepts (e.g., Holt, 2009). Recent definitions of adaptive capacity from the ecological literature specifically address responses to environmental change, such as "the ability of a species or population to cope with climate changes and is characterized by… phenotypic plasticity, dispersal ability, and genetic diversity" (Beever et al., 2016). Thus, past definitions vary in breadth, focusing on ecological processes within "natural systems," definitions considering the effects of environmental change on ecological populations (most frequently climate change), and broader definitions which include the influence of human impacts on adaptive potential of "natural systems" and feedbacks via adaptation within human systems. Because of the variation in definitions, there have been some arguments against using it (Fortini & Schubert, 2017). Consequently, we suggest "biological" definitions of adaptive capacity can be conceived as a subset of broader definitions that include SES factors (Figure 1).

Clarifying definitions and concepts will require connections with SES research to better understand future anthropogenic change. For example, the requirements for societal adaptive capacity can be described as the societal traits necessary for successful adaptation to environmental change. These societal traits include the willingness and intention to respond to change, possession of knowledge about anticipated adaptive change, adoption of proactive behavior, and the ability to modify existing behavior (Fazey et al., 2007). A subset of these (willingness to respond and ability to change) equate to the capacity of societies to enact changes in traits in response to changing environmental conditions, that is, societal adaptive potential. This, by definition, includes a teleological component (purposeful intent toward an outcome), in contrast to so-called natural systems where such intent does not exist. Strong feedbacks are also likely whereby, for example, information on the status of ecosystems and ecosystem services affects human social processes.

Adaptive potential can be considered a component of biological adaptive capacity as defined above. Adaptive potential is a concept from evolutionary biology that predates adaptive capacity and has strong parallels with the concept of evolvability (e.g., Brookfield, 2009; Kirschner & Gerhart, 1998). Notably, two primary processes contribute to adaptive potential acting at different time scales: mutation and standing genetic variance. The former is key to the generation of novel traits, often through changes in regulatory or developmental processes and evolutionary potential itself may be under selection (Kirschner & Gerhart, 1998). However, the original definition from Fieher (1922) as additive genetic variance related to fitness continues to be used today (e.g., Mittell et al., 2015). The widespread use of adaptive potential in the conservation literature emerged in the 1990s with the emergence of conservation genetics (Franklin & Frankham, 1998) and has been discussed for species in a wide variety of conservation goals (La Haye et al., 2017). This also parallels research in evolutionary biology, such as work on mutation and effective population size by Lande (1995). More recent use and definitions of adaptive potential include Funk et al.,'s (2019) "Capacity to evolve genetically-based changes in traits in

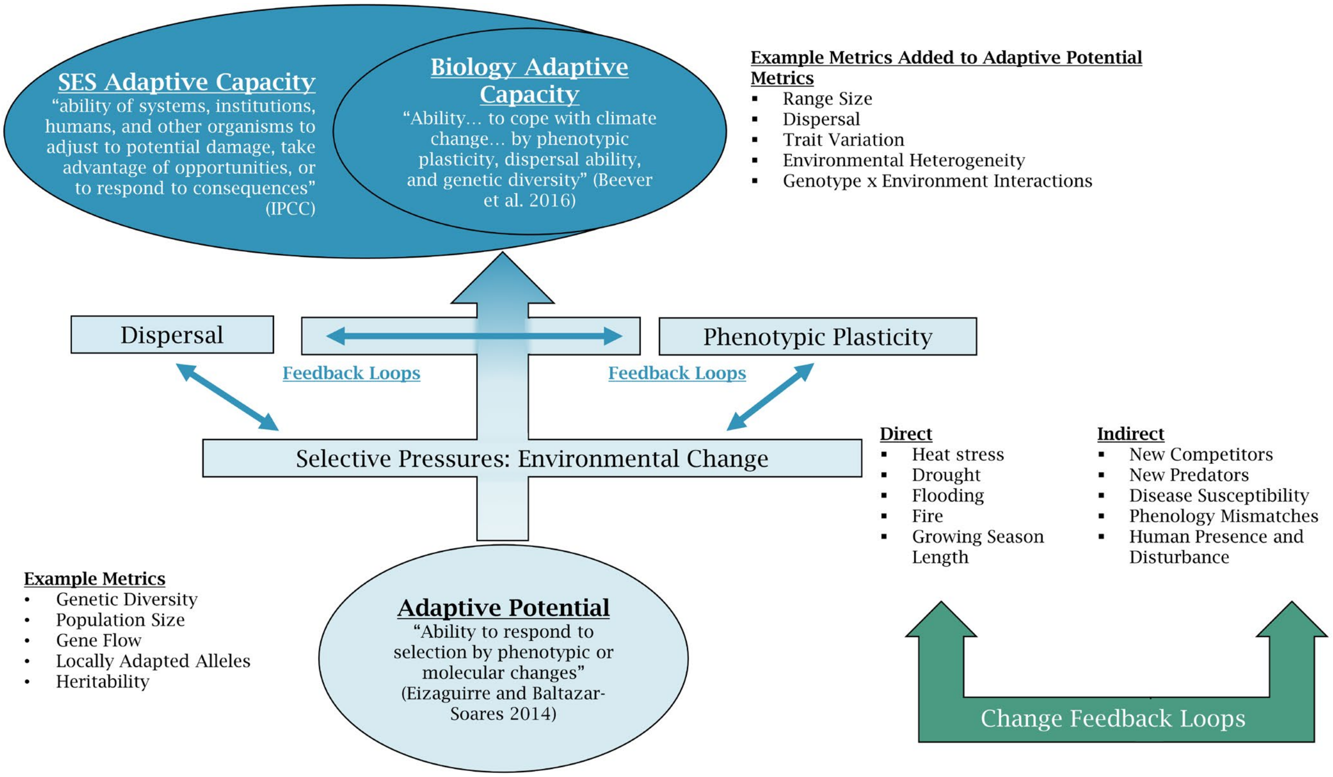

FIGURE 1 Conceptual diagram hierarchically linking adaptive capacity and adaptive potential, terms broadly linked with conservation biology and evolutionary biology, respectively. Adaptive capacity concepts integrate adaptive potential with regards to environmental change, plasticity, and dispersal processes while accounting for feedback loops of potential selective pressures. Adaptive capacity definitions also focus on climate change, but that varies by researcher. Here, feedback loops designate processes that may interact with each other to change local environments in the system environment or adaptive capacity of populations in those locations. SES, social-ecological systems, which incorporates both the biological and social components [Colour figure can be viewed at wileyonlinelibrary.com]

response to changing environmental conditions" and Eizaguirre and Baltazar-Soares's (2014) "ability of species/populations to respond to selection by means of phenotypic or molecular changes." Thus, adaptive potential research has emphasized the genetic basis of phenotypes and the ability of a species to persist through evolution of genetically based phenotypes, sometimes referred to as adapt-in-place in more recent literature. This also ties to the expansion, or conversely conservatism, of the fundamental niche space of a species (Wiens & Graham, 2005). Adaptive potential is closely related or synonymous to other terms including "evolvability" (Brookfield, 2009). Brookfield's (2009) general definition of the "ability of populations to evolve in an adaptive way" draws parallels with some definitions of adaptive potential, but not in all cases. Evolvability also has been tied to robustness—the ability of a species to achieve increased fitness in some environments—which begins to parallel some definitions of adaptive capacity as the biological scale moves to higher levels (but see Brookfield, 2009 for variations in definitions of robustness). In other words, adaptive potential may be thought of as the ability of a species to evolve in the future when conditions change. Thus, like adaptive capacity, the history of use of adaptive potential by researchers is complex and not completely resolved. Hence, we encourage authors to explicitly identify underlying mechanisms when possible for conceptual and operational reasons. For example, the standing genetic diversity component is more likely to contribute to adaptive potential than mutational processes at time scales relevant to anthropogenic environmental change for most species. Regardless, clarifying definitions and underlying processes relates directly to the effective selection of metrics of adaptive capacity.

One challenge in using either of these terms lies in the various ways that researchers use the term "adaptive" and the different approaches researchers take to understand the fitness of a population. These discussions have occurred when comparing the fields of adaptive dynamics and population genetics (Kokko, 2005), and some of the same issues arise when considering these two terms. One challenge is the "adaptive" part of terms actually has three broad sets of definitions because of the history of use of the terms adaptive capacity and adaptive potential, ranging from evolutionary applications focusing on the matching of biological traits to the environment among individuals and within populations, to ecological and systems theory concepts applied to higher scales of organization (communities, ecosystems), and to SES definitions that focus on the ability of a system to change and maintain ability to support human well-being or other specific human-centric outcomes (e.g., the IPCC definition). An instructive example within evolutionary ecology is the concept of "evolutionary suicide" whereby selection can drive the evolution of traits conferring relatively higher fitness for those individuals possessing those "adaptations" compared to others in the population, but those same traits cause a mismatch with the broader environment, reduced average fitness, population decline and extinction. Clearly, in the context of conservation, "adaptation" refers to factors increasing average fitness. Notably, because of the variety of definitions, underlying assumptions and scales applied to "adaptive," "capacity," and to a lesser extent "potential," the terms can become too broad to rigorously assess and measure.

Both adaptive capacity and adaptive potential incorporate the goals of evolutionary conservation (Eizaguirre & Baltazar-Soares, 2014) and it is important to understand the history of adaptive potential (as reviewed by Mable, 2019) to properly integrate it with concepts of adaptive capacity. We suggest adaptive potential is one of three primary components of adaptive capacity (Figure 1), recognizing strict partitioning of the terms is not accurate. For instance, other components of adaptive capacity such as the expression of phenotypic plasticity and dispersal may contribute to adaptive capacity and also influence adaptive potential via eco-evolutionary feedback loops. Specifically, the evolution of the reaction norms of a trait may change the breadth of phenotypic plasticity, but the range of phenotypic plasticity may also influence the future change of those reaction norms (Oostra et al., 2018; Senner et al., 2018). In these cases, feedback loops describe processes and their outcomes which influence other processes and outcomes, such as dispersal influencing the selective pressure experienced by a species and the environmental change then also shifting the patterns and physiological constraints of dispersal. Together, movement, plasticity, adaptation, and the feedback with SES may or may not buffer populations or allow ranges to shift, and such nonlinearities may be key system drivers and are also problematic for assessments using climate envelope approaches (Valladares et al., 2014; Whitney et al., 2017).

The study of adaptation as a response to climate is a broad and interdisciplinary field (Adger & Vincent, 2005; Brooke, 2008) and future research collaboration will benefit from better understanding the use of these terms and how they may be integrated. Applying a hierarchical framework with adaptive potential as a component of adaptive capacity (Figure 1), the range, relationships, and connections among fields are clarified. Moreover, the framework highlights another potential difference of the terms and fields: adaptive capacity applies to research across a larger number of disciplines and typically at broader spatial scales (e.g., single population vs. range-wide). For example, adaptive capacity can be applied to ecosystems, but adaptive potential cannot if using classic definitions as adaptive potential is considered a trait of a population.

To better understand adaptive capacity and adaptive potential, we: (1) summarize the history and use of each term; (2) assess and compare methodologies, metrics, taxa biases, climate change focus, and geographic scale of studies used in adaptive capacity and adaptive potential research; and (3) present refined definitions of the two concepts in an attempt to bridge conservation ecological, evolutionary biological, and SES research. We used a systematic literature review to compare use of the terms "adaptive capacity" and "adaptive potential" through the lens of conservation to address these first two goals.

2 | BIBLIOGRAPHIC AND SYSTEMATIC LITERATURE REVIEW METHODS

We conducted a literature review following methods of Lortie and Bonte (2016) and others with the Topic Search topics "adaptive capacity" or "adaptive potential" and with the Topic Search "conservation" through Web of Science in August 2019 (string: "adaptive capacity" OR "adaptive potential" AND "conservation"). Topic searches include titles, keywords, abstracts, and the Web of Science assigned "keywords plus." We followed the preferred reporting items for systematic reviews and meta-analyses (PRISMA) format, including number of papers removed at each step (Moher et al., 2010; Figure S1). Of note, the earliest paper returned was from 2001. This likely occurred because of the additional topic "conservation," because both "adaptive capacity" and "adaptive potential" were used prior to 2001. We chose to include the topic conservation as a unifying field to maximize shared research goals and understand potential collaborative efforts across biological fields and methodologies. Although these search methods may not have produced a completely exhaustive list, they did provide a representative sample of the literature related to conservation broadly defined. After obtaining our original search results, we used the refine tool to remove non-biology topics and review papers, news articles, books, and symposium papers. Articles were categorized by year published, number of times the term was used, taxa studied, and methodologies used. During this process, we also removed articles not focused on conservation or social science by reading each paper or the paper's abstract. In addition, we estimated the geographic range of each study by creating a box around the study points and estimating either directly on maps provided by the authors or by importing locality data or study site maps into ArcGIS Pro (ESRI, 2020).

3 | PUBLICATION AND TOPIC PATTERNS REVEAL DISJOINTED FIELDS

In general, adaptive capacity and adaptive potential publications have been increasing between 2001 and 2019 (Figure 2a). Only 15 papers used both terms. The articles using adaptive capacity and/or adaptive potential were spread across a wide range of journal titles and were rarely repeated within the same journal. This highlighted the diversity of research disciplines and publication targets related to the terms. The top 10 journals by count of number of publications showed low numbers of articles within the same journal and minimal crossover among the terms (Table 1), revealing a coherent literature has not coalesced within a journal or set of journals. The top journals reflected that adaptive capacity has been primarily used by conservation ecologists, while adaptive potential has been used primarily by evolutionary biologists. When looking at top journals, the overall proportion of papers remained relatively consistent through the sample period, with only adaptive potential showing a positive trend (Figure 2b). We excluded Scientific Reports and PLOS One from analyses of proportions because these two journals had orders of magnitude higher number of articles published across a range of disciplines (mean 5000 for all journals across disciplines, *N* = 199,792 and 362,198, Scientific Reports and PLOS One, respectively). Most articles used either term infrequently across the paper and its abstract (Figure 3; mode = 1; median = 4, 2, and 3 for AC, AP, and Both, respectively), indicating the concepts were not the primary focus of the studies. Articles including adaptive capacity were associated with the term climate change 63% of the time whereas adaptive potential papers focused on climate change in 8.6% of the sample, potentially reflecting generally broader definitions of adaptive capacity, explicit linkage of adaptive capacity to climate change in the

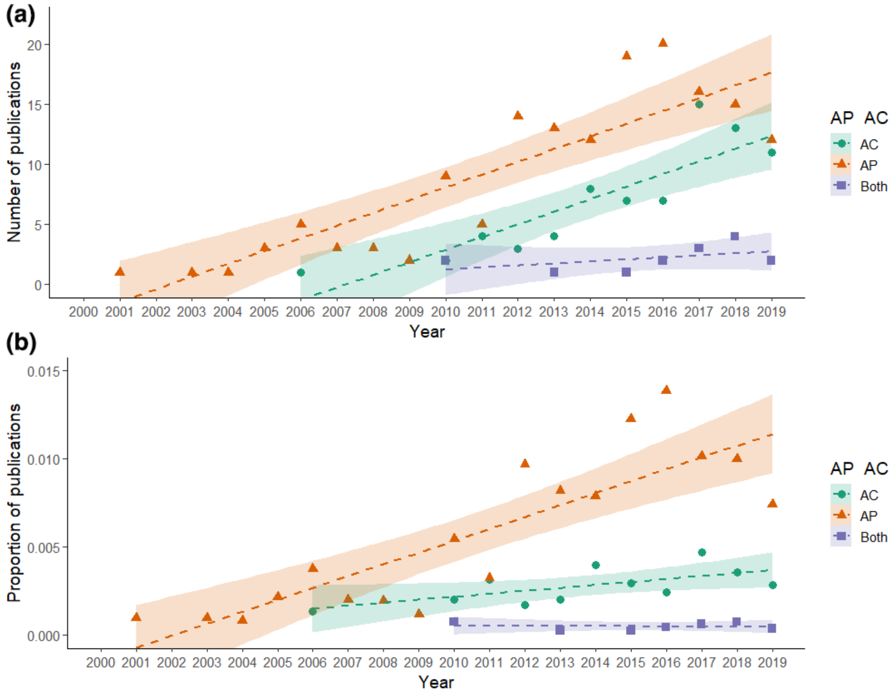

FIGURE 2 (a) Raw count and (b) proportion of publications using the terms "conservation" and "adaptive potential" (AP, *N* = 150) or "adaptive capacity" (AC, *N* = 73) or both terms (*N* = 15) through time. Proportion was calculated as total number of papers from the search divided by the total number of papers published in the 10 most frequent journals for each term (excluding *PLoS ONE*) [Colour figure can be viewed at wileyonlinelibrary.com]

IPCC assessments starting from the second report, and inclusion of social and SES elements in past definitions of adaptive capacity. However, the use of adaptive capacity by the IPCC across the assessments did not lead to any notable spikes in use of the term when a new assessment was released (Figure 2). The higher use of adaptive capacity in climate change studies may also explain the larger geographic scope of studies citing adaptive capacity compared to adaptive potential (Figure 4). This difference in geographic scope is also likely due to the biological scale these terms attempt to describe. Adaptive potential was often considered as an attribute of a population, whereas adaptive capacity was most often applied to the individual species. We note some evidence of integration among adaptive capacity and adaptive potential research when environmental change was the focus of the research, because a slight majority of papers using both terms (eight of 15 papers) were focused on climate change.

TABLE 1 Counts of the number of publications during the study period for the 10 most frequent journals

Term			
Adaptive capacity		**Adaptive potential**	
Journal	**Number**	**Journal**	**Number**
Global Change Biology	6	*Conservation Genetics*	21
PLOS One	5	*Evolutionary Applications*	10
Ecology and Evolution	4	*Biological Conservation*	7
Ecosphere	4	*Molecular Ecology*	7
Climatic Change	3	*Ecology and Evolution*	6
Diversity and Distributions	3	*PLOS One*	6
Global Ecology and Conservation	3	*Journal of Heredity*	5
Scientific Reports	3	*Conservation Biology*	4
Biodiversity and Conservation	2	*Animal Conservation*	3
Ecological Indicators	2	*Heredity*	3

4 | COMPARISON OF ADAPTIVE CAPACITY AND ADAPTIVE POTENTIAL RESEARCH

4.1 | Research system

Most papers focused on the species. Although this aligns with the definition of adaptive potential, some adaptive capacity papers focused above species (e.g., ecosystem). There were no clear differences in composition of study taxa between adaptive potential and adaptive capacity (Figure S2), with the exception of a higher number of studies on ecotypes or species assemblages for adaptive capacity, generally consistent with a focus on traits or phenotypes within adaptive capacity research. Regardless, the intraspecific focus of research on both topics may miss important components in some systems because adaptive genetic variants may cross species boundaries through hybridization (Hamilton & Miller, 2016) and eco-evolutionary dynamics between species can affect population viability (Hendry, 2016). Focus on ecotypes or ecosystems was rare and used metrics similar to species-level studies. For

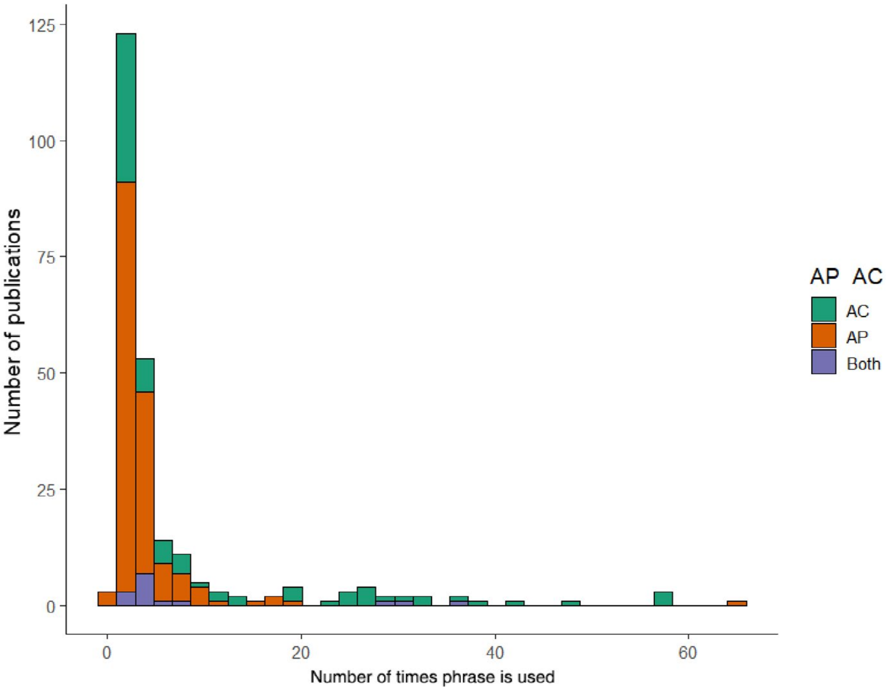

FIGURE 3 Stacked histogram of the number of times the phrases "adaptive capacity" (AC) or "adaptive potential" (AP) or both were used by each paper. Publications with zero use of the word are papers which only used the term in their key words [Colour figure can be viewed at wileyonlinelibrary.com]

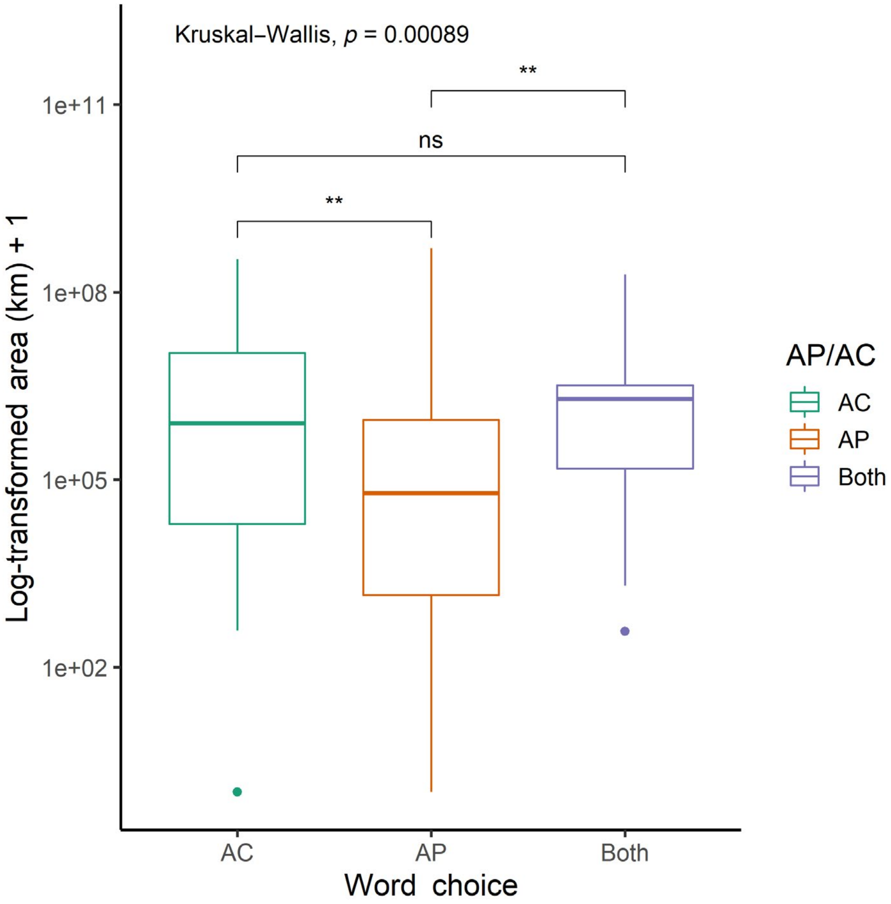

FIGURE 4 Boxplot of rough estimated geographic scale of the research by the term of either adaptive capacity (AC) or adaptive potential (AP) or both [Colour figure can be viewed at wileyonlinelibrary.com]

example, range size and expected exposure to changing temperature has been applied to ecosystems (Virah-Sawmy et al., 2016). Often ecosystem or habitat category approaches were found within SES research (e.g., Gunderson et al., 2014; Whitney et al., 2017) perhaps because the term adaptive capacity stems from ecosystem resilience and systems research (as reviewed in Angeler et al., 2019).

4.2 | Metrics of adaptive potential and adaptive capacity

An ongoing challenge is identifying quantifiable metrics for either adaptive potential or capacity. The most frequent single metrics in past research have been phenotypic variation, range size, and neutral genetic diversity. Encouragingly, studies often incorporate more than one metric, and our analysis found a large overlap between adaptive capacity and adaptive potential metrics (Figure S3). One common theme is the need for interdisciplinary research to properly address assessments of adaptive capacity, and the need has been reviewed previously (e.g., Nicotra et al., 2015). We provide a very brief overview of the metrics used in both adaptive potential and adaptive capacity research, considering the former a subset of the latter. Overall, the metrics focused explicitly or implicitly on components of fitness and many included potential for eco-evolutionary feedbacks.

4.2.1 | Genetic diversity

Increased genetic diversity supplies a larger range of phenotypes for selection to act upon, thus increasing adaptive potential. Estimation of genetic diversity is a well-established concept and has been reviewed previously, including linkages to the concepts of adaptive capacity and adaptive potential (Beever et al., 2016; Willi et al., 2006). Genetic monitoring may include adaptive and/or neutral variation, as defined by Holderegger et al., (2006), and generally, with neutral variation, many researchers operate under the assumption more genetic diversity is better. It had been argued that adaptive variation may be a more direct way to assess adaptive potential (Holderegger et al., 2006) because neutral variation might be a poor proxy for the capacity of a population to evolve in response to natural selection. Genomic data may continue to improve our understanding of adaptive potential (Aravanopoulos, 2016), specifically through the identification of adaptive variation as sequencing technologies continue to improve (Benestan et al., 2016; see Hohenlohe et al., 2019 for a review of examples). In more recent papers, authors used a combination of neutral and adaptive genetic diversity to better understand the adaptive potential of a species, and different inferences may result if only a single genetic data type is used (Eizaguirre & Baltazar-Soares, 2014; Prince et al., 2017). One important note is that multiple metrics of genetic diversity are used and specific methods of analyses with molecular data can impact estimates of adaptive potential, for example, heterozygosity versus allelic richness

(Vilas et al., 2015). There are also multiple assumptions when relating genetic data to the adaptive potential or capacity of a species, such as whether genetic variation is representative of phenotypic variation. Quantitative traits are poorly correlated with neutral genetic variation (Holderegger et al., 2006; Reed & Frankham, 2001), which is particularly true for life history and behavioral traits. In one meta-analysis, Mittell et al., (2015) found that molecular genetic diversity explained about 0.26 of the quantitative genetic variation. In contrast, selective sweeps may reduce overall genetic diversity by fixing regions of the genome beyond the genomic region where selection is occurring (Smith & Haigh, 1974). Lastly, an emerging concept is the use of genetic data and molecular dating to discuss the adaptive potential of a species based on how long it has been present as a metric of adaptive potential. In a rare example, Biersma et al., (2018) used molecular dating of the internal transcribed spacer region in *Schistidium mosses*, and highlight that adaptive potential is likely high in species which have occurred for multiple millions of years across varying climates. Such metrics may be more closely tied to mutation rate and genetic mechanisms generating novel traits over evolutionary time scales than within population genetic variance. With continued advances in sequencing and analysis methods, genomic data will be an important key to understanding neutral and adaptive genetic diversity and their relationship to fitness and population demography in rapidly changing environments.

4.2.2 | Phenotypic variation/trait assessment

Whereas genetic diversity is closely tied to adaptive potential, trait-based vulnerability assessments have a rich history for evaluating threats with climate change (see table 1 of Willis et al., 2015). Phenotypic variation and other trait-based assessments were slightly more common within adaptive capacity research. The focus of trait-based assessments often considered either (1) presence or absence of traits of interest; (2) plasticity (specifically gene by environment interactions); (3) or indirect measures focused on environmental heterogeneity. The general assumption has been that trait variation provides populations with the ability to persist under heterogenous environments, including when conditions move outside historical conditions (e.g., under climate change). In the first case, variation should be related to measures of genetic diversity whereas in the second case, genetically based norms of reaction can produce a greater degree of phenotypic variation than expected from genetic variation alone. For example, differences in phenotypic plasticity and reaction norms of hypoxia tolerance in salmon across populations indicate differences in adaptive potential (Côte et al., 2012). However, this is only true if the differences in reaction norms have some genetic basis and are not strictly controlled by the environment (e.g., maternal effects or early life experience). Under circumstances of complete environmental control, plastic responses and the capacity for adaptive evolution will not be linked. The timing and heritability of trait expression is also critically important, and phenology may also drive the success of a species (Olson et al., 2013). In some systems, fitness-related traits can have low heritability (Hendry et al., 2018; Rogell et al., 2010), which may slow the ability of a species to adapt when facing change. Degree of plasticity in traits is an important, but difficult to measure, factor affecting the ability of populations to persist with environmental change (Nicotra et al., 2015) and the underlying mechanisms and evolvability of plasticity are an active area of research. Environmental heterogeneity has been used as an indirect measure of trait variation because heterogeneity can cause adapted family lines which may influence population persistence (Huang et al., 2016). However, beyond the reasonable assumption that heterogeneity increases persistence, metrics of environmental heterogeneity are especially challenging to standardize and compare across taxa and systems.

4.2.3 | Connectivity

Adaptive potential, and thereby adaptive capacity, may be positively or negatively impacted by connectivity: gene flow can introduce adaptive genetic variation to a population or impede local adaptation. However, it is important to again consider eco-evolutionary feedbacks within the system. For example, evolution can alter the speed of species' range shifts and thus any attempts to estimate range shifts need to account for evolution (Miller et al., 2020; Nadeau & Urban, 2019). Our review revealed an array of methods for estimating connectivity, including telemetry, movement ecology modeling, and gene flow estimation. Modeling approaches included systems modeling and dispersal kernels (Bonte & Bafort, 2019; Summers et al., 2012). Gene flow estimates are well established in the literature for understanding connectivity, and were measured through landscape genetics approaches, which have been applied to other conservation questions, such as restoration (Kaus et al., 2019; Manel et al., 2003; Proft et al., 2018). Importantly, connectivity estimates are beholden to the assumptions of the genetic markers used and examples exist where neutral markers may show no population structure, but traits show clear local adaptation (Fjellheim et al., 2015). High connectivity will reduce the effects of drift, but may not always confer high adaptive capacity and adaptive potential either; more movement slows local adaptation with potential for outbreeding depression (Blanquart et al., 2012). In addition, different types of genetic variation can respond differently to habitat fragmentation (Young et al., 1996).

The influence of connectivity on adaptive capacity beyond metapopulation dynamics, range expansion, or increased adaptive potential is complicated because adaptive capacity encompasses a wider range of factors than adaptive potential, including SES factors. For example, connectivity may be important in maintaining ecosystem services flowing from biocomplexity, which can in turn affect social drivers on ecological systems. As an example, the biocomplexity of a large sockeye salmon metapopulation, including ecological traits such as timing of spawning, egg size, and energetic allocation play an important role in maintaining a large stable and highly regulated fishery in southeast Alaska (Hilborn et al., 2003; Schindler et al., 2010).

If this intraspecies variation is isolated, then the biocomplexity of a species may break down, resulting in less reliable fisheries returns and potential changes in fishing practices. Connectivity likely is also important to the portfolio effect, which establishes that the stability of a system is often greater than the individual parts and the covariance of those parts (Schindler et al., 2015). If connectivity is reduced, then the adaptive capacity of the population, species, or system will likely be reduced.

4.2.4 | Population dynamics and range size

Large population size, a large number of subpopulations, higher population growth rate, and larger range size are considered positive correlates with adaptive capacity (Wade et al., 2017). A positive relationship with adaptive potential is also generally, but not always, observed (reviewed by Hoffmann et al., 2017; Lanfear et al., 2014). Although models show support for higher adaptive potential in larger populations, empirical research is mixed (Willi et al., 2006). Population growth rate is likely important, as declining populations lose genetic variation, which may be important for persistence (Willi et al., 2006). In addition, the strength and form of density dependence may be important metrics for understanding population trajectories in changing environments because eco-evolutionary dynamics depend on the interactions of density, population growth rate, and selection (Catullo et al., 2015). Range size is often a proxy for total number of individuals of a species and may also be a metric for the degree of environmental heterogeneity currently experienced by a species. Distribution models have been used to estimate potential loss and gain in range size (Kubisch et al., 2013; Willis et al., 2015). In addition to range size, genetic variation across the range is an important consideration, as adaptive potential may be lower in certain areas of the range (Volis et al., 2014). Conversely, philopatry may conserve adaptive potential along range margins, highlighting interactions between dispersal and genetics (Stiebens et al., 2013) and may result in enhanced tracking of the local environmental conditions in dynamic landscapes through adaptation (Hendry & Stearns, 2004). In addition to population size and dynamics, generation time and fecundity within the populations are important, as shorter generation time and higher fecundity may result in increased adaptive potential, and consequently adaptive capacity (Catullo et al., 2015). Inbreeding and mating systems can reduce adaptive potential: complete hybridization with immigrants may not increase adaptive potential to theoretical levels (Swindell & Bouzat, 2006), but this is not always the case (Willi et al., 2006), and thus inbreeding may have positive or negative effects on adaptive capacity. Although a wide array of demographic metrics is possible, most papers focused on metrics such as population size that may be easier to estimate than parameters such as density-dependent population growth rates which may be more predictive of population trajectories. Understanding the trade-offs between ease of quantification and reliability among metrics is an important consideration because, for instance, a small census size may imply poor adaptive potential and capacity, whereas a large range at low density would indicate higher adaptive capacity for a given population size if the large range is a surrogate for physiological tolerances of the species.

4.3 | Comprehensive adaptive capacity assessments: A predictive and interdisciplinary endeavor

While reviewing the literature, we found a few robust estimates of adaptive capacity, which always required interdisciplinary research and generally included, at a minimum, proxies of adaptive potential. Using multiple metrics can help provide a holistic understanding less sensitive to individual metric assumptions, though factor selection or weighting can greatly change the vulnerability assessments of different species and it is important not to underestimate the sensitivity of the predictor inputs (Wade et al., 2017). Adaptive capacity assessments have combined metrics such as reproduction, movement, range, and niche breadth estimates (Butt & Gallagher, 2018) or combined genetic estimates of connectivity with predictions of range dynamics (Razgour et al., 2018).

One key part of many comprehensive assessments is the application of simulation modeling. Landscape resistance models, dispersal models, and landscape genomics can help understand the flow of adaptive genetic variation across the landscape (Bay et al., 2017; Creech et al., 2017; Razgour et al., 2019). One important point emerging from genomic studies (Ahrens et al., 2019) is that the environmental factor inducing the highest levels of selection varies among species. Consequently, understanding the response and strength of selection of multiple species from multiple environmental variables will be important to robust assessments of system adaptive capacity. Beyond differences in genetic selection on traits among species, future efforts should aspire to integrate the role of plastic trait expression as well. Further, we encourage consideration of study geographic extent and boundaries, for example, during reserve design, because of the challenges associated with delineating ecological systems in some scenarios. Specifically, discrete systems may be embedded or connected to other systems with strong influence (e.g., terrestrial ecosystems on oceanic islands, Polis et al., 1997; or "riverscapes," Fausch et al., 2002). Regardless, a trade-off exists between model complexity and focusing on the most important aspects of the system, and similar conversations have occurred surrounding assumptions and complexity in the adaptive modeling literature (Kokko, 2005).

4.4 | Bridging concepts and best practices: Integrating adaptive potential into adaptive capacity

We contend that adaptive potential is one of the three pillars of adaptive capacity and that recognition of the hierarchical interrelationships among system elements conferring system potential and capacity is important (Figure 1). In addition, the exclusion or inclusion of human intention and action as direct or indirect system factors is a key difference between adaptive capacity definitions in the ecological versus SES literatures, and that the former can be partly subsumed under the latter. After reviewing the literature, we identified several steps to developing a robust estimate of adaptive capacity and identification of the ecological and social factors required for a species to persist. First, researchers need to understand species' response to environmental change across landscapes, the magnitude of anticipated environmental change, and the temporal rate and pattern of change. This can be done through range-wide mapping of environmental change to determine not only how much change might occur but where it may occur. Shifts in range size and shape can then be estimated with distribution models based on information about species traits limiting range. Second, researchers will need to understand limitations of local adaptation and phenotypic plasticity at threatened or near-threatened sites to buffer projected loss. This can be achieved by identifying adaptive alleles, patterns of heritability, and common garden estimates of phenotypic plasticity. Common gardens are often used for understanding the additive genetic variation of a trait, but controlled manipulation of the environment when using siblings or relatedness indices also makes it a useful tool for phenotypic plasticity. Third, it will be important to estimate connectivity to elucidate whether individuals can track their current climate envelope or whether genetic or phenotypic traits can move into populations to alter niches and prevent local extinction. Connectivity assessments can be done using an array of spatially explicit simulations in conjunction with either telemetry or gene flow estimates from neutral markers. An important component can be the use of sensitivity analyses to simultaneously identify parameters with the largest influence on systems and/or effects of measurement error on model outcome and efficiently allocate future empirical efforts toward those parameters. One important note for all the steps above is that accurate inferences will be limited by the measurements we can make in the field or lab. As Beever et al., (2016) state, the adaptive capacity of a species can be classified as either fundamental or realized, similar to niche space, and that current observations of realized space may not encapsulate the full fundamental capacity of the species. Trade-offs in a system may also result from interactions among species and linking how one species' adaptive capacity changes another species' adaptive capacity is an essential question to explore to better understand the conservation implications of environmental change. Fourth, defining key SES elements, drivers, and feedbacks will be necessary for predicting a species' response to a given environmental change. SES elements may influence the ability of a species to respond either directly, such as through causing direct mortality of individuals or reducing connectivity, or indirectly, such as increasing the rate of environmental change. Finally, once the data are collected, one of the biggest challenges will be creating a single, cohesive adaptive capacity analysis framework. Such integrative efforts will likely be species specific and involve many (sub)models and data gaps may be extensive for some species of conservation concern. Nonetheless, integrated analyses will be key for identifying conditions that provide "surprises"—outcomes that are nonintuitive caused by, for example, nonlinear dynamics, facilitation, or other feedbacks not obvious using typical bioclimatic projection approaches.

When managing for adaptive capacity and adaptive potential, there are two broad approaches once the above steps are completed. The first is "organism-focused," where the goal may be to identify populations with high adaptive capacity and aim to support those populations. This may involve individual protections for populations or using these individuals to support populations with lower adaptive capacity where the species may be threatened by environmental change through conservation breeding or translocation programs. The second is "habitat- or system-focused," aiming to identify the factors which are important for adaptive capacity, particularly any limits to social adaptive potential as defined above, so that steps and policies can be implemented to ensure that adaptive capacity does not decrease in the future. Given the current non-stationarity of socio-ecological systems, the factors influencing adaptive capacity may change over time, and the dynamics and feedback loops will need to be understood.

5 | CONCLUSION

Understanding adaptive capacity is paramount to mitigating the effects of environmental change, but currently a consensus is lacking on the appropriate methods and definitions. Our results comparing and linking adaptive capacity with adaptive potential across the fields of conservation biology and evolutionary biology reveal how the integration of evolution and social system drivers may be lacking in some conservation plans. Although adaptive capacity and adaptive potential have been conflated in some cases, there is support for considering adaptive potential as a subcomponent of adaptive capacity. The complex eco-evolutionary feedbacks of these subjects make determining metrics and integrating across disciplines challenging, yet these same feedbacks and potential for nonlinear dynamics highlight the need for mechanistic understanding. Some of the barriers between conservation practitioners, either conservation biologists or managers, and evolutionary biologists has been explored elsewhere (Cook & Sgrò, 2017, 2019). The general gap between these fields is particularly prevalent when comparing the understanding of adaptive capacity between academia and stakeholders (Mcleod et al., 2016). Although linking evolutionary biologists and conservation biologists through interdisciplinary research on adaptive capacity may help with the conservation of imperiled taxa, increasing participation of researchers from across disciplines will take a concentrated effort to maximize intellectual progress. Most current environmental change is anthropogenic and elucidating the key social drivers and constraints will be critical. Explicitly recognizing human planning, actions, and responses as components of a fully integrated definition of adaptive capacity may help reconcile "ecological" and "sociological" definitions and provide fruitful research and conservation paths.

Our review is intended to increase understanding of appropriate methods while encouraging robust interdisciplinary analysis.

By linking evolutionary biologists, conservation biologists, systems theorists, and social scientists, interdisciplinary research on adaptive capacity may help with the conservation of imperiled taxa while continuing the foundational research of adaptive potential. One persistent issue across these fields and terms is missing definitions and, at minimum, we recommend researchers explicitly define terms when addressing concepts of adaptive potential and capacity. Even if a single unifying definition does not exist, it will be imperative to make sure that at least the working definition for a particular study is always obvious. As working definitions and transdisciplinary research occurs, adaptive potential and adaptive capacity researchers can learn from each other to maximize growth of the field. This is only beneficial to broad conservation goals if a better understanding of the implementation of vulnerability assessment is improved (Engle, 2011; Petersen et al., 2018).

Interdisciplinary research among these fields of biology should occur along with SES research because effective conservation will need to involve an understanding of policy and human–environment feedback loops. Fully understanding the adaptive capacity of a species is a resource heavy endeavor, which will require engagement beyond the biological landscape. Furthermore, social and political systems are currently the primary drivers of the environmental change that adaptive capacity research is focused on addressing, and a continuing challenge will be to efficiently allocate limited conservation resources between increasing mechanistic understanding and implementation of conservation action. In the absence of being able to fully describe the adaptive capacity of a species or ecosystem, mitigation may need to be focused on limiting the environmental change itself through social and political systems.

ACKNOWLEDGMENTS

We thank attendees at the EPSCoR GEM3 seminar where preliminary results were shared for their feedback and discussion. In addition, we thank Andrew Child for help with data management and storage. We also thank the work of the reviewers toward improving the original manuscript. This publication was made possible by the NSF Idaho EPSCoR Program and by the National Science Foundation under award number OIA-1757324.

CONFLICT OF INTEREST

The authors report no conflict of interest.

DATA AVAILABILITY STATEMENT

Web of Science export results available through the Northwest Knowledge Network (Seaborn, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Seaborn T, Griffith D, Kliskey A, Caudill CC. Building a bridge between adaptive capacity and adaptive potential to understand responses to environmental change. *Glob Change Biol*. 2021;27:2656–2668. https://doi.org/10.1111/gcb.15579