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Assisting adaptation in a changing world

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Today, all ecosystems are undergoing environmental change due to human activity, and in many cases the rate of change is accelerating due to climate change. Consequently, conservation programs are increasingly focused on the response of organisms, populations, and ecosystems to novel conditions. In parallel, the field of conservation biology is developing and deploying new tools to assist adaptation, which we define as aiming to increase the probability that organisms, populations, and ecosystems successfully adapt to ongoing change in biotic and abiotic conditions. Practitioners are aiming to assist a suite of adaptive processes, including acclimatization, range shifts, and evolution, at the individual and population level, while influencing the aggregate of these responses to assist ecosystem reorganization. The practice of assisting adaptation holds promise for environmental conservation, but effective policy and implementation will require thoughtful consideration of potential social and biological benefits and risks.

KEYWORDS

assisting adaptation, acclimatization, range shifts, evolution, ecosystem reorganization

1 Introduction

The natural world has changed so quickly that many practitioners would argue that we have entered a new, human-dominated geological epoch called the Anthropocene (Corlett, 2015). The causes of these changes are diverse, including human land use practices, pollution, invasive species, natural resource extraction, and global climate change, and many of them are accelerating (Halpern et al., 2015; Venter et al., 2016). While some drivers of change can be mitigated locally, global climate change is not locally avoidable. Ultimately, global solutions to climate change are needed; however, even if people effectively curb greenhouse emissions in the near future, the climate will

continue to change for decades to come (Thomas, 2011; Pecl et al., 2017; IPCC, 2022). In the meantime, to mitigate the loss of biodiversity and ecosystem services, the field of conservation biology is ramping up efforts to develop new theories and tools that explicitly assist the adaptation of organisms, populations, and ecosystems to the cumulative impacts of environmental change.

Our goal in this paper is to summarize what we refer to as assisting adaptation, which is the range of potential management interventions available to help organisms, populations, and ecosystems adjust to ongoing, and especially climate-driven, environmental change while highlighting some of their potential benefits and risks. Organisms, populations, and ecosystems respond to environmental change through a suite of biological processes that occur across a range of scales of organization—including acclimatization, evolution, range shifts, and ecological reorganization—that we collectively refer to as adaptation because they are all processes by which biological systems adjust to environmental change (Webster et al., 2017). Note that this definition is broader than the evolutionary definition of adaptation that refers only to genetic changes, but is consistent with the growing use of the term in conservation biology to refer to how human and non-human organisms adjust to environmental change (e.g., Morecroft et al., 2019; Tittensor et al., 2019; Wilson et al., 2020; Jacquemont et al., 2022). Under this definition, adaptation is simply the process of responding to change, with no normative evaluation of whether it is positive or negative; however, efforts to assist adaptation are typically normative because they promote particular adaptive outcomes that people view as preferable to others (e.g., species persistence or continued provisioning of ecosystem services).

The practice of assisting adaptation builds on decades of theory and practice in conservation. For example, many conservation initiatives focus on reducing acute threats so that populations or ecosystems can maintain or return to a more desirable state (Carwardine et al., 2019). Under stable environmental conditions, threat reduction alone might produce long-lasting positive benefits. However, under changing environmental conditions, additional interventions that deliberately boost the rate, scope, and scale of adaptive processes may be required to achieve desirable conservation outcomes (Pressey et al., 2007; Stein et al., 2013; Abrahms et al., 2017).

Stakeholders considering possible management interventions to assist adaptation have a growing list of options to consider. While some options focus on facilitating adaptive processes through passive interventions that promote the conditions under which adaptation can occur but allowing natural processes to determine the outcome, other options more actively direct adaptation, whereby the practitioner actively drives organisms or ecosystems toward a particular outcome (Gaitán-Espitia and Hobday, 2021). Implementing any effort to assist adaptation will require appropriate policies (Scheffers and Pecl, 2019) and should stem from inclusive decision-making processes that consider the potential social and biological benefits and risk of alternative actions (Kaplan-Hallam and Bennett, 2018; Raymond et al., 2022).

2 Assisting the adaptation of organisms and populations

In the last few decades, conservation biologists have been vigorously developing new theories and tools for assisting organisms and populations in their response to local and global change (Stein et al., 2014). Primary motivators for this work include reducing the risk that individual species or populations go extinct and ensuring they continue to provide benefits to humans and other species. At the individual organism and population level, the management tools for assisting adaptation have focused on influencing three key biological processes: acclimatization, range shifts, and evolution. Below, we discuss each of these processes individually; however, we recognize that they are likely to interact with each other in determining a population's adaptive response (Donelson et al., 2019). Indeed, it is the fact of these interactions that makes a broader focus on the processes that collectively underly adaptation so important to contemporary conservation.

2.1 Assisting acclimatization

Acclimatization is the process whereby individual organisms automatically adjust their phenotype, which we define as the observable traits of an organism, including their morphology, physiology, and behavior, in response to changing biotic and abiotic conditions. While acclimatization is an individual response to environmental change, it can play an important role in conservation if the sum of individual responses dampens the adverse effects of stressors on populations. Acclimatization can occur quickly, often well within the lifespan of an individual, so it is thought to be a first response for many organisms as the environment changes (Fox et al., 2019).

Conservation efforts can take advantage of acclimatization through long-standing conservation practices, like reducing local threats or prioritizing actions in places where populations experience less environmental change. While these actions do not directly manipulate acclimatization, they may create conditions whereby individuals are more likely to successfully acclimatize. For example, conservation efforts can focus on areas that are predicted to be less affected by climate change (Keppel et al., 2015; Lawler et al., 2020; Arafeh-Dalmau et al., 2021). Within such climate change refugia the rate and magnitude of environmental change may be small enough that organisms can successfully acclimatize; in the absence of the refuge, they might instead perish. In another example, behavioral acclimatization, the shifting of behavior in response to environmental change, can be facilitated by designing protected areas to include a diversity of habitat conditions that provide individuals with access to alternative food resources, favorable temperature conditions, and a variety of breeding sites (Beier et al., 2015; Beever et al., 2017).

Practitioners can directly boost acclimatization by inducing organisms to express new phenotypes. For example, California condors have been trained to avoid dangerous electrical wires and poles through behavioral conditioning (Mee and Snyder, 2007). Similarly, vaccinating wild organisms induces the phenotypic expression of pathogen resistance (Barnett and Civitello, 2020). New phenotypes can also be induced by stress

conditioning. For example, once transplanted into the wild, corals that were previously subjected to sub-lethal thermal stress in a controlled environment may have a greater ability to survive similar stressful conditions in the future and this ability might be heritable for several generations through epigenetic mechanisms (van Oppen et al., 2015).

While acclimatization can occur rapidly and is likely to be helping many organisms adjust to environmental change, there are concerns that acclimatization by itself, which is inherently constrained by an organism's genome, will not be sufficient to allow many populations and species to persist as climate change intensifies (van Oppen et al., 2015; Beever et al., 2017). Furthermore, under certain circumstances, acclimatization can slow the rate of evolution or even be maladaptive, particularly if environmental conditions become more variable (Fox et al., 2019). Therefore, many conservation biologists and managers are considering a broader range of adaptive processes to target with management actions.

2.2 Assisting range shifts

Conservation biologists have recognized that many populations will need to shift their geographic distribution to remain in environments within their physiological tolerances (Schwartz and Martin, 2013; Thomas, 2015; Scheffers and Pecl, 2019). Managers can assist such relocation in at least three distinct ways: 1) facilitating natural range shifts, 2) directly redistributing individuals within their recent historical range, and 3) moving individuals to locations outside their historical range.

The most simplistic expectation for climate-driven changes in species distribution is that populations will tend to move poleward, up in elevation on land, inland in coastal environments, and deeper in aquatic environment, to conditions that better approximate what they experienced in their recent evolutionary history (Chen et al., 2011; Pecl et al., 2017). Indeed, there is ample evidence that these kinds of changes in range shifts are already extensive (Lenoir et al., 2020). Networks of protected areas can be designed or expanded to facilitate range shifts by including connectivity attributes. Examples include ensuring that populations can move through habitat corridors or disperse from steppingstone habitats to areas that might become suitable in the future (Bonebrake et al., 2018; Brito-Morales et al., 2018; Scheffers and Pecl, 2019; Belote et al., 2020).

Managers can directly manipulate range shifts by moving wild or releasing captive-bred individuals within their recent geographic range. Such directed relocations can be used for a variety of purposes, including re-establishing extirpated populations (Houde et al., 2015) demographically rescuing target populations (Hufbauer et al., 2015), concentrating populations in predicted climate change refugia (Keppel et al., 2015), and influencing local evolution (discussed in the next section). Whether to move individuals within their recent geographic range must be balanced against the potential risks such as disrupting the extant genetic or ecosystem structure (Butt et al., 2021).

In many cases, managers are concerned that natural dispersal will not be adequate to facilitate the movement of populations to new geographic areas (Carroll et al., 2015). Significant advances in

predictive species distribution modeling of future environments allows managers to anticipate where suitable environmental conditions might exist in the future (Morán-Ordóñez et al., 2017) or how population dynamics may play out across a landscape (Briscoe et al., 2019), fueling a fast-growing branch of conservation biology focused on the questions of whether and where to move populations to new places as environmental conditions change (Thomas, 2011).

Assisted range shifts have the potential for widespread implementation because, at least in principle, the whole world is searchable for potentially suitable locations for populations to occupy in the future. However, deliberate relocations are likely to be constrained by the high costs of identifying suitable locations and conducting the relocation process, the ecological risks of introduced and potentially invasive new species, the uncertainty associated with modeling future climate and future ecological responses, and the possibility that successfully relocated populations may need to relocate again as the environment continues to change. Moreover, prior to moving forward with assisted range shifts, managers will need to carefully weigh the risks of not moving a population (e.g., risk of extinction, extirpation, or loss of diversity) relative to the risks it poses to other species and ecosystems if relocated (Butt et al., 2021), and consult closely with potential recipient communities. In many cases, the decision of whether to proceed will be controversial (Thomas, 2011; Weeks et al., 2011; Kracke et al., 2021).

2.3 Assisting evolution

In recent decades, the evidence of contemporary evolution, with significant changes to gene frequencies occurring on the scale of years to centuries, has grown tremendously (Stockwell et al., 2003; Stuart et al., 2014; Hoffmann et al., 2015). Building on these observations, conservation biologists are increasingly exploring whether and how to assist evolutionary processes to help species persist (Hoffmann and Sgró, 2011).

Conservation biologists are exploring two primary approaches to assisting evolution. First, species can be managed to maintain or increase local population size and metapopulation connectivity to indirectly influence the amount of genetic variance available for natural selection (Sgró et al., 2011; Webster et al., 2017; Walsworth et al., 2019; Colton et al., 2022). The assumption in this case is that enough genetic variation exists within a metapopulation to support evolutionary adaptation, provided that management actions increase local abundance and/or facilitate natural geneflow.

Second, conservation biologists and managers can directly introduce new individuals of the same species from another population to wild populations to increase the potential for evolutionary adaptation through natural selection; a strategy commonly called assisted gene flow (Aitken and Whitlock, 2013). The simplest form of assisted gene flow involves adding individuals to focal populations under the assumption that they will increase the overall genetic variance, thereby increasing the range of genotypes available for local evolution by natural selection. Practitioners can take this approach a step further by introducing specific genotypes that they predict will fare better under current or future conditions, which could theoretically boost the rate of evolution of favorable

traits (e.g., Aitken and Whitlock, 2013; van Oppen et al., 2015). Evolution can also be assisted by attempting to increase adaptive genetic variation through transgenic modification, which can purposely insert entirely new genes into an individual's genome (e.g., Powell et al., 2019). Efforts to assist evolution also have possible downsides. For example, if the new individuals entering the population are locally less fit than those already present, then they can cause outbreeding depression that undermines local evolutionary adaptation (Aitken and Whitlock, 2013). Therefore, successfully assisting evolution may require a careful titration of gene flow so that it enhances, rather than hinders, local selection.

Efforts to directly manipulate evolution are among the most controversial approaches to assisted adaptation for several reasons. First, deliberately altering genetic structure of populations has long been considered anathema to the basic conservation goal of preserving extant biodiversity and is opposed by many groups, including many Indigenous Peoples (e.g., Mead, 2016), for ethical reasons. Second, many populations may not have favorable conditions for successful rapid evolution (Bell, 2012; Stewart et al., 2017). Third, even when assisted evolution is theoretically possible, we lack empirical demonstrations of our ability to drive evolutionary adaptation in wild populations. Finally, the widespread application of assisted evolution can involve expensive management actions, like captive breeding and subsequent releases into the wild (Snyder et al., 1996), possibly pulling resources from other conservation actions. A good first step in potentially navigating some of this controversy would be some case study demonstrations that rapid evolution can be successfully assisted in wild populations to achieve conservation outcomes (Filbee-Dexter and Smajdor, 2019). However, even with such empirical evidence, the choice of whether to proceed with manipulations of population genetic structure will require a careful consideration of whether the benefits outweigh the costs.

3 Assisting the adaptation of ecosystems

Ecosystems respond to environmental change through a process of reorganization, whereby the composition, relative abundance, and functional role of species change over time. Managing for ecosystem adaptation aims to guide this kind of reorganization, making it distinct from other ecosystem management approaches that aim to either prevent ecosystems from changing or return them to a past state. Despite the assumption of ongoing reorganization, managing for ecosystem adaptation can have measurable goals—like the provisioning of certain ecosystem services—but it recognizes that the way goals are achieved might change over time, perhaps with a different composition of species (Beier and Brost, 2010).

Managing for ecosystem adaptation can use some of the same tools used for facilitating population and species adaptation. For example, managing large, connected, and abiotically representative networks of protected areas can preserve the processes that promote the adaptation (i.e., acclimatization, range shifts, and evolution) of multiple species in ways that may result in shifts in community composition and species' functional roles (e.g., Beier and Brost, 2010; Webster et al., 2017). It is also possible to direct the reorganization of an ecosystem by actively manipulating the abundance and composition of select species over

time to achieve a particular goal, as exemplified theoretically in renewal ecology (Bowman et al., 2017) and the creation of designer ecosystems (Aswani et al., 2018), and in specific case examples like forestry (Ontl et al., 2020).

Ultimately, the influences of acclimatization, range shifts, evolution, and ecosystem reorganization are not independent (Donelson et al., 2019), and efforts to manage natural systems that are experiencing environmental change will likely have to consider more than one of these adaptive processes as they simultaneously affect individual species and the ecosystem as a whole.

4 Discussion

All management interventions raise questions about their potential risks and benefits to wild organisms, ecosystems, and people (McShane et al., 2011). Purposefully assisting adaptation amplifies many of these questions because, in addition to longstanding and well-tested conservation practices, it adds new, rarely-if-ever-tested, kinds of interventions, some of which are based on new and emerging technology. Furthermore, assisting adaptation recognizes that inaction is risky because the underlying environmental conditions are changing and will continue to change. Therefore, efforts to assist the adaptation of organisms, populations, and ecosystems warrant careful consideration of the social, economic, and biological implications of action and inaction.

On the biological side, assisted adaptation efforts have great promise for helping to realize important goals, like species persistence. However, these interventions necessarily come with biological risks; in some cases these efforts may simply not work, but in others they might create new, but unintended, problems. Assisting adaptation also presents a whole host of potential social benefits and risks. For example, potential interventions may have important economic ramifications, both positive and negative, for people whose livelihoods are tied to the structure and function of biological systems. Furthermore, assisting adaptation can create risks and benefits to cultural values and practices. For example, in some cases, people may understandably reject efforts to assist adaptation because the methods are considered unethical or because of potential harm to existing cultural values, such as those that might be associated with native species assemblages or population genetic structure.

Given the complex set of potential risks and benefits, decisions about whether and how to move forward with assisted adaptation will likely need to be considered on a case-by-case basis that explicitly considers local biological and social ramifications. Furthermore, recent research indicates that the implementation of conservation actions may be more equitable and successful if it is based on inclusive processes that effectively weigh the economic, social, and cultural values of diverse groups of stakeholders continuously, from early planning stages, through project implementation, and later evaluation and adaptive management (Raymond et al., 2022).

Implementation may be further complicated by the fact that many environmental laws and policies have been established prior to the development of some assisted adaptation tools. As stakeholders face the challenge of whether and how to assist adaptation, they will likely be looking to policymakers and regulators for guidance on how to either interpret or update existing regulations in light of methodological advances and growing urgency (Brodie et al., 2021). In some cases,

existing policy and management frameworks may be vague or explicitly forbid certain interventions, indicating that regulatory or legal changes might be needed before some interventions are attempted (Sansilvestri et al., 2015).

Conservation biologists can help inform whether and how to move forward with assisting adaptation by developing and testing potential management options and helping to clarify the biological benefits and risks of possible interventions. For example, deliberately moving a species outside of its recent historical range may reduce the probability of that species' extinction, while simultaneously affecting the species already present in the new environment (Thomas, 2011; Schwartz and Martin, 2013). Similarly, the extirpation of local species can have ripple effects on the entire ecosystem, putting cultural and economic values at risk. Thus, a priority going forward is to build mathematical models and risk assessments for alternate management scenarios that consider the full range of biological processes and management options for assisting adaptation. With this kind of information in hand, conservation biologists can help stakeholders make better-informed decisions about whether and how to proceed with management actions aimed at assisting adaptation.

Ultimately, assisting adaptation is about helping species, ecosystems, and people through a bottleneck during an era of rapid environmental change. However, even with human assistance, the scope of adaptation will always have limits. Therefore, in parallel to assisting species and ecosystems in individual cases, the highest long-term priority for conservation should be mitigating the drivers of change to reduce the need for rapid adaptation.

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MW, BT, and MC initially conceived the topic and MW led the process of drafting and revising the manuscript. All

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