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Understanding local adaptation to prepare populations for climate change

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Abstract:

Adaptation within species to local environments is widespread in nature. Better understanding this local adaptation is critical to conserving biodiversity. However, conservation practices can rely on species' trait averages, or broadly assume homogeneity across the range, to inform management. Recent methodological advances for studying local adaptation provide the opportunity to fine-tune efforts for managing and conserving species. Implementation of these advances will allow us to better identify populations at greatest risk of decline due to climate change, as well as highlight possible strategies for improving the likelihood of population persistence amidst climate change. Here, we review recent advances in the study of local adaptation and highlight ways these tools can be applied in conservation efforts. Cutting-edge tools are available to help better identify and characterize local adaptation. Indeed, increased incorporation of local adaptation in management decisions may help meet imminent demands of managing species amidst a rapidly changing world.

I. **Local adaptation (LA) can be better incorporated in conservation efforts**

Local adaptation (Williams 2018) is pervasive across ecological systems, and is a key evolutionary process that has generated much of the world's biodiversity. LA is the process by which populations have traits that confer higher survival and reproduction in the local environment compared to elsewhere due to the spatial match between adaptive genetic variation and environmental variation (Blanquart *et al.* 2013). LA is generally a result of divergent selection over one or more traits, which, if combined with geographical isolation, can lead to different evolutionary trajectories, including reproductive isolation and speciation (White and Butlin 2021). LA has been widely investigated across the tree of life (e.g. Kawecki and Ebert 2004; Blanquart *et al.* 2013), and we are rapidly increasing our understanding of the scale and pervasiveness of LA (Sork 2017).

As our understanding of the processes that generate and maintain diversity has rapidly expanded, so has our interest in the consequences of LA (Hereford 2009; Savolainen *et al.* 2013). One of the most-important outcomes of LA may be the maintenance of ecologically important genetic variation, which can be vital for species' persistence amidst changing ecological conditions (Whitlock 2015). However, much of the spatial variability in adaptive genetic diversity generated by LA may be threatened by the multifaceted effects of global and anthropogenic change. Additionally, adaptation to non-climatic factors, such as other abiotic and biotic interactions (e.g., soil and water characteristics, diseases, food resources, predation, and competition), may be disrupted by climate change (Delph 2017). A shift from local adaptation to maladaptation (i.e., reduced fitness and survival of individuals, given a mismatch between genetically determined traits and the current environment) under fast-changing environments likely contributes to staggering losses of populations worldwide (Derry *et al.* 2019). Thus, an improved understanding of LA can help guide conservation actions to better conserve the world's biodiversity (e.g., Fig. 1). One caveat in this discussion of LA and conservation, however, is that in extremely small populations, the larger forces of genetic drift and mutational load may prevent local adaptation from occurring (Willi *et al.* 2022). Therefore, managers in such situations may find more benefit from focusing on increasing overall genetic diversity and census size (Willi et al. 2022). Information on LA, however, can provide valuable insights for improving the adaptive potential of populations that are not on the very brink of extinction, to maximize their likelihood of long-term persistence (Bay *et al.* 2018; Flanagan *et al.* 2018). Additionally, utilizing LA to inform translocations, reintroductions, captive breeding, and identification of conservation units and critical habitat may substantially increase the likelihood of successful outcomes (Flanagan *et al.* 2018). Despite this importance, relatively few studies have incorporated LA into predictions of how species' distributions and abundances will be affected by climate change (Smith *et al.* 2019) or taken LA into account when designing conservation and recovery plans (Peterson *et al.* 2019).

The time is ripe to evaluate LA as a standard component of conservation planning and integrate it into conservation actions (Hellmann and Pfrender 2011). Herein, our objectives are to provide a primer on LA and its potential incorporation in conservation by: 1) highlighting the ways conservation biologists can merge classic and emerging tools to detect LA; 2) exemplifying methods for incorporating LA in conservation actions to better help populations withstand changing climate and other ecological stressors; and 3) describing the implications and applications of LA to policy, management, and conservation and future directions for promoting the strategic incorporation of LA into conservation decision-making. We acknowledge that numerous other ecological disturbances (e.g., land-use change, over-harvest, pollution, disease) have all contributed to losses of biodiversity (Díaz *et al.* 2019). Given this, we primarily focus here on climate change because of its iteratively increasing pace, near-ubiquity, interaction with the above-mentioned factors, and clear influence on fitness and population persistence.

II. **Integrating classic and emerging tools to characterize and quantify LA**

Common-garden experiments and reciprocal transplants have been the gold standard for identifying LA and separating genetic contributions from phenotypic plasticity. However, these studies tend to be biased toward abundant, well-studied, easy-to-translocate species, and parsing traits with complex genetic architecture requires using many study individuals (Ghalambor *et al.* 2018). Until recently, this limited the ability to incorporate LA in conservation because species of conservation interest are generally understudied and rare, and many traits of conservation interest are likely controlled by a suite of genes, rather than by single genes of strong effect (Savolainen *et al.* 2013).

The conservation toolbox is now rapidly expanding as new technologies emerge for studying genomes (i.e., the entirety of an organism's genetic material) and as our understanding of the genomic basis for traits increases. We now have the tools to identify and incorporate LA into conservation and management by integrating cutting-edge genomic data with traditional methods of studying LA, such as common-garden experiments (Hoban *et al.* 2016). We can generate high-resolution genomic data for almost any species (Whitlock 2015). Further, many of these methods do not necessitate rearing or growing organisms in the lab, such as species distribution modeling and landscape genetics, making an understanding of the causes and consequences of LA possible for most organisms of conservation importance (e.g., Fig. 2; Funk *et al.* 2019). We can identify genotypes that are locally adapted, determine the environmental variables driving population differentiation, and pinpoint the genetic variation for specific traits underlying LA, making it possible to then use that information to make predictions for future habitat suitability and guide conservation and restoration actions (Tiffin and Ross-Ibarra 2017). Increasing our understanding of the causes and consequences of LA in species of conservation focus will allow conservation biologists to better understand which populations may be limited in their adaptive potential and how phenotypes and fitness will respond to climate heterogeneity. Ultimately, this information can be used for improved conservation planning. See the **Supplemental Table** for further exploration of these methods.

III. Using LA to best equip populations for persistence under changing climates

Given the recent advances in our ability to identify LA, it is now possible to incorporate LA into species conservation and management to plan for future conditions under climate change (Capblancq *et al.* 2020). Managed gene flow and the incorporation of LA in relocation and reintroduction planning each provide options for ‘throwing a lifeline’ to populations that have become increasingly maladapted to their environment due to reduced genetic diversity or rapidly changing environments, or to restore resilient populations in places where they have become locally extinct. Cryopreservation of gametes and gene editing are two additional technological advances that, if informed by an improved understanding of LA, may provide options for saving species from the brink of extinction and allow a path for protecting species that are most vulnerable to the negative effects of global change. Below, we discuss the benefits and concerns regarding these options and highlight how the understanding of LA can inform these important conservation tools. We are not advocating that these tools should replace more classic conservation strategies, such as land and species protection and take prohibitions, which will continue to constitute pivotal approaches for biodiversity conservation. Rather, we aim to demonstrate that we also now have new tools to combat biodiversity loss.

Managed gene flow and translocations/reintroductions

Translocation, the human-assisted movement of individuals, has a long history of use in managing populations for conservation objectives (Griffith *et al.* 1989). Today, it can also be a potentially powerful management strategy for mitigating maladaptation due to rapidly changing climate conditions (Hoffmann *et al.* 2021). This can occur through the intentional translocation of individuals within a species' range to reintroduce populations that have gone locally extinct, or to facilitate gene flow of locally adaptive alleles into existing populations. Additionally, locally adapted individuals can be translocated to areas outside their current or historical range that are projected to provide suitable habitat under future climatic conditions based on assessments of adaptive capacity (actions reviewed by Thurman *et al.* 2022).

More specifically, translocation is an option for assisted gene flow to benefit maladapted populations and promote increased local adaptation through a number of non-mutually-exclusive mechanisms (Aitken and Whitlock 2013). For example, immigrant genotypes can be sourced from an environment that matches projected future climate conditions, such that "preadapted" alleles are used for translocation or introduction into a maladapted recipient population (Catullo *et al.* 2019, Chen *et al.* 2021). These alleles may be locally adapted to these future conditions. This is most often discussed for longlived and dispersal-limited species that are unlikely to otherwise keep pace with changes in local climate, such as trees (Browne *et al.* 2019) or corals (Bay and Palumbi 2014). A large body of literature also now supports the idea that gene flow into populations that have become small and isolated due to habitat fragmentation can facilitate 'genetic rescue' – an increase in population growth due to the immigration of new genetic material (see Panel). Finally, over a longer timeframe, increased genetic variation provided by assisted gene flow may be a critical source of raw genetic material that allows populations to adapt to novel selection pressures (Derry *et al.* 2019).

Although assisted gene flow and movement of individuals have many potential benefits, they also pose a number of possible risks. Outbreeding depression can occur if immigrants are too distantly related (particularly if they have differences in chromosomal structure or number) and/or if they introduce traits that are not well-suited for the new environment (Frankham *et al.* 2011; Leroy *et al.* 2018). For example, reduced hybrid survival was observed when geographically separated salmon populations with distinct spawning phenotypes (even- vs odd-year spawn timing) were crossed (Gilk *et al.* 2004), highlighting the critical importance of a strong understanding of organismal natural history before carrying out assisted gene flow. Another concern is loss of local genetic lineages through genetic swamping (Rhymer and Simberloff 1996; Gilk *et al.* 2004). This may occur if too many individuals with higher fitness than local individuals are introduced. It has also been shown that strong selection can maintain locally favored alleles, even in the face of high gene flow (Fitzpatrick *et al.* 2020). Although the benefits of assisted gene flow and genetic rescue within a species' range are increasingly recognized, movement of individuals to areas outside of the historical range of a species should be treated cautiously (Schwartz *et al.* 2012). Thus, building on the lessons from empirical studies, demographic modeling and simulations are increasingly used as powerful tools to both 1) forecast the interaction of LA with demographic, biotic and abiotic factors (Landguth *et al.* 2020), and 2) predict the spatial distribution of adaptive genetic variants and thus, determine appropriate current and future geographic areas for translocations (Razgour *et al.* 2019; Rochat *et al.* 2021). Simulations of assisted gene flow have shown that multiple translocations over several generations can lead to smaller reductions of fitness, especially if outbreeding depression is strong (Grummer *et al.* 2021). However, when traits are polygenic (i.e., controlled by multiple loci of small effect), the beneficial effects of assisted gene flow may only be tangible on a longer time scale than that necessary for most climate-related actions (Grummer *et al.* 2021). Given that “the stage” and “evolutionary play” are iteratively changing as noted by G.E. Hutchinson, conservation practitioners must also ensure that viability of source populations is not compromised by assisted migration. These above-described concerns deserve increased research to continue to increase the applicability of this important conservation tool (Fitzpatrick *et al.* 2020; Brodie *et al.* 2021).

Cryopreservation and seed banking

Another emerging tool that can be used to help support incorporation of LA in conservation is seed banking and the cryopreservation (freezing) of gametes, embryos, or somatic cells (Fig. 3). These methods have been increasingly implemented in species where *in-situ* conservation methods have failed to maintain viable populations (Holt *et al.* 1996; Ryder and Onuma 2018). There are around 1,300 seed banks world-wide, and ecologists are gaining an understanding of how best to design and sample populations to increase the utility of seed banks for promoting LA (Rajasekharan 2015; Hoban 2019). Additionally, there have been rapid advances in cryopreservation techniques that allow maintenance of genetic material for animals and plants (e.g., tropical species) whose seed can't be stored (e.g., maintenance of tissue culture stocks; Ryder and Onuma 2018). Cryopreserved cells can theoretically be stored indefinitely, and can serve as "back-ups" to preserve the genotypes of individuals. When combined with *in-vitro* fertilization techniques, this approach can produce new offspring (Charlton *et al.* 2018; Ryder and Onuma 2018), which may then be used in genetic-rescue and reintroduction efforts.

Seed banks and cryopreserved cells not only serve as genetic resource banks to conserve genetic diversity overall in an imperiled species, but can also preserve locally adapted genotypes that are important for future adaptive potential (Holt *et al.* 1996). In black-footed ferrets, a species reliant on *ex-situ* conservation and whose extremely low population sizes have led to strong inbreeding effects, the use of frozen spermatozoa and artificial-insemination techniques increased genetic diversity and lowered measures of inbreeding in released individuals (Howard *et al.* 2016). This approach can be combined with genomic analyses to identify and target genetic variants that are, or will be, important for promoting LA. The northern white rhinoceros is extinct in the wild, but cells from multiple individuals have been cryopreserved. These cells have been tested not only for measures of genetic diversity, but also signatures of selection that may reflect locally adapted genotypes (Tunstall *et al.* 2018). These data can be used to prioritize cells that will lead to offspring with the greatest chance of success in the reintroduction effort (Howard *et al.* 2016; Tunstall *et al.* 2018). This approach was recently proven successful by cloning an individual black-footed ferret from cells that had been cryopreserved for over 30 years (U.S. Fish and Wildlife Service, 2021a). Promoting LA amidst ongoing global change via cryopreservation might specifically include: a) ensuring that individuals from disjunct populations are well represented; b) including individuals from numerous edges of the bioclimatic envelope (or that have wide moisture and temperature tolerances), particularly from trailing-edge populations; c) preserving populations that naturally experienced higher frequencies of extreme events; d) including individuals from transition zones; and e) including individuals from more populations of poorly dispersing species associated with past climates, such as cryosphere-associated species (Thurman et al. 2022). However, it will be important to also ensure any of these targets of cryopreservation also come from populations with high levels of overall genomic diversity to avoid the negative effects of bottlenecks.

Cryopreservation, however, requires technical knowledge from specialist veterinarians and regular maintenance at designated facilities. Additionally, there is significant variation among species in the viability of frozen gametes for fertilization (Charlton *et al.* 2018; Ryder and Onuma 2018). Cryopreservation has also been shown to have negative effects on the morphology of some species, including effects that can reduce the survivorship and reproductive output of individuals (Poo and Hinkson 2020). Nonetheless, seed banks and ‘frozen zoos’ may be the last option for the future of some species, and research on how to improve seed banking and cryopreservation techniques to support future adaptation seems poised to provide invaluable insights.

Gene editing

Gene-editing technology has also emerged as a potentially viable tool for conservation biology in recent years, especially with the explosion of versatile CRISPR gene-editing techniques (Phelps *et al.* 2020). An example of gene-editing utility for conservation can be found in the ‘I’iwi (Hawaiian honeycreeper). Simulation models of ‘I’iwi reintroductions after devastating population loss driven by non-native malaria suggest that the species has a much higher chance of success if genetically edited, malaria-resistant individuals were to be introduced (Samuel *et al.* 2020). Although the I’iwi has not yet been gene-edited, this study demonstrates the strong potential for this tool to assist conservation efforts if a gene for malaria resistance can be identified. This solution is especially important because future warming is projected to increase the rate of malaria-driven extinctions of other species of Hawaiian birds, which may require analogous conservation efforts (Paxton *et al.* 2016). Similar gene-editing schemes have been proposed for other conservation scenarios, such as introducing genes for temperature resistance in coral species, fungal-disease resistance in bats and amphibians, and plague resistance in black-footed ferrets (Piaggio *et al.* 2017). As gene-editing tools become more accessible, and the ability to identify regions of the genome associated with adaptive traits becomes more precise, these technologies will become a more feasible part of the conservation toolkit (Supple and Shapiro 2018; Derry *et al.* 2019). For example, it is not outside the realm of possibility that one day we could identify adaptive genetic variation for thermal tolerance in an organism, using the techniques outlined in the Supplemental Table, and then introduce this variation into populations that will likely need it under future warming, but are currently lacking it, using gene-editing techniques (Thomas et al. 2013). This approach could have the added benefit of preserving the unique, local genetic diversity present in the population while introducing important alleles for future persistence. However, as with all the above-mentioned conservation actions, it will be important, and non-trivial, for sufficient overall genetic variation to be produced and maintained in any gene-edited population to avoid inbreeding and promote long-term persistence and resilience. LA-oriented gene editing might specifically include: a) seeking conservation of allelic diversity at multiple spatio-temporal scales; b) seeking maintenance of the evolutionary processes and pathways that maintain LA; and c) balancing concerns about swamping and hybrid vigor with desire to facilitate population persistence in a warmer, drier, and/or more-erratic future climate. Additionally, any use of genome-editing in a conservation context would benefit from being implemented in an adaptive management framework, with sufficient data collection before, during, and after actions, to ensure learning and the possibility for future refinement of techniques.

Gene editing also has limitations and requires ethical considerations and community engagement before being implemented as a regular conservation tool (Kardos and Shafer 2018, Barnhill-Dilling and Delborne 2021). Gene-editing technologies have progressed rapidly, but still depend on the ability to accurately identify regions of the genome that are adaptive and loci that have large effects on the trait of interest (Phelps *et al.* 2020). This approach is unlikely to work well for traits that are determined by many loci of small effect. In addition, there is some public resistance to the use of gene-editing technologies for conservation purposes, and many people remain skeptical that the techniques are safe and/or ethical (Kohl *et al.* 2019). Thus, it is important to engage with multiple stakeholders when considering genetically modifying organisms for conservation purposes (Kofler *et al.* 2018). Ethical analyses of other genomic technologies, such as cloning, have been conducted, and could be adapted to evaluate gene-editing as well (Sandler *et al.* 2021). Additionally, we presume that specific policies around the use of gene-editing for conservation will be developed iteratively over time (Burgiel *et al.* 2021). Although the practical and ethical considerations of gene editing should be carefully weighed, this technology may constitute the last chance for species when all other conservation efforts have failed. Conservation biologists may benefit from increasing engagement with these emerging technologies to reduce future biodiversity loss and plan for future climatic conditions (Piaggio *et al.* 2017).

IV. Implications and applications for policy, management, and conservation

LA has profound implications for a wide array of conservation actions, as described above. However, the full incorporation of LA into the conservation toolbox will require both emphasizing the identification of LA and having policies that promote the incorporation of LA in conservation planning (Hällfors *et al.* 2016). This includes having flexibility in the legal and regulatory mechanisms for preserving biodiversity under future climate conditions, while also providing clear directives. The European Union's Birds and Habitats Directive, for instance, provides regulatory agencies numerous options for planning and implementing actions to assist natural populations with adaptation to climate change. This flexibility, however, also has its limitations, as it does not require any specific actions or protections; consequently, planning for climate change is possible but voluntary (Verschuuren 2010).

Genomic advances are reshaping how we identify conservation units. There is ongoing vigorous debate among scientists and practitioners regarding how to weigh patterns shown in a small number of genes versus genome-wide patterns in conservation decisions and policy (Teixeira and Huber 2021; Kardos *et al.* 2021; Waples *et al.* 2022). For example, genomic research has recently identified one genomic region (GREB1L to ROCK1) as being tightly linked with migration timing, an important life-history trait driven by LA, in Pacific salmon (Prince *et al.* 2017; Waples and Lindley 2018). Researchers have demonstrated dramatic reductions in diversity at this locus after anthropogenic habitat modification, potentially reducing fitness and population sustainability (Thompson *et al.* 2019). Other components of fitness in salmonids, however, including growth rate and age at maturity, appear to be less homogeneous in their genetic basis (Waters *et al.* 2018). Consequently, it can be challenging to determine how much weight should be given to single genomic regions versus genome-wide patterns when designing conservation actions, particularly given that overall genomic diversity will provide the building blocks for future adaptation (García-Dorado and Caballero 2021; DeWoody *et al.* 2021).

Assisted gene flow and assisted colonization, as discussed above, are potentially powerful methods for helping dispersal-limited species to cope with climate change and increase overall genetic diversity (Williams *et al.* 2021). However, for assisted gene flow and assisted colonization to become effective policy, clear protocols and benchmarks will be needed to guide when and how translocations can occur (Schwartz *et al.* 2012). Translocations triggered by clear population declines, high likelihood of future declines, or loss of ecosystem function are consistent with the preventive principle (addressing known ongoing declines in threatened species) and precautionary principle (addressing anticipated or hypothetical future declines) outlined by the Rio Declaration on Environment and Development (Sansilvestri *et al.* 2015).

In addition to directly assisting movement, another critical component of conservation planning relevant to local adaptation is reserve design that helps assist movement through human-dominated habitats, assuming that organisms (and their associated traits) can disperse sufficiently quickly (Kostyack et al. 2011). Reserves can be designed to both promote movement between important habitats and to conserve the highest number of adaptively differentiated populations. Reserve design and conservation planning can combine methods for identifying and mapping out local adaptation (outlined in Section II above) with spatial analyses of climate refugia (see Saunders *et al.* 2022, Stralberg *et al.* 2020, Michalak *et al.* 2020) to prioritize areas for protection. For example, Saunders *et. al* (2022) conduct a reserve-selection prioritization to highlight priority areas for reserve design that both complement the current protected area network and would protect climate refugia for the highest number of taxonomic groups. One could expand on this analysis further to ensure adaptively differentiated populations within species are represented across the reserve network. Such combinations would improve our ability to conserve adaptive variation that will be important for species persistence now and into the future.

Under national laws aimed at species conservation, such as the USA's Endangered Species Act (ESA), addressing extant conventional threats has arguably often garnered higher priority than pre-emptive management in the face of climate change (Delach *et* *al.* 2019). Nonetheless, the U.S. Fish and Wildlife Service (USFWS) is evaluating (as of Nov. 2021) use of techniques such as translocations, reintroductions, genetic supplementation of *in-situ* populations, and use of captive breeding to create *ex-situ* insurance populations and 'head-starting' of offspring for numerous species whose range has become markedly more fragmented than the historical range and for which local adaptation was used to help delineate conservation or recovery units (e.g., rusty-patched bumble bee (USFWS 2021b), Eastern massasauga rattlesnake (USFWS 2021c), Dakota skipper (USFWS 2019)). Such actions seek to achieve persistence of locally adapted populations across diverse selective regimes, higher genetic diversity, avoidance of inbreeding depression, and long-term persistence amidst increasingly stochastic environmental conditions. Analogously, given declining population sizes and declining heterozygosity, and after considering risks of genetic swamping and loss of local adaptation, translocations of numerous mountain pygmy possum (an endangered Australian marsupial) individuals from a genetically diverged population achieved genetic rescue and demographic recovery of 1 of the 3 remaining extant populations of the species (Weeks et al. 2017).

The IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN 2013) can be used for developing national and more-localized guidance for using these tools amidst climate change. The Guidelines acknowledge the importance of information on adaptations to local ecological conditions, yet many other factors also warrant attention when considering human-assisted movement of individuals for conservation. Similarly, Weeks et al. (2011) provided pragmatic decision trees to evaluate possible translocations (see Fig. 2, Table 2), suggesting that local adaptation would constitute one of seven suites of factors governing the likelihood of both resilience and persistence of translocated populations. Determining whether and how translocated individuals will be moved may require modification of existing laws and/or policies. For example, the ESA provisions governing the movement of endangered or threatened plants are currently much less restrictive than those for animals, and may warrant new or revised guidelines or policy to be able to apply more broadly to animals (Shirey and Lamberti 2010). Aitken and Whitlock (2013) argued in their incisive review that to robustly weigh the risks of translocations (i.e., outbreeding depression and disrupting local adaptation to non-climatic factors) against their ability to mitigate maladaptation due to climate change, both pattern of gene flow and extent of LA need to be known.

Looking forward, conservation actions necessitating and enabling the movement of individuals and genes due to climate change-induced shifts in suitable habitat will at times require collaboration among multiple governmental and non-governmental organizations, and in many cases across national boundaries. Current transboundary agreements for climate change often fail to accommodate this reality (Trouwborst 2012). A logical early step for transboundary collaborations would involve synthesizing data gathered by scientists and managers across species' ranges to identify patterns of LA. This approach can help in 1) assessing potential benefits and risks of assisted migration or colonization across borders to reduce extinction risk, 2) approaching reserve design at a continental scale, 3) identifying alleles associated with higher fitness under different climatic conditions, and 4) determining populations for which seed banking/cryopreservation ought to be given high priority to preserve options for future conservation efforts. Organizations such as zoos, botanical gardens, or biobanks involved in cryopreservation or captive propagation of threatened species constitute key partners in coordinating efforts and providing genetic material or individuals for translocations. Additionally, the resources required to prepare populations for climate-change threats will be much greater than the resources available to meet the need for all taxa threatened by climate change. Consequently, conservation practitioners will necessarily have to prioritize actions and employ cost-benefit analyses to inform when to apply these tools. Collaborations across the researcher-practitioner-policy spectrum may be beneficial to help managers identify the best combination of strategies, tools, and resources for adaptively managing species with local adaptation in mind.

V. Conclusions

We now have the technical capabilities to meaningfully integrate local adaptation (LA) into conservation planning. Although taking an LA-focused conservation approach may necessitate greater initial investment in funds and human resources, we believe taking this approach will often have large returns on investment in terms of higher mean fitness, long-term sustainability, and greater effectiveness in buffering against the negative effects of climate change. Thorough and nuanced understanding of local adaptation is increasingly pivotal to inform the climate-adaptation conservation and management actions described herein, such as assisted migration, seed sourcing for restoration, active management of fragmented metapopulations and low-dispersal species, identification of conservation units, reserve design, and more-accurate predictions of climate-mediated range shifts. Indeed, LA tools and approaches may provide the best last-ditch option for some species, such as those with long generation times, and/or limited and infrequent gene flow. We acknowledge, however, that LA-relevant data are lacking for many species, including climate-sensitive species and despite massive advances in tools, data, and analytical approaches, numerous research frontiers remain. The climatic factors and mechanisms involved, critical life-stages, and population dynamics most strongly affecting persistence can be unknown, for parts or all of a species' range. In such cases, prioritizing the collection of such data could reap large rewards, and it is our hope that the information provided in our Supplemental table can help in that data generation process. Ultimately, land and wildlife managers and other conservation practitioners must weave LA information into an amalgamation of climate-change vulnerability involving not only adaptive capacity, but also sensitivity, exposure, and anthropogenic disturbances. Indeed, a recent conceptual framework suggested that a primary pathway for reducing a species' adaptive capacity (including its evolutionary potential to create LA) from its fundamental to realized level was mediated by extrinsic factors such as pollution, habitat fragmentation, and invasive species (see Fig. 1 of Beever et al. 2016). However, by thoroughly considering LA, conservation practitioners will be better equipped to incorporate the myriad factors involved and prepare populations for long-term persistence under a changing climate.

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Glossary

Adaptive capacity: the ability of a species or its populations to cope with or accommodate a given change (e.g., climate change) by persisting *in situ* or shifting to more-suitable ranges or microhabitats

Adaptive potential: the ability of a species or population to adapt via evolutionary change

Assisted gene flow: intentional translocation of individuals to facilitate adaptation to anticipated local conditions

Common garden experiment: a method of assessing differential responses to environmental variables by placing two populations into the same environment. Variations of this include reciprocal transplants and provenance plots.

Genetic rescue: an increase in population fitness caused by gene flow inferred from some demographic vital rate or phenotypic trait, by more than can be attributed to the demographic contribution of immigrants

Inbreeding depression: reduced fitness of individuals with related parents due to lower survival and/or reproduction

Maladaptation: Suboptimal fitness, either in absolute terms or relative to another population

Outbreeding depression: reduced fitness (compared to the parental fitness) caused by crossing distantly related individuals

Phenotypic plasticity: in which a single genotype produces multiple phenotypes in response to environmental changes

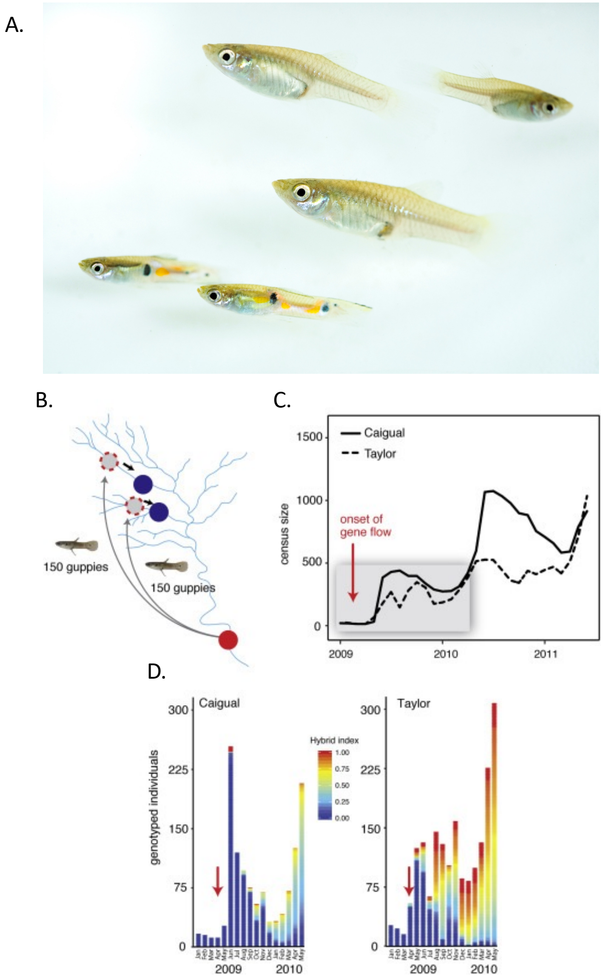
Reciprocal transplant: a method of evaluating local adaptation by swapping individuals among locations and comparing their fitnesses in their home versus foreign environments. This method requires local and non-local individuals be tested in each habitat of interest, whereas provenance plots do not.

Panel: Does genetic rescue constrain or facilitate local adaptation?

Human-assisted gene flow resulting in genetic rescue has aided the recovery of several iconic species such as Florida panthers (Johnson *et al.* 2010), bighorn sheep (Hogg *et al.* 2006), and Australian marsupials (Weeks *et al.* 2017). Yet, despite increased evidence for its potential to reverse population declines in small and isolated populations, genetic rescue is not a widely used management strategy (Ralls *et al.* 2018). Genetic rescue is primarily thought to increase fitness through masking of deleterious alleles that become exposed in small and inbred populations. However, the genetic architecture underlying genetic rescue is rarely known. In addition to masking deleterious alleles, beneficial genetic variation introduced by gene flow could rescue populations through heterozygote advantage, adaptive evolution, or a combination of these processes (Scott *et al.* 2020).

One of the main concerns with gene-flow augmentation in management is the possibility that gene flow may constrain local adaptation (Edmands 2006). This concern warrants re-evaluation in the context of (1) overwhelming evidence for inbreeding depression when populations become isolated and are rapidly reduced in size; (2) increasing evidence that gene flow increases fitness under a wider set of conditions than what theory predicts (Whiteley *et al.* 2015); and (3) the extent of maladaptation that many natural populations now face, given the pace of environmental change (Hoffmann and Sgrò 2011). In fact, gene flow may actually facilitate local adaptation, especially in cases where populations lack the variation needed to respond to selection.

Recent empirical work supports the idea that moderate rates of gene flow, even from adaptively differentiated source populations, can maintain or even facilitate adaptation within recipient populations (Panel Figure). For example, experiments using Trinidadian guppies in the wild and in mesocosms showed increases in population growth without the loss of locally adapted traits (Fitzpatrick *et al.* 2016; Kronenberger *et al.* 2018). In fact, gene flow caused shifts in some traits in the predicted adaptive direction (Fitzpatrick *et al.* 2017). In addition, greenhouse crosses using the annual wildflower *Clarkia pulchella* found strongest benefits of gene flow during an anomalously warm year, highlighting the potential role of gene flow in aiding adaptation to warming climates (Bontrager and Angert 2019). As natural populations become fragmented *and* exposed to severe environmental stressors, gene flow may be an increasingly important source of variation necessary for persistence.



Panel Figure

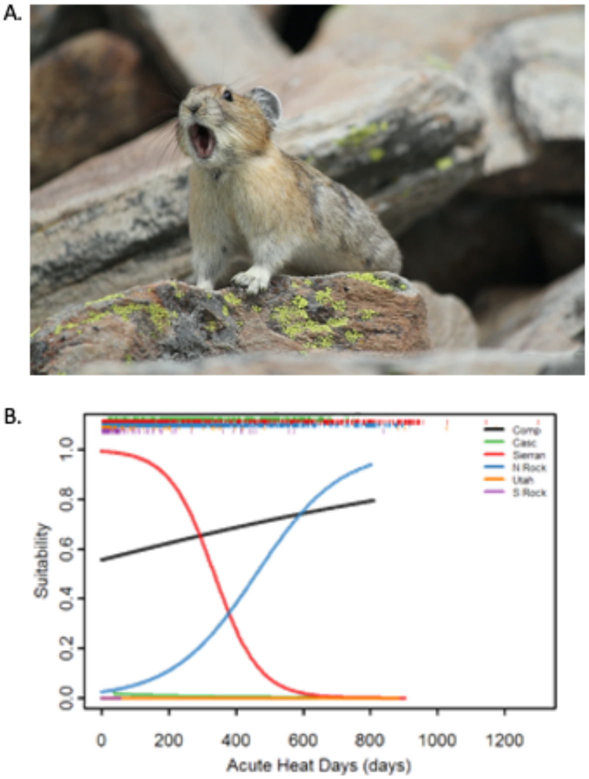

A.
B.
Comp
Casc
Sierran
N Rock
Utah
S Rock
Suitability
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
1000
1200
Acute Heat Days (days)

Figure 1.

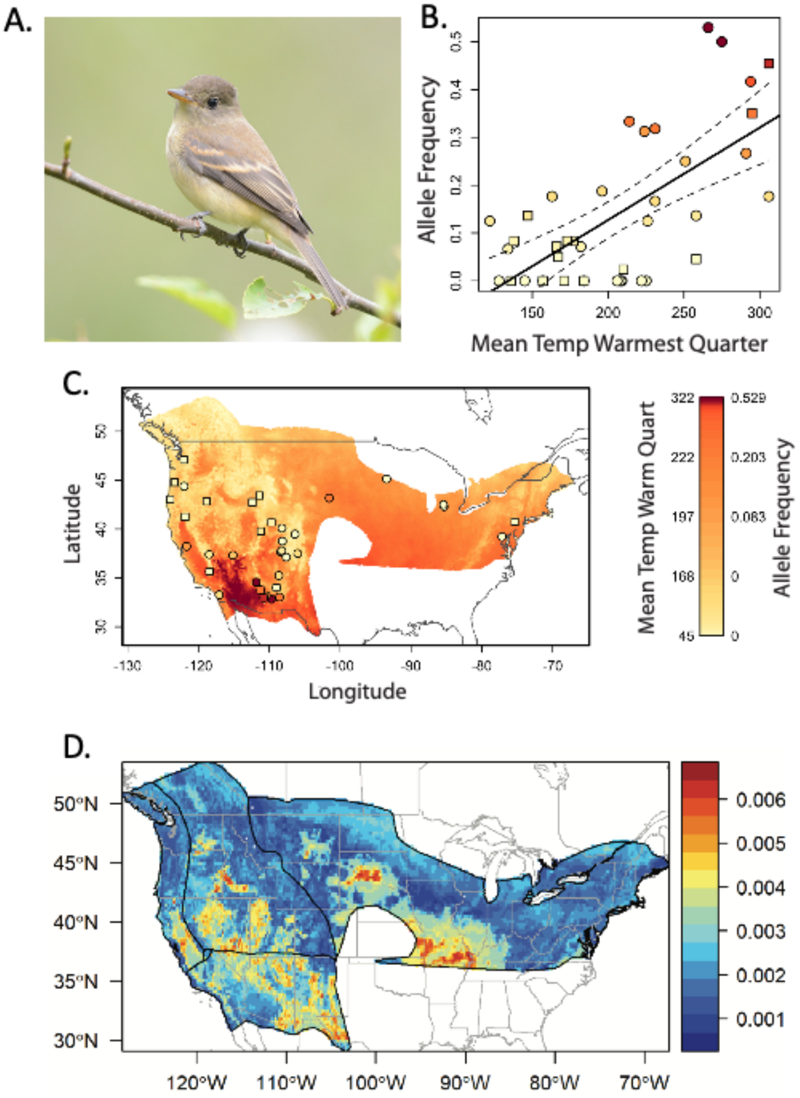

A.
B.
Allele Frequency
0.0
0.1
0.2
0.3
0.4
0.5
150
200
250
300
Mean Temp Warmest Quarter
C.
Latitude
50
45
40
35
30
-130
-120
-110
-100
-90
-80
-70
Longitude
Mean Temp Warm Quart
322
222
197
168
45
0.529
0.203
0.083
0
0
Allele Frequency
D.
50°N
45°N
40°N
35°N
30°N
120°W
110°W
100°W
90°W
80°W
70°W
0.006
0.005
0.004
0.003
0.002
0.001

Figure 2.

Figure 3.

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Figure Legends:

Panel Figure: A) Trinidad guppies (photo credit: David Herasimtschuk). B) Populations have benefitted from gene flow from adaptively differentiated source populations. Gray arrows indicate initial translocations. Black arrows indicate direction of gene flow. C) Work by Fitzpatrick et al. (2020) showed increases in C) census size after gene flow in both populations. D) Incorporation of new genotypes from translocation is shown by the increase in hybrid index in each population over time.

Figure 1. (A)The importance of incorporating LA in conservation planning is highlighted by research on the American pika (*Ochotona princeps*). A juvenile pika from Darkhorse Creek Canyon, Beaverhead Mountains in the central-northern Rocky Mountain chain, along the Montana-Idaho border. Photo taken by P. Billman, Montana State University. (B) Different populations show different responses to the *same range* of values *in the same climatic aspect*. Plot shows the marginal response of each lineage to acute heat days, ignoring the effect of all other variables. Specifically, increasing frequency of hotter days is beneficial to pikas in the northern Rocky Mountains (blue line); it strongly decreases habitat suitability for pikas in the Sierra Nevada (red line); and has no or nearly no effect on pikas in the three other genetic lineages (green, orange, and purple lines). Note that the composite model (black line) masks this intra-specific diversity in how populations respond heterogeneously to climate. Output is from a LARS (least angle regression) model calibrated with an elastic net to obtain the optimal level of regularization. By design, the coefficients are biased toward 0 (unpublished analysis associated with Smith et al. 2019).

Figure 2: (A) Candidate single nucleotide polymorphisms (SNPs) appear tightly linked to temperature in the Willow Flycatcher; the Southwestern Willow Flycatcher has been federally designated as endangered since 1995 (only an estimated 900-1100 pairs existed, as of 2002, USFWS 1995, 2013). Photo credit (A.): V.J. Anderson, CC BY-SA 4.0 <https://creativecommons.org/licenses/by-sa/4.0>, via Wikimedia Commons. (B) As mean temperature of the warmest quarter increases, so does the allele frequency of the temperature-associated SNP. The allele frequencies from the original genome scan data are indicated by squares, whereas allele frequencies based upon the validation set are denoted by circles. The highly significant relationship between this SNP and 7 of the 8 top-ranked climate variables in both the genome scan and validation results suggests a potential role for the SNP in climate adaptation across the region. (C) The geographically explicit representation of panel B, showing the association between Mean Temperature of the Warmest Quarter (BIO10) and the SNP allele frequency across western North America; population allele frequencies are color-coded from high frequency (red) to low (yellow). (D) Map showing the genomic vulnerability (amount of mismatch between current and predicted future genotype-environment relationships) across the Willow Flycatcher breeding range; red=high genomic vulnerability and blue=low genomic vulnerability. Reprinted from Ruegg et al. (2018).

Figure 3: Organisms that have been cryopreserved in order to save genetic material and aid conservation efforts. A) Semen from male Hawaiian ʻalalā is preserved by the

Maui Bird Conservation Center to bank genetic diversity for the recovery effort, photo credit: Lianne Hedditch. B) Black-footed ferret: World Wildlife Fund Northern Great Plains biologist and black-footed ferret expert Kristy Bly prepares to release a black-footed ferret at Snake Butte on the Fort Belknap Reservation, northern Montana. Photo credit: © Clay Bolt / WWF-US. C) San Diego Zoo Global has cells from 12 individual northern white rhinos cryopreserved in the Frozen Zoo® to help recover the species, photo credit: Lianne Hedditch. D) Endangered *Dudleya brevifolia* seed is stored at the San Diego Zoo Wildlife Alliance Native Plant Seed Bank, photo credit: Matthew Luskin, wikimedia.