Linking evolutionary potential to extinction risk: applications and future directions

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Extinction-risk assessments play a major role in prioritizing conservation action at national and international levels. However, quantifying extinction risk is challenging, especially when including the full suite of adaptive responses to environmental change. In particular, evolutionary potential (EP) – the capacity to evolve genetically based changes that increase fitness under changing conditions – has proven difficult to evaluate, limiting its inclusion in risk assessments. Theory, experiments, simulations, and field studies all highlight the importance of EP in characterizing and mitigating extinction risk. Disregarding EP can therefore result in ineffective allocation of resources and inadequate recovery planning. Fortunately, proxies for EP can be estimated from environmental, phenotypic, and genetic data. Some proxies can be incorporated into quantitative extinction-risk assessments, whereas others better inform basic conservation actions that maximize resilience to future change. Integration of EP into conservation decision making is challenging but essential and remains an important issue for innovation in applied conservation science.

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The profound transformation of the biosphere by humans is driving population extirpations and species extinctions (Ceballos *et al*. 2017; Sage 2020). Adaptive capacity – the ability to accommodate, cope with, or respond to dynamic conditions – fundamentally determines whether and how species will persist or decline in response to ecological disturbances (Figure 1; Panel 1; Foden *et al*. 2019; Thurman *et al*. 2020). These disturbances are diverse and interacting, and include habitat degradation and loss, climate change, overharvest, pollution, invasive species, and novel diseases. However, adaptive capacity in response to disturbance is poorly understood, and is therefore often ignored in assessments of vulnerability and extinction risk.

In a nutshell:

- Evolutionary potential (EP) can reduce a species' extinction risk by facilitating adaptive responses to environmental change; although challenging to quantify, EP can be estimated from environmental, phenotypic, and genetic data
- Including EP in extinction-risk assessments is rare; the best available models integrate demographic and evolutionary dynamics with environmental change
- Where data are limited, best practices for maintaining EP remain essential: conserving across the breadth of adaptive diversity and protecting the integrity of processes that drive evolutionary change
- Considering EP in conservation decision making will improve extinction-risk assessments and conservation planning to ensure resilience in the face of complex environmental change

In particular, the evolutionary potential (EP) component of adaptive capacity has proven difficult to evaluate for species of conservation concern, given its complexity and multidimensionality (Panel 2). We define EP as the capacity to evolve genetically based changes in traits that increase population-level fitness in response to novel or changing environmental conditions. Theory, experiments, simulations, and studies of wild populations all corroborate the importance of EP in mitigating extinction risk (reviewed below). Consequently, integrating available data on EP into vulnerability assessments is essential for effective prioritization of limited conservation resources amidst accelerating biodiversity losses. Because a comprehensive evaluation of EP is pragmatically impossible for any species (Panel 2), some uncertainty will accompany efforts to integrate EP into extinction-risk estimates. However, ignoring advances in our ability to estimate EP will only increase uncertainty and subsequently the potential for flawed decision making (Funk *et al*. 2019). We focus here on EP and extinction risk for several reasons: species-level extinctions are irreversible and accelerating (Wiens 2016; Ceballos *et al*. 2017), many legislative frameworks rely on extinction-risk estimates to prioritize conservation efforts (WebTable 1), and extinction-risk assessments that include genetic factors focus on inbreeding depression and rarely integrate EP.

Here, we examine the relationship between EP and extinction risk from theoretical and applied perspectives, and review proxies for EP, address their strengths and weaknesses, and discuss current approaches for integrating EP into

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Panel 1. Adaptive capacity, vulnerability, and extinction risk

A species' vulnerability to ecological disturbance is often assessed in terms of its exposure and sensitivity to changing conditions, and its adaptive capacity in response (Figure 1). Although these terms originated in the climate-change literature (eg Foden *et al.* 2019), they are useful in framing species' responses to disturbance more generally. Exposure defines the magnitude of disturbance (ie departure from levels that the species has evolved with). Sensitivity reflects how closely tied survival, performance, or fitness is to changes in prevailing conditions (Dawson *et al.* 2011). Adaptive capacity defines the innate ability to cope with, accommodate, or evolve in response to disturbance. Because species must continually adapt to changing environments, adaptive capacity is essential for resilience and viability (Sgro *et al.* 2011). It is most commonly summarized by three attributes: dispersal and colonization abilities, phenotypic plasticity, and evolutionary potential (EP) (Foden *et al.* 2019). This depiction arguably oversimplifies adaptive capacity, and other definitions include attributes like ecological role and life history (Thurman *et al.* 2020). In practice, these attributes are context-specific, interacting with factors that promote or constrain their expression. Using a framework analogous to ecological niche theory, a species' "fundamental" adaptive capacity can be reduced to a "realized" level by numerous aggravating/synergistic extrinsic factors such as habitat fragmentation and biotic interactions (Figure 1; Beever *et al.* 2016). This realized adaptive capacity interacts with the cumulative impact of exposure and sensitivity, reducing vulnerability and mitigating extinction risk.

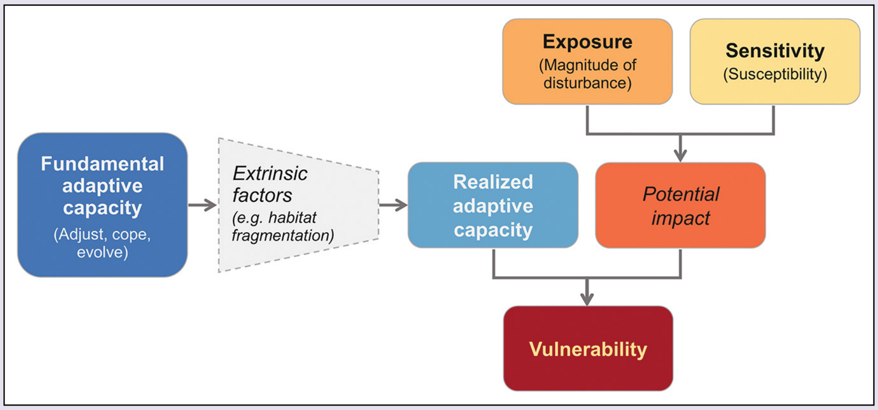

Figure 1. The vulnerability of a species to ecological disturbance is affected by the magnitude of exposure and the species' sensitivity to change, mitigated by the species' adaptive capacity. In most cases, a species' fundamental adaptive capacity will be constrained by extrinsic factors such as habitat fragmentation, such that the realized adaptive response is reduced.

extinction-risk assessments. These approaches are limited and represent an important challenge and opportunity for innovation in ecological–evolutionary research and conservation science.

The theoretical relationship between EP and extinction risk

Theory predicts that populations and species must have the capacity to adapt to persist in the face of ecological disturbance (Gilpin and Soulé 1986; Burger and Lynch 1995; Soulé and Mills 1998). Here, we distinguish extinction (the complete loss of all populations and individuals of a species) from extirpation (the loss of one or more populations within a species' range). Extirpation of populations is a common precursor to species extinctions (Gilpin and Soulé 1986; Hobbs and Mooney 1998). In this section, we summarize current theory underlying the importance of EP for persistence of populations and species.

The extinction vortex is a well-known concept in conservation biology that provides a useful framework for considering the roles of demographic and genetic factors in extirpation of a single population (Figure 2). First, ecological disturbances reduce age-specific vital rates and population growth rates, reducing census population size. Impacts of demographic stochasticity increase as census population size decreases, increasing variance in population size and creating a feedback, further reducing population size. Population size can also be reduced by environmental variation and catastrophes. Decreased census population size typically results in a concomitant reduction in effective population size (the size of an ideal population that would experience the same amount of genetic drift as the focal population). Genetic drift is greater in populations with small effective size, reducing both genetic diversity and the efficiency of selection. This further diminishes vital rates through two distinct genetic chains of causation that can act simultaneously: (1) increased inbreeding and inbreeding depression; and (2) reduced EP, which in turn results in maladaptive phenotypes and reduced fitness. Notably, current approaches for evaluating extinction risk rarely incorporate this second chain of causation.

These same population-level factors, along with metapopulation processes and environmental heterogeneity, collectively determine species-wide extinction risk (Figure 3). First, the size, number, and distribution of populations across a species' range affect extinction probabilities. Species with smaller ranges, and/or fewer and more-isolated populations (Figure 3, Species 1 and 2) are more likely to have populations subject to extinction-vortex processes, including reduced EP. All else being equal, species with larger ranges, larger population sizes, and/or more continuously

Panel 2. Challenges and advances in estimating EP

Comprehensively evaluating EP in any species is virtually impossible given the complexity of the genetic, demographic, environmental, and ecological factors that influence it. This is especially true for at-risk species, which are often difficult to study and for which management decisions must be made with limited resources and under firm timelines. To assess EP, we first must know which stressors (eg climate change, disease, habitat loss, or, more commonly, some interaction of these) are most important in driving population trajectories, and how their importance may shift over time. Second, we must identify the traits that mediate responses to those stressors and then quantify relationships among traits, individual fitness, population growth rates, and extinction probabilities. Finally, we must quantify the additive genetic variation (variation that is responsive to selection) in these traits, and the distribution of this variation within and among populations. In addition, complicating factors can affect these estimates of EP, including plasticity and genotype by environment interactions, epigenetic variation, and biotic interactions (Bonduriansky *et al.* 2012; O'Brien *et al.* 2017). Attaining a thorough understanding of EP is therefore a formidable task even for model species and is essentially impossible for species of conservation concern.

Although a comprehensive understanding of EP is likely not possible, advances in sequencing technology have democratized the quantification of useful proxies for EP in at-risk species (Table 1; WebTable 3; Harrisson *et al.* 2014; Funk *et al.* 2019). Before these advances, the gold-standard methods for quantifying EP required controlled crosses, long-term studies of marked individuals, rearing individuals in controlled environments, and/or reciprocal transplants, none of which are typically feasible for fragile, declining populations or mobile animals. Genomics has improved our ability to quantify the genetic basis of trait variation and adaptive differences among populations in almost any species of interest (see "Proxies for EP" section). In addition, the increasing availability of high-quality annotated reference genomes (ie chromosome-level genome assemblies with biological information associated with sequences) for species of conservation concern (or close relatives) is improving the quality of genomic inferences of EP. Like all proxies for EP, genomic approaches have assumptions and caveats, but the palette of options these data provide has dramatically augmented our ability to estimate EP in at-risk species and incorporate those estimates into extinction-risk assessments.

distributed populations (Figure 3, Species 3) will have larger census population and effective population sizes, reduced genetic drift, increased EP, and higher birth and survival rates. Gene flow can act to either reduce EP (ie swamping out locally adaptive variants), or increase EP (ie introduce beneficial adaptive variants) (Lenormand 2002; Weiss-Lehman and Shaw 2019). Lack of gene flow (Figure 3, Species 1 and 2) can prevent movement of beneficial genetic variation, reducing EP and increasing inbreeding depression in small populations (Hanski *et al.* 2011).

Second, species with minimal variability in environmental conditions across their geographic range (Figure 3, Species 1) will tend to have reduced EP at the species level compared to more widely distributed species whose ranges span selective conditions (Forester *et al.* 2016). Species with greater environmental heterogeneity across the range but composed of small, isolated populations (Figure 3, Species 2) will also have reduced EP at the species level due to the overriding influence of genetic drift. Larger, better-connected, and more continuously distributed populations spanning greater environmental heterogeneity (Figure 3, Species 3) will typically maintain higher levels of EP. The interaction of these population-level and range-wide processes determine susceptibility to extirpation and extinction during ecological disturbance (Figure 3, shift from left to right panel), such that species with higher EP are more likely to show an evolutionary response to change (Figure 3, Species 3), whereas species with lower EP are more likely to have maladapted populations subject to extirpation (Figure 3, Species 1 and 2).

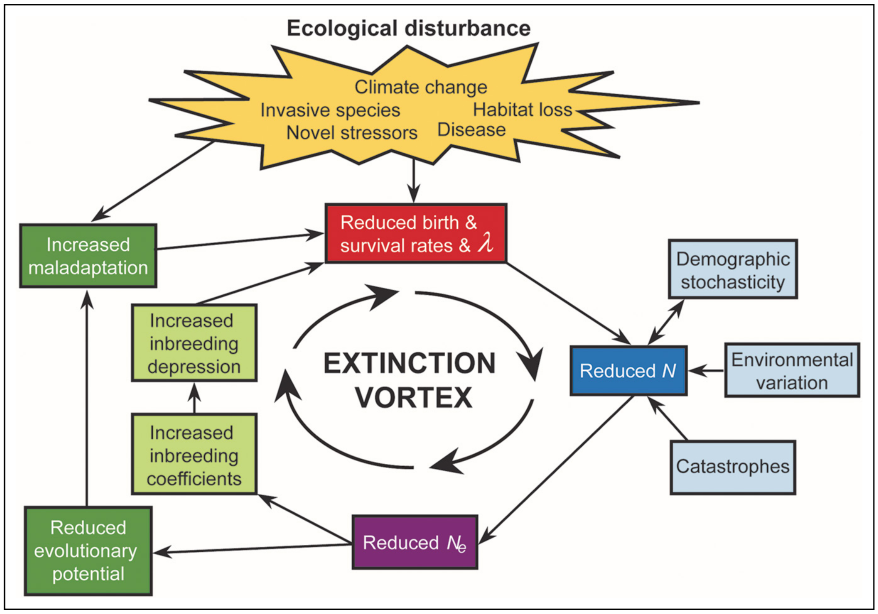

Figure 2. An extinction vortex incorporating effects of loss of evolutionary potential (EP; dark green boxes) on extinction risk for a single population (ie extirpation risk). Ecological disturbances (yellow) reduce vital rates, population growth rate (λ, red), and census population size (N, dark blue). Demographic stochasticity (the impacts of which increase as N decreases), environmental variation, and catastrophes (light blue) further reduce N. This reduces effective population size (N_e, purple), further diminishing vital rates through two distinct genetic mechanisms: increased inbreeding depression (light green); and reduced EP, resulting in maladaptation. Modified from Gilpin and Soulé (1986); Soulé and Mills (1998); Frankham *et al.* (2002).

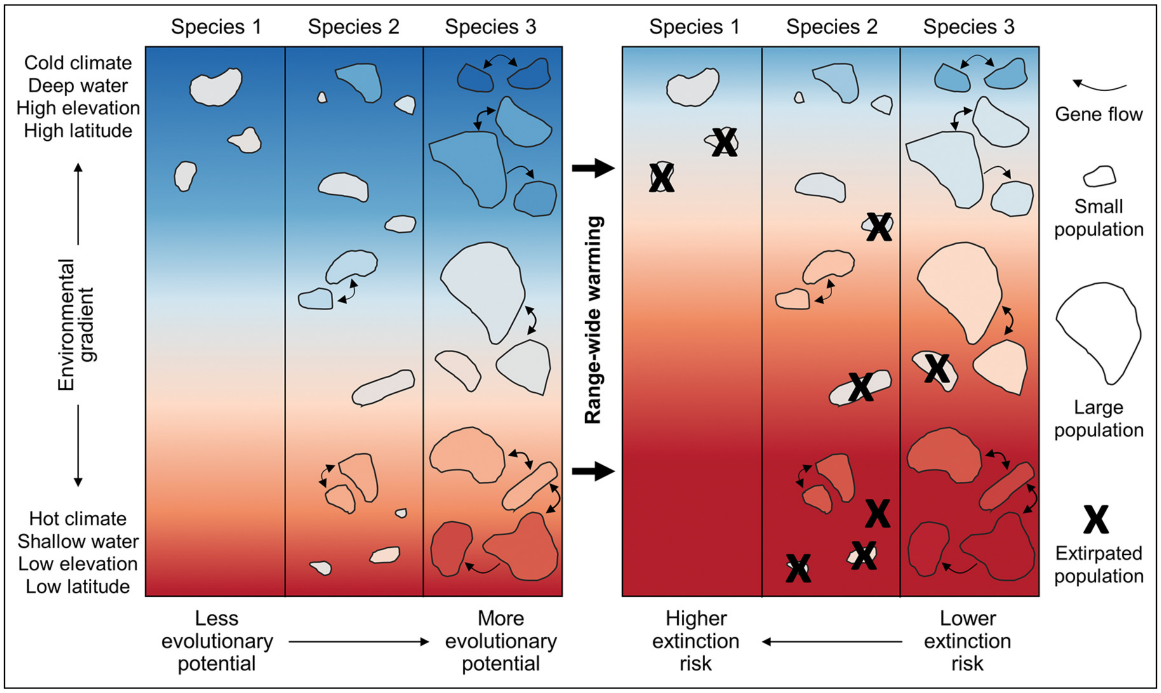

Figure 3. Species-wide EP (left panel) and extinction risk (right panel) depend on the distribution and size of populations, gene flow, and range-wide environmental heterogeneity (color gradient). Populations are adapted to the local environment (match between polygon and background color), given appropriate conditions (eg sufficient effective size and gene flow); otherwise, they are maladapted (color mismatch). In response to warming (right panel), Species 1 faces high extinction risk because its small, isolated populations have low EP. Species 3 faces lower risk due to its many large, well-connected populations and high EP, facilitating an evolutionary response to warming (color change to match background).

This theory points to a set of simple best practices for maintaining EP (Panel 3).

Evidence linking EP to extinction risk

Beyond theoretical predictions, evidence from simulations, experimental studies, and research in wild populations supports the importance of EP in buffering extinction risk. Here, we present a few recent examples (additional studies are presented in WebTable 2).

In a simulation study of two reef-building corals, Walsworth *et al.* (2019) modeled EP as additive genetic variation – the amount of total genetic variation that responds to natural selection (Table 1). They found that warming temperatures drove corals to rapid functional extinction in the absence of EP. In contrast, even low levels of EP allowed corals to maintain high cover and support ecosystem function in the face of rising temperatures. Conserving populations across trait (thermal tolerance) and environmental (temperature) variability while protecting intervening reefs that maintained gene flow promoted resilience to ongoing and unpredictable warming. Similarly, Walters and Berger (2019) used a framework linking EP, demography, and environmental change to determine how EP across a simulated species' range influenced extinction risk; they found that EP, modeled as local adaptation across an environmental gradient (Table 1), increased time to extinction up to threefold across a range of carrying capacities and rates of environmental change. In their model, key determinants of species persistence time included the availability of standing genetic variation to provide preadapted variants, and sufficient connectivity to facilitate gene flow as the environment changed.

Experimental studies have also confirmed the importance of EP in buffering extinction risk. Ørsted *et al.* (2019) used replicated experiments with fruit flies (*Drosophila melanogaster*) to investigate relationships among population bottlenecks, loss of genome-wide variation, EP, and extinction risk. Populations with high genome-wide genetic diversity (Table 1) exhibited a strong evolutionary response under stressful conditions, whereas populations with low genome-wide genetic diversity showed reduced EP and experienced high rates of extinction. In another example, Morgan *et al.* (2020) found that wild-caught tropical zebrafish (*Danio rerio*) had a limited ability to increase their thermal tolerance (ie low evolvability for thermal tolerance) (Table 1). Although thermal acclimation (plasticity) allowed individuals to increase their thermal tolerance, acclimation capacity declined over multiple generations of selection for higher thermal tolerance. Because these populations already live close to their thermal limit, a hard constraint on upper thermal tolerance puts warm-water populations at higher risk of extirpation as climate change increases the frequency, duration, and magnitude of heat waves.

Studies in wild populations have also illustrated the importance of EP in mitigating extinction risk. Little brown bats (*Myotis lucifugus*) were widely distributed across North America before

Table 1. Examples of proxies for estimating evolutionary potential (EP), including their data requirements, strengths, and weaknesses

Proxy	Data requirements	Strengths for quantifying EP	Weaknesses for quantifying EP
Narrow-sense heritability or evolvability of a trait	Fitness-relevant trait data; pedigrees or genomic data	Directly assesses short-term EP of a trait in a population by quantifying additive genetic variance	Estimates are trait-, population-, and environment-specific; trait might not reflect those most important for future adaptation; data can be difficult or impossible to collect for at-risk species
Genetic markers identified through genotype–environment associations	Genomic data; environmental data	Identifies genetic markers associated with environmental variation; can identify local adaptation, reflecting spatially variable EP across landscapes; generality (ie not trait-specific) might better capture species-wide EP	Relevant traits and heritability are unknown; results are correlative without further validation
Genome-wide genetic diversity	Genomic data	Quantifies overall genetic diversity across populations that might be correlated with EP; generality (ie not trait- or environment-specific) might better capture species-wide EP	Does not always reflect EP (eg EP in some traits can be retained even with low genome-wide diversity); difficult to incorporate into quantitative extinction-risk assessments
Ecotypes	Phenotypes; environmental data; sometimes genetic/genomic data	Links phenotypic and environmental variation reflecting potential functional variation that might correlate with species-wide EP; sometimes includes genetic distinctiveness	Phenotypes might not be heritable (ie phenotypic variation can be due to plasticity); trait(s) might not reflect those needed for future adaptations; relationships are correlative
Full breadth of ecological variation	Environmental data	Reflects variable environmental selection that might correlate with species-wide EP; can be estimated for any species with location data; generality (ie not trait-specific) might better capture species-wide EP	Populations inhabiting different environments might not be locally adapted; relevant traits and heritability are unknown; difficult to incorporate into quantitative extinction-risk assessments

Notes: a full list of proxies and references is provided in WebTable 3.

precipitous declines and extirpations of populations due to the spread of white-nose syndrome, an infectious disease caused by an invasive fungal pathogen. Two studies conducted in different parts of the species' range compared non-survivors and survivors, and detected selection on standing genetic variation despite population bottlenecks and strong genetic drift (Auteri and Knowles 2020; Gignoux-Wolfsohn *et al*. 2021). Candidate genes associated with survival included those related to immunity, regulation of hibernation, metabolism, and breakdown of fat, although the exact genes identified differed across studies and regions. Strong selection associated with mass mortalities might have acted on variable standing genetic variation distributed across the range, resulting in evolutionary responses through distinct genetic pathways. Little brown bats remain vulnerable to extinction, but slow recovery of populations in certain locations demonstrates the importance of high levels of standing genetic variation to maintain EP in widespread species in the face of known (eg climate change) and unknown (eg novel diseases) threats (Panel 3).

Proxies for EP

As demonstrated above, EP can be an important parameter buffering species from extinction during ecological disturbance. But how do we quantify EP within and across populations? Because a comprehensive assessment of EP is impossible (Panel 2), we must use proxies reflecting population-level and/or species-wide EP in conservation assessments (Table 1; WebTable 3). These proxies provide different levels of evidence for EP, are associated with tradeoffs based on their degree of specificity versus generality, and vary in their practicality for informing quantitative models of extinction risk (next section). For example, estimating the heritability of a fitness-relevant trait (ie the proportion of phenotypic variation among individuals due to additive genetic variation) is considered a gold standard for quantifying EP. However, heritability estimates are trait-, population-, and environment-specific; require large sample sizes; and are unlikely to reflect the full suite of EP required for future adaptation. Although genomics has improved our ability to estimate heritability in wild populations (Gienapp *et al*. 2017), its practicality as a proxy for EP in at-risk species is likely to remain relatively low.

Fortunately, there are proxies that provide broader insights into EP such as genotype-environment associations (GEAs), which identify genetic markers associated with environmental variation, and differentiation-based tests, which identify markers showing signatures of divergent selection. Given that GEAs do not require large sample sizes, sampling designs can be optimized to evaluate adaptation across a species range (eg Ruegg *et al*. 2018). Differentiation-based tests complement GEAs by identifying markers unrelated to chosen environmental predictors that may reflect adaptation in response to unknown selective pressures. In both cases, results are correlative without further validation (eg through common garden experiments: Lasky *et al*. 2015; de Villemereuil *et al*. 2016), although an annotated reference genome can provide insight into the function of candidate markers. Scaling observed relationships between genotypes and environment and linking those to fitness (Bay *et al*. 2017b) provides an option for parameterizing extinction-risk models when functional relationships are unknown. In these cases, testing the sensitivity of extinction-risk profiles to these uncertain parameters is essential.

Other proxies, such as conserving populations across the full breadth of ecological variation, can be used in cases where

Panel 3. Simple best practices for maintaining EP

Given the complexity of estimating EP within populations and across species' ranges, conservation practitioners will need to rely on first principles to ensure that a species' EP is sufficiently protected to support adaptive responses to change. Foremost is to conserve populations across the full breadth of adaptive diversity. Because we do not always know what species will have to adapt to in the near- and long-term future (eg bats and white-nose syndrome), comprehensive conservation of EP is the best approach to reducing extinction risk in response to known and unknown threats (Sgro *et al.* 2011). At the species level, this means maintaining phenotypic, genetic, and environmental diversity across the species' geographic range (Figure 3). At the population level, this means maintaining large population sizes that reduce the impacts of demographic stochasticity, genetic drift, and inbreeding, and maximize EP (Figure 2). A second, related principle is to ensure the maintenance of evolutionary processes that drive adaptive evolutionary change: namely, natural selection and gene flow (Moritz 2002). This includes conserving climate/niche diversity range-wide to allow for persistence in the face of a variety of selective forces, maintaining patterns and levels of gene flow and connectivity, and conserving sufficient habitat (both quantity and quality) to ensure maintenance of population sizes that are robust to demographic stochasticity and genetic drift.

other data are not available. Because environmental heterogeneity can maintain genetic variation through differential selection and local adaptation (Forester *et al.* 2016), this approach can maximize EP by maintaining standing genetic variation, improving the capacity to respond to changing conditions (Figure 3; Panel 3; Huang *et al.* 2016; Walters and Berger 2019; Walsworth *et al.* 2019). A limitation is that levels of environmental heterogeneity cannot be quantitatively tied to EP, and consequently its utility in extinction-risk assessments is relatively low (but see the monarch butterfly example discussed below). However, this simple proxy does provide a basis for conserving EP in other management frameworks, such as spatial conservation planning (Hanson *et al.* 2017).

Recent experimental research in the model annual plant *Arabidopsis thaliana* reinforces the value of more generalizable proxies for EP in conservation practice. Fournier-Level *et al.* (2016) combined common garden experiments and simulations to predict evolutionary responses of multiple traits across climate-change scenarios. The genetic basis and dynamics of trait adaptation varied among the scenarios, highlighting the difficulty of predicting the molecular basis of EP, even in a model species. Still, populations with higher genetic diversity exhibited increased EP across all scenarios, reinforcing the utility of a basic approach to conserving EP: protecting standing genetic variation within populations and across environments that are as diverse as possible (Panel 3; Kardos *et al.* 2021). These results also illustrate how conservation-relevant estimates of EP are not necessarily improved by understanding the genetic basis and heritability of traits (but see Kardos and Luikart 2021). Instead, more inclusive proxies of EP might capture more variance in adaptive responses to complex environmental drivers, yielding more comprehensive evaluations of EP and its relationship with extinction risk.

Integrating proxies for EP into extinction-risk assessments

Evaluating extinction risk is challenging, given the complexity of ecological and evolutionary interactions operating across scales (Figures 2 and 3). This is compounded by uncertainty regarding future trajectories of ecological disturbances, their interaction with population persistence, and the complications of unknown threats, such as novel diseases. Given this complexity, EP is usually overlooked when assessing extinction risk. However, EP is increasingly being incorporated into other conservation frameworks, such as species distribution models, which forecast range shifts in response to stressors like climate change (eg Bush *et al.* 2016; Razgour *et al.* 2019; Selmoni *et al.* 2020). Although these evolutionarily informed species distribution models are improvements over their static counterparts, their results cannot generally be extrapolated to quantify extinction risk (Foden *et al.* 2019), the parameter most commonly used to assign conservation status under legislative frameworks (WebTable 1).

Recent work to inform US Endangered Species Act decision making has attempted to bridge this gap by evaluating ecotype-level extirpation risk in the monarch butterfly (*Danaus plexippus*). This study delineated eight "adaptive capacity units" or ecotypes based on phenotypic diversity, genetic variation, and ecological setting (USFWS 2020). For the data-rich eastern and western North American ecotypes (Figure 4, a and b), extirpation risk was evaluated independently using population viability analysis. The projected persistence of both ecotypes under future conditions was only 10% over 30 years. Extirpation of these ecotypes would represent loss of the largest monarch populations globally, and substantial loss of EP species-wide, due to loss of the ancestral migratory phenotype. Although this approach does not quantify contributions of EP to mitigating extirpation risk within ecotypes, it provides a qualitative assessment of how their loss could reduce species-wide EP, contributing to extinction risk.

Studies that explicitly incorporate proxies for EP into species-level extinction-risk assessments are rare (we found no examples in the published or gray literature), making this an important area for research and methods development. Estimates of extinction risk that include EP will require integration of demographic and evolutionary dynamics in response to shifting environmental conditions, an approach referred to as dynamic ecological–evolutionary modeling (DEEM). The most comprehensive of these models will be spatially explicit, and capable of including demographic and reproductive processes, landscape and environmental heterogeneity and change, biotic interactions, dispersal dynamics and range shifts, neutral genetic processes, and proxies for EP. There are a number of simulation programs that accommodate most, if not all, of the above characteristics (WebTable 4). DEEMs require extensive data, and might need to be parameterized using expert elicitation in combination with sensitivity analyses to determine how parameter uncertainty impacts model trajectories (Funk *et al*. 2019).

To our knowledge, only one study (Bay *et al*. 2017b) has incorporated proxies for EP into an assessment of population extirpation risk, providing a model for future work covering entire species ranges. Bay *et al*. (2017b) used a DEEM to forecast extirpation risk of a population of *Acropora hyacinthus* coral (Figure 4, c and d) by integrating genomic data related to thermal tolerance with demographic parameters and climate-change scenarios. The proxies for EP used in the Bay *et al*. (2017b) study were candidate genetic markers related to temperature, identified using GEA and differentiation-based tests. The authors modeled a link between these markers and sea-surface temperature, including a sensitivity analysis given uncertainty in the relationship to population fitness. Under low-emissions climate-change scenarios, the population persisted via adaptive shifts in genetic markers, whereas higher emissions scenarios caused population extirpation due to maladaptation and negative growth rates. Translocation of warm-tolerant "preadapted" corals accelerated evolutionary responses and prevented population extirpation under high-emissions scenarios. Extending this work in a spatially explicit framework to incorporate metapopulation dynamics and range shifts is an important next step in estimating regional or species-wide extinction risk in response to warming. Other studies have used DEEMs to investigate EP and extinction risk, although they lacked empirical data to parameterize proxies for EP (eg Reed *et al*. 2011; Cotto *et al*. 2017; Matz *et al*. 2020; McManus *et al*. 2021). These studies provide additional evidence for the importance of EP in buffering extinction, and proof of concept for the utility of integrative simulations.

Although DEEMs will not be feasible to parameterize for data-deficient species, they are currently one of the best tools available for incorporating proxies for EP into extinction-risk assessments. As with any method for evaluating extinction risk, simulations are limited to the parameterizations and scenarios tested, and cannot represent all factors that contribute to species vulnerability. They should therefore represent part of a comprehensive approach to assessing extinction risk and ensuring the conservation of EP across species' ranges. Expanding the use of ecological–evolutionary modeling and developing new approaches to integrate EP into extinction-risk assessments will enable valuable science-based decision support in the face of ongoing and unprecedented losses of global biodiversity (Chevin *et al*. 2010; Pierson *et al*. 2015; Bay *et al*. 2017a).

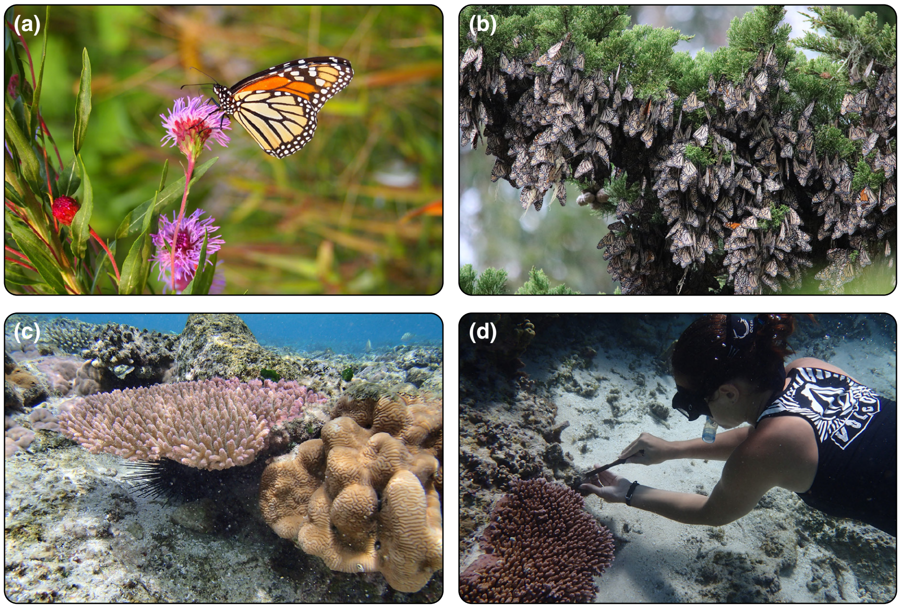

Figure 4. (a) Eastern monarch butterfly (*Danaus plexippus*) in the Midwestern US before migrating to Mexico (K Nail; USFWS). (b) Western monarch butterflies overwintering in Pacific Grove, California (J Gilkeson, USFWS). (c) *Acropora hyacinthus* (pink) among other corals in Rarotonga, Cook Islands (R Bay). (d) Sampling *A hyacinthus* for genomic analysis (M Morikawa).

Conclusions

EP can have profound implications for extinction risk. Once species-wide EP is lost, it is extremely difficult to restore (de Villemereuil *et al*. 2019; Jaramillo-Correa *et al*. 2020), underscoring the importance of implementing basic practices for maintaining EP, most notably conserving populations across the full breadth of species-wide adaptive diversity and protecting the integrity of processes that drive evolutionary change. Beyond these best practices, proxies for EP provide valuable information to inform both extinction-risk assessments and recovery efforts in the face of global change. If information on EP is ignored, conservation prioritization can be misdirected and actions to improve long-term persistence may be misguided (Funk *et al*. 2019; Walsworth *et al*. 2019). For example, extinction-risk estimates could be biased high if EP is disregarded, elevating protection status and shifting scarce resources away from species at higher risk. Similarly, if EP is not considered in recovery planning, opportunities to mitigate extinction risk through actions such as assisted gene flow could be missed (Aitken and Whitlock 2013). Frameworks that incorporate EP into quantitative extinction-risk assessments remain at the frontier of ecological–evolutionary research, providing opportunities for innovation and advancement in applied conservation science.

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Data Availability Statement

No data were collected for this study.

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