

# **Linking evolutionary potential to extinction risk: applications and future directions**

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Running head: Evolutionary potential and extinction risk

Key words/phrases: adaptive capacity, climate change, conservation, dynamic eco-evolutionary models, environmental disturbance, evolutionary potential, extinction risk, genetics, global change, simulations

Open Research Statement: No data were collected for this study.

*In Press*, Frontiers in Ecology and the Environment. Accepted November 4, 2021.

## **Abstract**

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 area for innovation in applied conservation science.

## **In a nutshell**

- Evolutionary potential (EP) can reduce a species' extinction risk by facilitating adaptive responses to environmental change. EP is challenging to quantify, but 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.

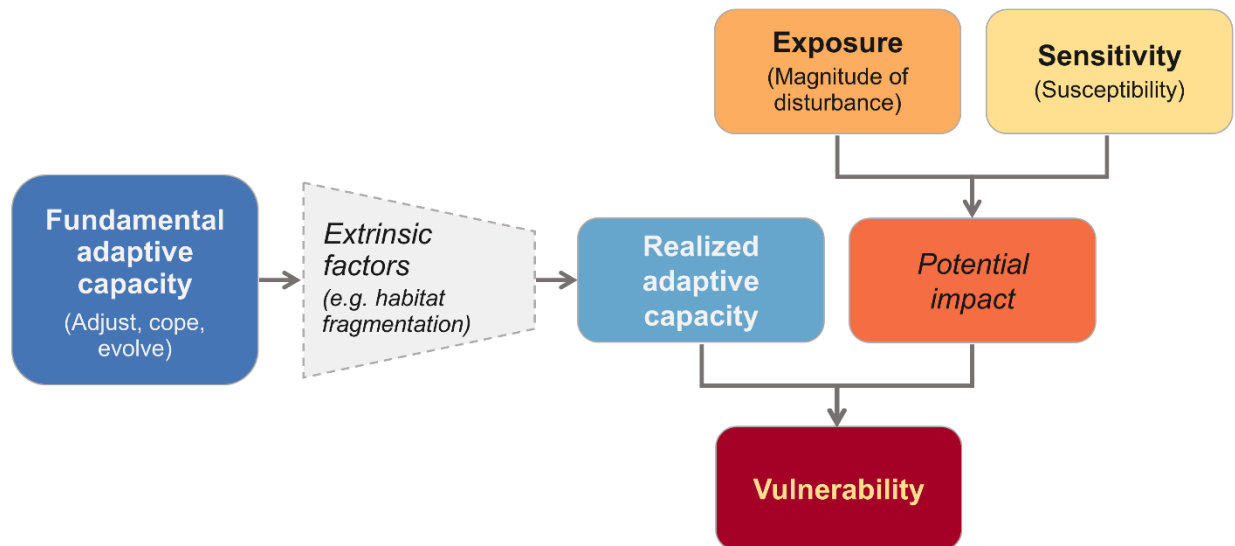
The profound transformation of the biosphere by human actions is driving population extirpations and species extinctions (Ceballos *et al.* 2017; Sage 2020). Adaptive capacity—the ability to accommodate, cope with, or respond to dynamic conditions—fundamentally determines whether and how species will persist or decline in response to ecological disturbances (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. Unfortunately, adaptive capacity in response to disturbance is poorly understood and is thus often ignored in assessments of vulnerability and extinction risk.

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 in 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 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.

In this review, we examine the relationship between EP and extinction risk from theoretical and applied perspectives. We review proxies for EP, address their strengths and weaknesses, and discuss current approaches for integrating EP into extinction-risk assessments. These approaches are limited and represent an important challenge and opportunity for innovation in ecological-evolutionary research and conservation science.

### 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 originate in the climate change literature (e.g., Foden *et al.* 2019), they are useful in framing species' responses to disturbance more generally. Exposure defines the magnitude of disturbance, i.e., 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 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.

## **PANEL 2: Challenges and advances in estimating evolutionary potential**

Comprehensively evaluating EP in any species is virtually impossible given the complexity of 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 tight timelines. To assess EP, we first must know which stressors (e.g. 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 thus a formidable task even for model species and is essentially impossible for species of conservation concern.

Although a comprehensive understanding of EP is out of reach, advances in sequencing technology have democratized the quantification of useful proxies for EP in at-risk species (Table 1; Harrison *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 evolutionary potential”). Additionally, the increasing availability of high-quality annotated reference genomes (i.e., 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 improved our ability to estimate EP in at-risk species and incorporate those estimates into extinction-risk assessments.

**Table 1.** Examples of proxies for estimating EP, including their data requirements, strengths, and weaknesses. A full list of proxies and references can be found in WebTable 3.

<b>Proxy</b>	<b>Data requirements</b>	<b>Strengths for quantifying evolutionary potential</b>	<b>Weaknesses for quantifying evolutionary potential</b>
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 in 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 (i.e., 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 (i.e., not trait or environment specific) might better capture species-wide EP.	Does not always reflect EP (e.g., 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.	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 (i.e., 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 (i.e., 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.

## The theoretical relationship between evolutionary potential and extinction risk

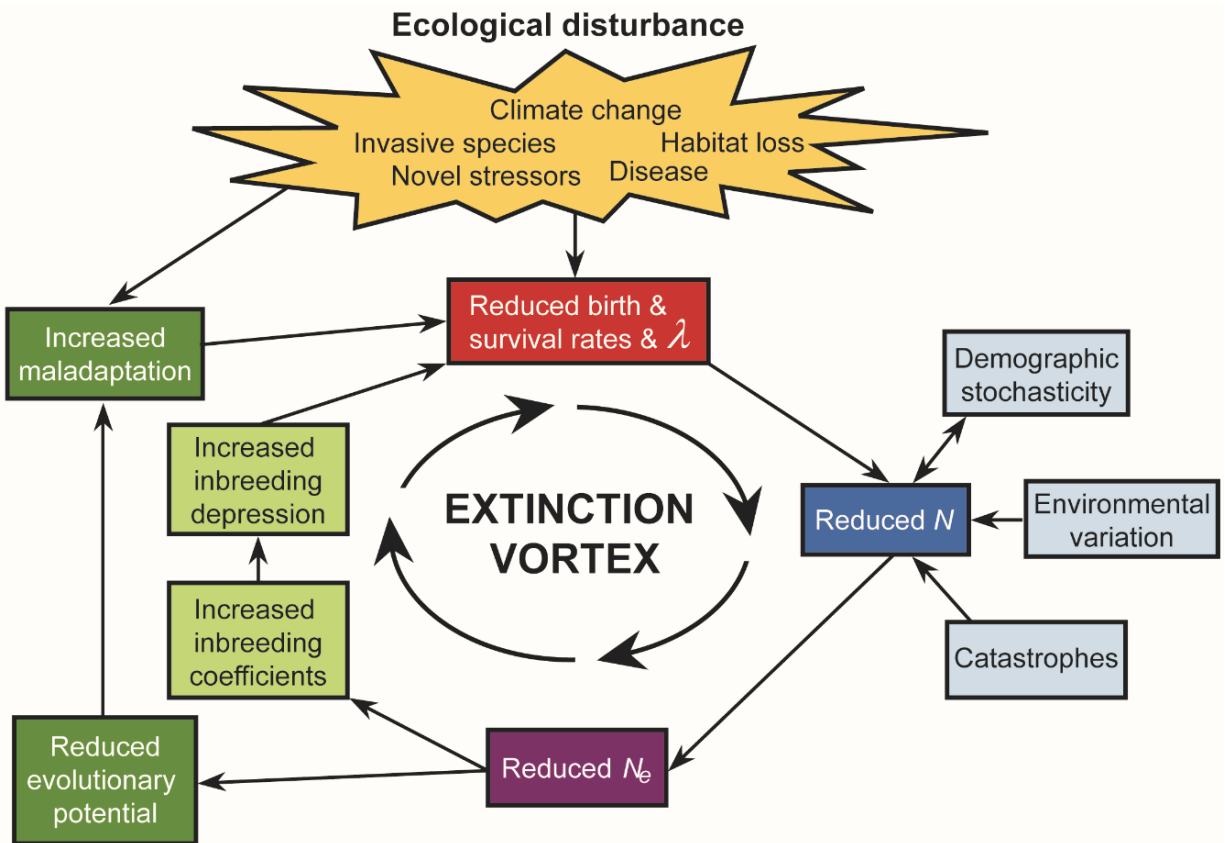
Theory predicts that populations and species must have the capacity to adapt to persist in the face of ecological disturbance (Gilpin and Soulé 1986; Burger and Lynch 1995; Soulé and Mills 1998). Here, we distinguish extinction, which is complete loss of all populations and individuals of a species, from extirpation, which is 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 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 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 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, both decreasing genetic diversity and reducing the efficiency of selection. This further reduces vital rates through two distinct genetic chains of causation that can act simultaneously: (1) increasing inbreeding and inbreeding depression and (2) reducing EP, which in turn results in maladaptive phenotypes and reduced fitness. Importantly, current approaches for evaluating extinction risk rarely incorporate this second chain of causation.

These same population-level factors, plus 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 distributed populations (Figure 3, Species 3) will have larger census and effective sizes, reduced genetic drift, increased EP, and higher birth and survival rates. Gene flow can act to either reduce EP (i.e., swamping out locally adaptive variants), or increase EP (i.e., 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).

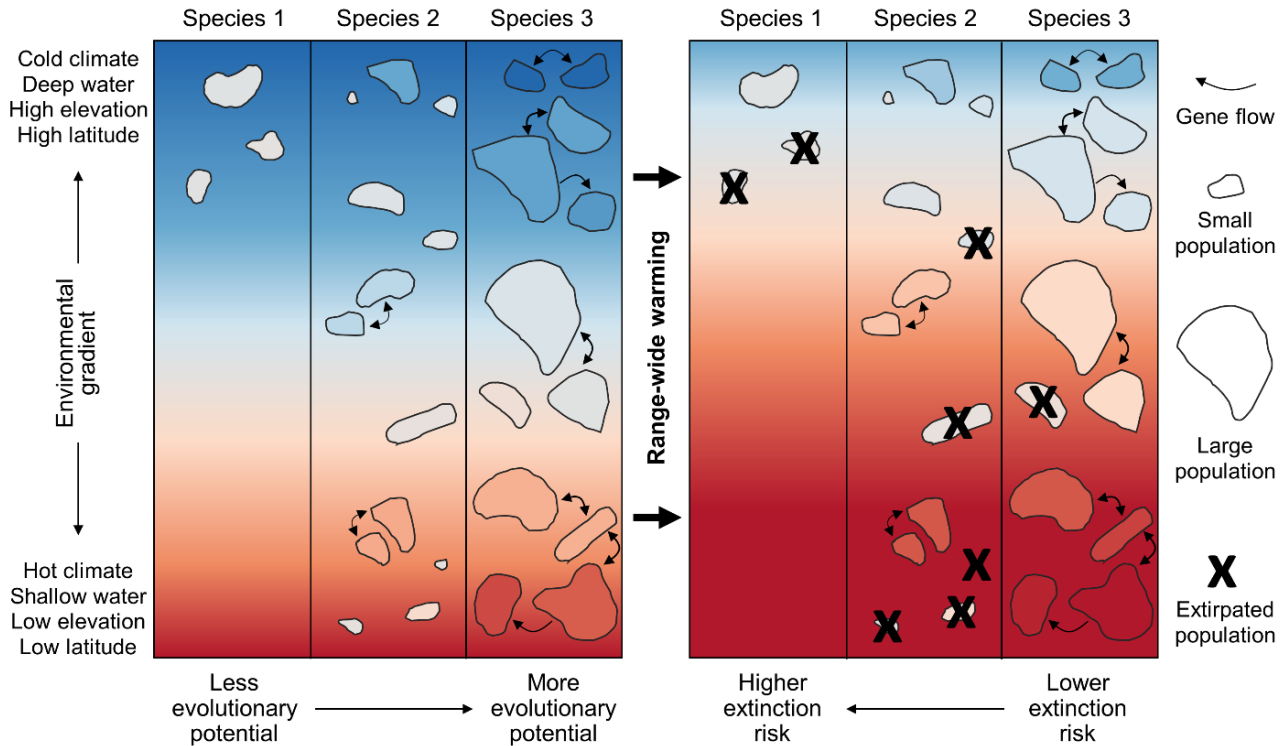
Second, species with minimal variability in environmental conditions across their geographic range (Figure 3, Species 1) will tend to have reduced EP at the species level compared to more-widely distributed species whose ranges span selective conditions (Forester *et al.* 2016). Species with greater 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 (Species 3), whereas species with lower EP are more likely to have maladapted populations subject to extirpation (Species 1 and 2). This theory points to a set of simple best practices for maintaining EP (Panel 3).



**Figure 2.** An extinction vortex incorporating effects of loss of EP (dark-green boxes) on extinction risk for a single population (i.e., extirpation risk). Ecological disturbances (yellow) reduce vital rates, population growth rate ( $\lambda$ , 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 decreases effective population size ( $N_e$ , purple), further reducing 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; and 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 (e.g., 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).

### PANEL 3: Simple best practices for maintaining evolutionary potential

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 (e.g., bats and white-nose syndrome, see below), 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.

### **Evidence linking evolutionary potential 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 appear in WebTable 2.

In a simulation study of two reef-building corals, Walsworth and colleagues (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. By 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. 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 and colleagues (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 higher genome-wide genetic diversity (Table 1) exhibited a stronger evolutionary response under stressful conditions, whereas populations with low genetic diversity showed reduced EP and higher rates of extinction. Morgan and colleagues (2020) found that wild-caught tropical zebrafish (*Danio rerio*) had a limited ability to increase their thermal tolerance (i.e., 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 precipitous declines and extirpations caused by 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, though 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, though slow recovery in some locations demonstrates the importance of high levels of standing genetic variation to maintain EP in widespread species in the face of known (e.g., climate change) and unknown (e.g., novel diseases) threats (Panel 3).

### **Proxies for evolutionary potential**

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 vs. 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 (i.e., 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. GEAs do not require large sample sizes, so sampling designs can be optimized to evaluate adaptation across a species range (e.g., Ruegg *et al.* 2018). Differentiation-based tests complement GEAs by identifying markers not related to chosen environmental predictors that may reflect adaptation in response to unknown selective pressures. In both cases, results are correlative without further validation (e.g., through common garden experiments: Lasky *et al.* 2015; de Villemereuil *et al.* 2016), though 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 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, so their utility in extinction-risk assessments is relatively low (though see monarch example, next section). 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 and colleagues (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 across scenarios, highlighting the difficulty of predicting the molecular basis of EP, even in a model species. Despite this, populations with higher genetic diversity had 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). These results also illustrate how conservation-relevant estimates of EP are not necessarily improved by understanding the genetic basis and heritability of traits (though 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 evolutionary potential into extinction-risk assessments**

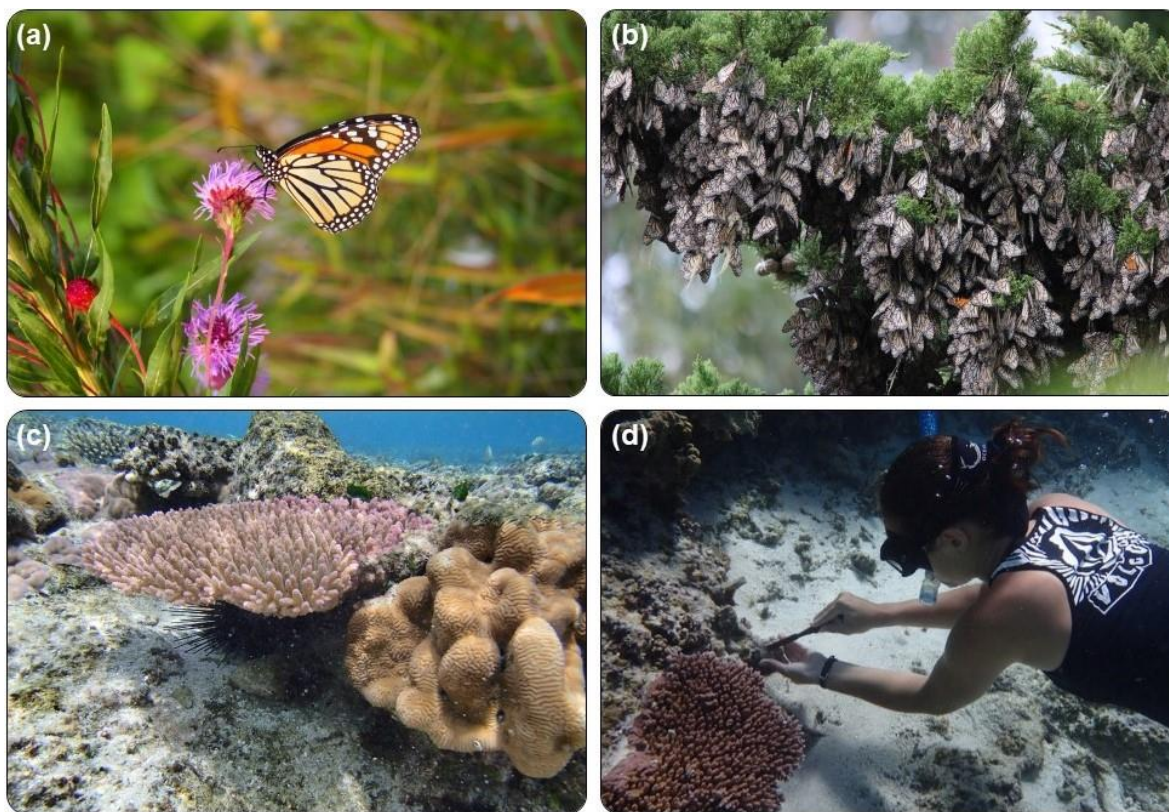
Evaluating extinction risk is challenging, given the complexity of ecological and evolutionary interactions operating across scales (Figures 2 and 3). This is compounded by uncertainty regarding future trajectories of ecological disturbances, their interaction with population persistence, and the complications 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 (e.g., Bush *et al.* 2016; Razgour *et al.* 2019; Selmoni *et al.* 2020). Although these evolutionarily-informed species distribution models provide 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 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 4a 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 (the authors found no examples in the published or grey 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, there is currently only one study that incorporates proxies for EP into population extirpation risk, providing a model for future work covering entire species ranges. Bay and colleagues (2017b) used a DEEM to forecast extirpation risk of a population of *Acropora hyacinthus* coral (Figure 4c and d) by integrating genomic data related to thermal tolerance with demographic parameters and climate change scenarios. The proxies for EP used in this 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, while 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, though they lacked empirical data to parameterize proxies for EP (e.g., 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. Like 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 on blazing star (Kelly Nail). (b) Western Monarch butterflies overwintering in Pacific Grove, California (Joanna Gilkeson, U.S. Fish and Wildlife Service). (c) *Acropora hyacinthus* (pink) among other corals in Rarotonga, Cook Islands (Rachael Bay). (d) Sampling *A. hyacinthus* for genomic analysis (Megan Morikawa).

## Conclusions

Evolutionary potential 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), highlighting the importance of basic practices for maintaining EP: 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 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 opportunity for innovation and advancement in applied conservation science.

## Acknowledgments

Funding for this research was provided by a David H. Smith Conservation Research Fellowship to BRF and an NSF grant to WCF (DEB 1838282). The authors thank Carly Cook and Tomoki Sakiyama for information on conservation legislation, and Robin Waples, Marty Kardos, and two anonymous reviewers for helpful feedback. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. This article has been peer reviewed and approved for publication consistent with USGS Fundamental Science Practices (<https://pubs.usgs.gov/circ/1367/>).

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WebTable 1. Selected conservation legislation and frameworks and how extinction risk is used to determine conservation status

Country	Conservation legislation or framework	Examples of how extinction risk is used to determine conservation status	References
International	Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	CITES is an international agreement with the goal of ensuring that "international trade in specimens of wild animals and plants does not threaten the survival of the species" ( <a href="https://cites.org/eng/disc/what.php">https://cites.org/eng/disc/what.php</a> , accessed 5/24/2021). Species protected under Appendix I of CITES include "...all species threatened with extinction which are or may be affected by trade", while Appendix II includes "...all species which although not necessarily now threatened with extinction may become so unless trade in specimens of such species is subject to strict regulation in order to avoid utilization incompatible with their survival" (CITES 1973, Article II).	CITES (1973)
International	International Union for the Conservation of Nature (IUCN) Red List of Threatened Species	The IUCN Red List uses categories to assign threat status to wild populations; the three threatened categories (critically endangered, endangered, and vulnerable) are characterized by extremely high, very high, and high risk of extinction in the wild, respectively, evaluated using five quantitative criteria.	IUCN (2012)
Australia	Environment Protection and Biodiversity Conservation Act 1999 (EPBC)	Uses extinction risk to assign threat categories (critically endangered, endangered, vulnerable) to both species and communities. For example, "A native species is eligible to be included in the critically endangered category at a particular time if, at that time, it is facing an extremely high risk of extinction in the wild in the immediate future, as determined in accordance with the prescribed criteria." (EPBC, Part 13, Division 1, Subdivision A, section 179-3).	EPBC (1999)
Canada	Species at Risk Act (SARA)	Defines an endangered species as "a wildlife species that is facing imminent extirpation or extinction" (SARA, S.C. 2002, c. 29, Interpretation, Definitions). Quantitative criteria for threatened or endangered status includes thresholds for probability of extinction in the wild defined by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).	SARA (2002); COSEWIC (2019)

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Costa Rica	Biodiversity Law of Costa Rica	Includes extinction risk for prioritization of conservation programs, e.g., "For the development of conservation programs, the State will give priority to the species threatened with extinction..." (Biodiversity Law, Article 55).	Legislative Assembly of the Republic of Costa Rica (1998)
Japan	Act on Conservation of Endangered Species of Wild Fauna and Flora and Basic Act on Biodiversity	The Act on Conservation of Endangered Species of Wild Fauna and Flora does not use the term extinction (in the English translation of the law), but does define as endangered those species with small populations that are deteriorating "to a level that would be detrimental to the survival of said species" (English language translation, Act on Conservation of Endangered Species of Wild Fauna and Flora, Article 4). The Basic Act on Biodiversity defines regulatory and conservation measures for species conservation as a function of "the likelihood of extinction" (English language translation, Basic Act on Biodiversity, Article 15).	Act on Conservation of Endangered Species of Wild Fauna and Flora (1992); Basic Act on Biodiversity (2008)
South Africa	National Environmental Management: Biodiversity Act, 2004	Uses extinction risk to assign threat categories (critically endangered, endangered, vulnerable) to species. For example, an endangered species is defined as "...any indigenous species facing an a high risk of extinction in the wild in the near future". (National Environmental Management: Biodiversity Act, 2004, Chapter 4, Part 2, Section 56).	National Environmental Management: Biodiversity Act (2004)
United States of America	Endangered Species Act (ESA)	Defines an endangered species as "any species which is in danger of extinction throughout all or a significant portion of its range" (ESA, Section 3, Definitions).	U.S. Endangered Species Act (1973)

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WebTable 2. Selected additional studies providing evidence linking evolutionary potential to extinction risk

References	Category of evidence	Brief description of the link between evolutionary potential and extinction risk
Cotto <i>et al.</i> (2017)	Simulation	Uses a dynamic eco-evolutionary simulation model parameterized with a mix of empirical data from four alpine plant species (e.g., demographic data) and simulated data (e.g., quantitative traits related to environmental variables). Models predict population and range declines over time due to maladaptation in response to climate change. Populations of the four species varied in their carrying capacities, and populations with smaller census sizes had reduced evolutionary potential. Species with long adult lifespans and limited dispersal showed signatures of extinction debt, with rapid loss of local adaptation.
Matz <i>et al.</i> (2020)	Simulation	Uses a dynamic eco-evolutionary simulation model to project the influence of local adaptation, standing genetic variation, migration, and future selection on the extinction risk of 680 coral reefs in the Central Indo-West Pacific in response to climate change. The majority of reefs were prone to decline and extirpation due to warming, especially those located in already warm conditions and those that did not receive migrants from warmer areas. By contrast, some reefs were able to adapt to warming conditions and persist over the 200 year simulation, particularly in populations where selection favored heat-tolerance alleles that already existed as standing variation prior to warming, and which were exchanged via migration.
McManus <i>et al.</i> (2021)	Simulation	Uses a dynamic eco-evolutionary simulation model applied to three coral reef regions around the globe. Incorporates regional dispersal patterns and eco-evolutionary dynamics for generalized coral species to investigate how evolution, dispersal, and selection (increasing temperature) influence coral reef persistence. Impacts of climate change varied across the three regions due to differences in habitat network characteristics, ecological setting, and evolutionary dynamics.
Nabutanyi and Wittmann (2021)	Simulation	Simulates positive feedbacks between reduced population size and loss of genetic variation at loci under balancing selection. Per capita rates of population decline and per-locus rates of loss of polymorphic loci increase with declining population size and declining numbers of polymorphic loci. Identifies a critical number of polymorphic loci and population size below which population size declines rapidly and extinction occurs.
Weiss-Lehman and Shaw (2019)	Simulation	Investigates the interaction of selection for increased dispersal (to facilitate range shifts during climate change) and population structure driven by local adaptation along a steep environmental gradient. The evolution of increased dispersal interacted negatively with adaptation along steep environmental gradients, reducing fitness. In this context, extinction was more likely in populations structured by these steep environmental gradients and/or stark range edges.

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Lachapelle and Bell (2012)	Experimental	Extinction risk in experimental populations of the green alga <i>Chlamydomonas reinhardtii</i> was lowest in populations with initially high genetic diversity and obligate sexuality due to an increased ability to respond to selection in response to a deteriorating environment.
Willi and Hoffmann (2009)	Experimental / Simulation	Experimental evolution in populations of the rainforest fruit fly ( <i>Drosophila birchii</i> ) compared the effect of census population size (20, 100, and 1000) on the response to five generations of heat-knockdown selection using simulations to model directional change in the thermal environment. Negative demographic effects (low growth rate and high stochasticity in growth rate) were most prominent in the smallest populations, which had the lowest additive genetic variance and highest extinction rates. Populations of intermediate size were negatively impacted by both demographic factors and reduced evolutionary potential despite higher genetic variance due to the interaction of increased demographic stochasticity, increased drift, and resulting reduction in evolutionary potential. Even the largest populations with highest reproductive output and lowest stochasticity were prone to eventual extinction due to relatively low levels of additive genetic variance and evolutionary potential.
Oziolor <i>et al.</i> (2019)	Wild population	Demonstrates hybridization as a mechanism for the introduction of adaptive variants crucial to adaptation to extreme environmental change (pollution); likely (unintentional) anthropogenic movement of Atlantic killifish to Gulf killifish range, facilitating adaptive introgression of toxicant resistance loci.
Thompson <i>et al.</i> (2019); Thompson <i>et al.</i> (2020)	Wild population	Degradation of river systems has resulted in loss of evolutionary potential in Chinook salmon via loss of the spring run phenotype and the corresponding “E lineage” genotype. Maintenance of the E lineage genotype in nearby basins means extirpation could be reversed, either through intrabasin migration (straying) or human-assisted translocation.
de Villemereuil <i>et al.</i> (2019)	Wild population	Lack of genome-wide genetic diversity, low heritability of traits under selection, and minimal additive genetic variance of fitness in the two remaining populations of endemic New Zealand hihi ( <i>Notiomystis cincta</i> ) indicate very low evolutionary potential species-wide to respond to environmental change. Avoiding extinction will depend on maximizing the number and size of populations as quickly as possible, which will also create conditions allowing for the regeneration of evolutionary potential over long periods of time.
Reed <i>et al.</i> (2011)	Wild population / Simulation	Using a simulation framework parameterized with empirical data from the population of interest and other populations and salmonid species, these authors tested how evolutionary potential in migration timing impacting population persistence under a range of climate change projections. They found that the ability to evolve earlier migration timing reduced future quasi-extinction risk by 83% compared to simulations where the population could not evolve.

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WebTable 3. Proxies for estimating evolutionary potential, including their data requirements, strengths, and weaknesses

Proxy	Data requirements	Strengths for quantifying evolutionary potential	Weaknesses for quantifying evolutionary potential	Selected references
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 may not reflect those most important for future adaptation. Data can be difficult or impossible to collect in at-risk species.	Hansen <i>et al.</i> (2011); Hoffmann <i>et al.</i> (2017); Gienapp <i>et al.</i> (2017)
Local adaptation of a trait via common gardens or reciprocal transplants	Fitness-relevant trait data obtained under common conditions.	Can demonstrate local adaptation in a trait. If replicated across environments, can reflect environmentally variable EP.	Estimates are trait-specific. Trait may not reflect those most important for future adaptation. Heritability is unknown. Data can be difficult or impossible to collect in at-risk species.	Lasky <i>et al.</i> (2015); de Villemereuil <i>et al.</i> (2016); Fournier-Level <i>et al.</i> (2016)
Genetic markers identified through genome-wide associations	Fitness-relevant trait data; genomic data.	Identifies genetic markers associated with a trait. Can identify local adaptation if evaluated across environments, reflecting environmentally variable EP.	Estimates are trait-specific. Genetic data may poorly explain trait variance. Trait may not reflect those most important for future adaptation. Results are correlative without further validation.	Auteri and Knowles (2020); Gignoux-Wolfsohn <i>et al.</i> (2021)
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 (i.e., not trait-specific) may better capture species-wide EP.	Relevant traits and heritability are unknown. Results are correlative without further validation.	Lasky <i>et al.</i> (2015); Bay <i>et al.</i> (2017); Ruegg <i>et al.</i> (2018); Capblancq <i>et al.</i> (2020)
Genetic markers identified through differentiation-based tests	Genomic data.	Identifies genetic markers with signatures of divergent selection. Can identify local adaptation. Generality (i.e., not trait- or environment-specific) may better capture species-wide EP in response to unknown stressors.	Relevant environmental drivers, traits, and heritability are unknown. Results are correlative without further validation.	Bay <i>et al.</i> (2017)

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Ecotypes	Phenotypes; environmental data.	Links phenotypic and environmental variation reflecting potential functional variation that may correlate with species-wide EP. Sometimes includes genetic distinctiveness.	Phenotypes may not be heritable (i.e., phenotypic variation may be due to plasticity). Trait(s) may not reflect those needed for future adaptations. Relationships are correlative.	Millien <i>et al.</i> (2006); Chen <i>et al.</i> (2018); Mahony <i>et al.</i> (2020)
Full breadth of ecological variation	Environmental data.	Reflects variable environmental selection that may correlate with species-wide EP. Can be estimated for any species with location data. Generality (i.e., not trait specific) may better capture species-wide EP.	Populations inhabiting different environments may not be locally adapted. Relevant traits and heritability are unknown. Difficult to incorporate into quantitative extinction-risk assessments.	Hampe and Petit (2005); Wilczek <i>et al.</i> (2014); Huang <i>et al.</i> (2016); Lee-Yaw <i>et al.</i> (2016); Hanson <i>et al.</i> (2017); Macdonald <i>et al.</i> (2017); Exposito-Alonso <i>et al.</i> (2018)
Full breadth of phenotypic variation	Phenotypes.	Reflects potentially functional trait variation that may correlate with species-wide EP.	Trait(s) underlying phenotype may not be heritable or may be plastic. Trait(s) may not reflect those most important for future adaptation. Difficult to incorporate into quantitative extinction-risk assessments.	Houle <i>et al.</i> (2010); Mills <i>et al.</i> (2018); Walters and Berger (2019); Walsworth <i>et al.</i> (2019)
Genome-wide genetic diversity	Genomic data.	Quantifies overall genetic diversity across populations that may be correlated with EP. Generality (i.e., not trait or environment specific) may better capture species-wide EP.	Does not always reflect EP (e.g., EP in some traits may be retained even with low genome-wide diversity). Difficult to incorporate into quantitative extinction-risk assessments.	Markert <i>et al.</i> (2010); Lohbeck <i>et al.</i> (2012); Lasky <i>et al.</i> (2015); Munshi-South <i>et al.</i> (2016); Exposito-Alonso <i>et al.</i> (2018); de Villedemereuil <i>et al.</i> (2019); Ørsted <i>et al.</i> (2019)
Ne 50/500 rule	Genetic or genomic data.	Ne > 500 is an established guideline for maintaining quantitative genetic variation for EP and future adaptation.	Does not provide a quantitative assessment of EP across populations. Difficult to incorporate into quantitative extinction risk assessments.	Jamieson and Allendorf (2012, 2013); Frankham <i>et al.</i> (2013); Hoffmann <i>et al.</i> (2017); Ørsted <i>et al.</i> (2019)

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WebTable 4. Selected dynamic eco-evolutionary simulation models

Model name	References
CDPOP	Landguth and Cushman (2010); Landguth <i>et al.</i> (2020)
CDmetaPOP	Landguth <i>et al.</i> (2017)
HexSim	Schumaker and Brookes (2018)
MetaPopGen 2.0	Andrello <i>et al.</i> (2021)
Nemo-age	Cotto <i>et al.</i> (2020)
QuantiNemo2	Neuenschwander <i>et al.</i> (2019)
SimAdapt	Rebaudo <i>et al.</i> (2013)
SLiM 3	Haller and Messer (2019)

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