

Title: Understanding organismal capacity to respond to anthropogenic change: Barriers and solutions

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Human activities are altering ecosystems across the planet at an unprecedented pace (Goudie 2006; Ellis & Ramankutty 2008; Sutherland et al. 2013; Aronson et al. 2014). The rapidity and scope of these changes challenge the ability of many species to cope, resulting in their decline and sometimes extinction (Parmesan 2006; Burkhead 2012; Beketov et al. 2013). Some species, however, are resilient to these changes while still others thrive in the altered or novel landscapes created by humans (McDonnell & Hahs 2013). At present, we have limited ability to predict which species will be winners and which will be losers in the face of anthropogenic change. This limitation highlights a fundamental gap in our understanding of what factors determine the capacity of organisms to adapt and acclimate to changes in the environment, and how these factors differ among species.

Here we first introduce the concept of multi-dimensional phenospace which undergirds our approach to describing and understanding evolutionary capacity. We then discuss existing barriers to research progress on this topic, and propose potential solutions to surmounting these barriers, many of which involve enhanced integration across biological disciplines. We end with a discussion of how an improved understanding of the evolutionary and ecological capacity of organisms to adapt would allow us to not only predict but potentially mitigate the accelerating impacts of human activity.

The Central Concept of Phenospace: Evolutionary capacity, or the lack of it, can be usefully considered in terms of multi-dimensional phenospace in which different dimensions represent the extent of possible variation in a particular phenotypic trait. These traits can be morphological, physiological, or behavioral. Figure 1a illustrates such phenospace for two different species, with the density maps representing the extent of phenotypic variation in two traits, X and Y. Phenospaces pose two related questions that are critical for understanding the capacity of species to evolve in response to changing environments. The first question is what determines the extent of phenospace that a species occupies? Are these limits determined by selection gradients such that values at the edge of a species distribution are sufficiently disfavored to be rarely seen? Or do they represent hard constraints to a species's ability to adapt? The second, and related, question is what is represented by the empty space between species distribution? Are they combinations that have low fitness values under present conditions? Or are they evolutionary unstable combinations of trait values that simply can not exist due to physical or other constraints? Alternatively, might they be combinations that simply have not been achieved due to the stochastic nature of evolution?

Importantly, such phenospace maps represent a single point in time. As environmental conditions change over time, some organismal trait combinations may become inviable. Some species may have the capacity to adapt to these new conditions by evolving different trait value combinations (Figure 1b- Species A), a process termed “Evolutionary rescue” (Carlson et al. 2014; McDermott 2019). Other species may not have this evolutionary capacity and may go extinct (Figure 1b- Species B). Evolutionary constraints on trait combinations along phylogenetic lineages (Figure 2) may inform which trait combinations are stable or unstable and therefore which organisms will persist under global change. However, our ability to link genotypic trait variation over evolutionary time with organismal traits and to understand how these traits predispose organismal ability to respond to global change remains one of the grand challenges in global change research.

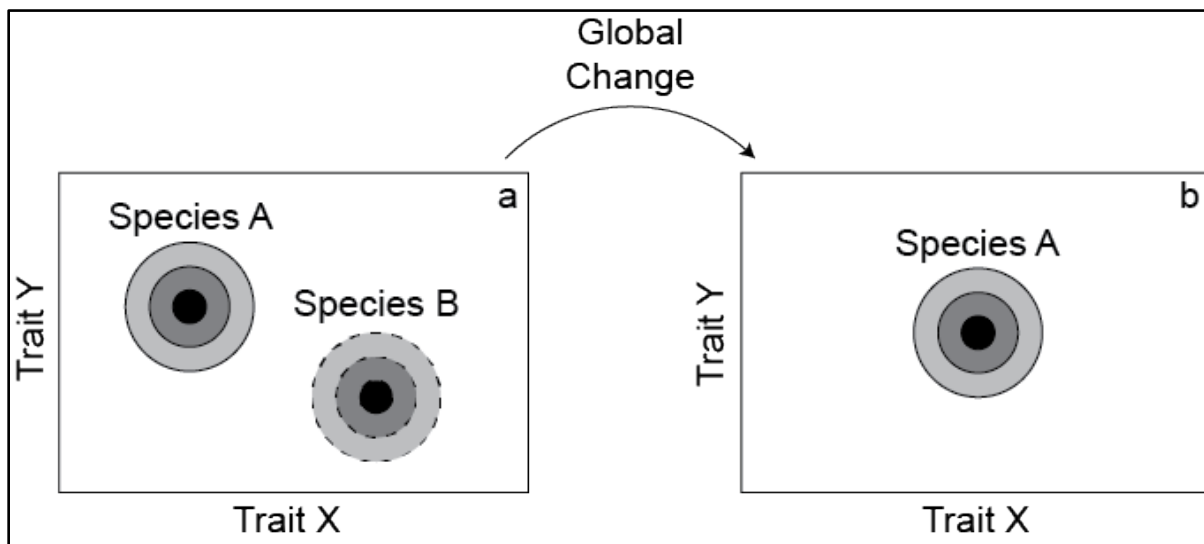
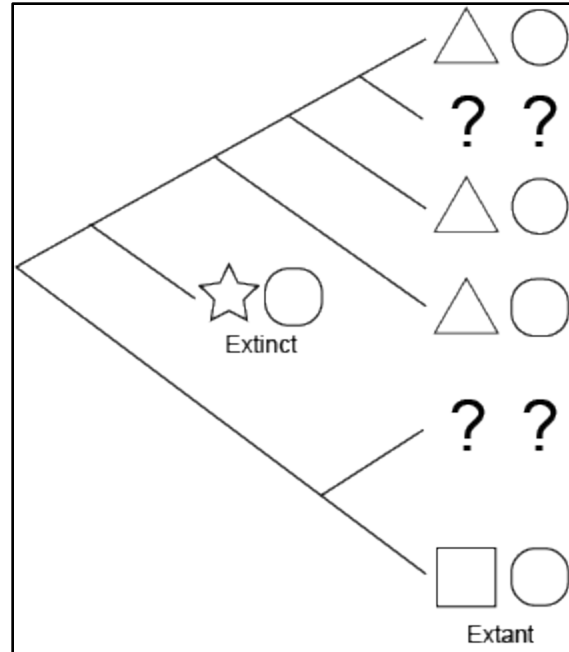


Figure 1. Phenospace of two species (A and B) in two traits (X and Y). Current position in phenospace may predict viability under anticipated global change.

Figure 2. Trait combinations vary among organisms. Accounting for this variation along evolutionary history may help predict which trait combinations are viable under current and future environmental conditions



Key Barriers: We see six key barriers that currently challenge our ability to understand why some organisms can adapt to anthropogenic change while others fail to do so. For each barrier we propose one or more solutions to overcome the challenge it represents.

Barrier 1: Documenting parameters of environmental change and their fitness effects:

The first key barrier to predicting winners and losers with anthropogenic change is a lack of understanding of the magnitude, frequency, and duration of predicted global change stressors and how these parameters vary across ecosystems. For example, some arctic and alpine ecosystems are clearly warming at faster rates than other biomes. Defining the global change context across ecosystems is fundamental to understanding how different abiotic conditions will alter organismal fitness.

- *Solution 1:* Data from remote sensing and ecological observation networks provide the global coverage necessary to address this problem. Coordinated NASA flyover data will allow us to collect fine grain data on environmental conditions and how they change over time. Paired with observations of organismal fitness collected from long-term observational networks such as NEON and LTER, we can begin to predict environmentally-dependent outcomes of organismal fitness. Because these coordinated observational networks are limited in scope, our predictable range will only be a fraction of the entire phenospace.

Barrier 2: Measure genotypic and phenotypic variation: Measuring existing genotypic and phenotypic variation across a species' range provides insights into the amount of standing variation that might contribute to the ability of an organism to respond to changing environments (Figure 3) but also depends on environmental variation (Charmantier & Garant 2005). Exploring the phenotypic variation allows us to place those organisms in their phenospace and track how it changes as the environment changes. Doing this retrospectively using museum collections and other existing long-term datasets will allow us to ascertain whether and how evolutionary rescue has already occurred. At present these data sets are relatively rare and not always widely accessible to the broader research community.

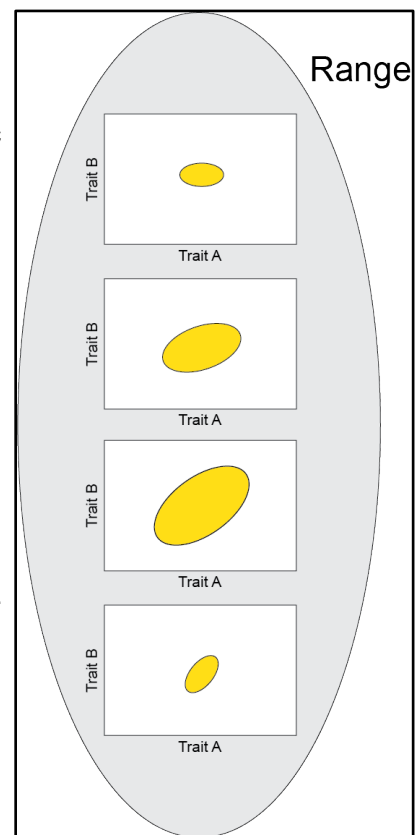
- *Solution 2:* Improving access to existing datasets on phenotypic variation could provide data to explore past and present levels of phenotypic variation in populations. It will allow us to explore the phenospace that an organism occupied in the past and possibly where it sits currently (depending on the data sets). If that species is a winner in successfully responding to environmental change then we may gain insights into the adaptive process that results in winners that we could then apply to other less successful species. It may also help us

understand constraints to phenotypic responses to rapid change. Computational improvements of spatial statistics will allow us to pair fitness landscapes with environmental gradients throughout a species range improving our understanding of how the fitness landscape changes across standing these abiotic gradients

Barrier 3: Linking genetic and phenotypic variation (and selection): If we can link the genetic basis to phenotypic variation we can begin to determine the genetic basis underlying adaptive responses (or winners). By understanding the genetic basis to evolutionary rescue we may be able to engineer winners in other organisms. Similarly, if we see new adaptive (or non adaptive) changes, we may be able to link those back to the genetic basis and begin to understand the process of selection and possibly to use this information to help alter non winner organisms (see create/engineer traits solution 6b).

- *Solution 3:* In addition to existing datasets, it will be necessary to generate new comprehensive data sets on genetic, phenotypic and environmental variation. Focusing on key target species will allow us to more quickly gain insights into genotypic and phenotypic basis to the ability to respond to environmental change, and help limit the costs associated with data collection. These data include a comprehensive description of phenotypic variation in each target species to understand the phenospace that describes that organism (Figure 3). They also include measuring genetic variation in these same target species to document standing genetic variation, provide a baseline for understanding evolutionary responses to rapid environmental change, and link genotype to phenotype.

Figure 3. Variation in a species' phenospace throughout its range.



Barrier 4: Understanding the role of cryptic variation in response to change: While genetic underpinning may play an important role in traits, phenotypic plasticity, and epigenetic processes such as methylation or alternative splicing may also aid in generating adaptive phenotypes that may respond well to novel environmental change.

While research in the areas of phenotypic plasticity and epigenetic have grown at a tremendous rate, efforts remain siloed across biological disciplines limiting our ability to understand how cryptic variation contributes to responses to environmental change. Given the rich history of phenotypic plasticity and epigenetic research across a diversity of disciplines, we are at an ideal time for reintegrating efforts across fields of biology to examine the contribution of cryptic variation to creating winning phenotypes. Doing so may help us to gain a better understanding of the processes that may aid in species responding and ultimately adapting to environmental change, or failing to adapt.

- *Solution 4:* One solution to understanding how some organisms cope with rapid environmental change, and the associated constraints, is to focus on target species. Focusing on target species will allow us to use natural systems to explore evolutionary and ecological capacity of species to respond to anthropogenic change. This focus may enhance our understanding of aspects of phenospace use and combinations of traits that may increase ability to respond or constraints to change. Focusing on target species can provide key insights from different perspectives (evolutionary history and multiple scales). We need to identify tractable and replicable models that would allow us to explore evolutionary and ecological capacity of species to respond to anthropogenic change. This may allow us to understand aspects of phenospace use and combinations of traits that may increase ability to respond or constraints to change. Below we highlight target species that can provide key insights from different perspectives (evolutionary history and multiple scales):

Focusing on species with long lineage may indicate that those species have been able to respond to change over evolutionary time. However, it may be that just one example will not provide enough insights. An ancient species such as horseshoe crabs that breed once a year (hence longer generation times) may not be able to evolve quickly enough for a scientist to understand what makes them successful. But they also have a good fossil record so that is useful to track their phenospace. Alternatively, one could focus on mycorrhizal fungi or ancient plant lineages that have quicker generation time that would allow one to more rapidly measure the response of these organisms, in the present, to rapid environmental change.

It would also be useful to focus on species of hybrid origin and or polyploids may be useful as they have greater genetic variation which enhances their ability to respond to rapid environmental change (ex. Plant polyploids). Some species that are of hybrid origin may have recently evolved so provide an example of a shorter term lineage such as recent lion fish hybrids. Hybrid vigor can provide genetic rescue rapidly such as with recent hybrids like red lionfish hybridization (Burford Reiskind et al. 2019). More ancient hybrids may also provide a mechanism for studying hybrid vigor. The all female gynogenetic Amazon molly, *Poecilia formosa*, arose via backcross hybridization with their parental species and maintains genetic variation in the “clonal” offspring for 100,000 years (Alberici da Barbiano et al. 2013). It may help to choose a species that has more data, both from the past and current data.

Another useful target would be to focus on species that are rapidly expanding beyond their native range would provide more recent insights into how species can respond to rapid environmental change (ex. mosquitofish, house sparrows, monk parrots, dandelions). It may be useful to choose a widespread invasive species that reproduces quickly and is well studied to use prior data sets. Comparisons between invasive populations and the native range, with a species such as mosquitofish, that have been introduced worldwide (Courtney & Meffe 1989), will help elucidate important mechanisms allowing organisms to respond to novel environments or insights into the genetic and phenotypic divergence that may aid in adaptive change and possible constraints. Alternatively, the rapid response to an invasive species may provide insights into how species can change rapidly. For example the relationship between invasive cane toads and black snake predators (Phillips & Shine 2006).

A few additional directions for exploring evolutionary and ecological capacity of species to respond to change includes focusing on convergent pairs or groups of species may aid in understanding convergent mechanisms to explore how species cope with rapid change. For example, multiple distantly related organisms may attain similar fitness peaks. Comparing related pairs of declining versus coping species could also provide insights into historical constraints and possible solutions to these constraints.

Barrier 5: Predicting consistency of genotype to phenotype patterns across space and time:

Links among genotypes and phenotypes are likely conditioned by the surrounding abiotic and biotic landscape. A universal framework of genotypes to phenotypes requires that we understand how the surrounding context shapes this relationship. For example, do populations that are peripheral respond to global change the same way as central populations? Peripheral populations may have more restricted phenospace due to increased environmental stress from abiotic and biotic conditions that make it increasingly difficult for populations to persist (Figure 3). If so, is this decreased phenospace a result of a smaller range of genetic variation, or decreased plasticity? At the same time, it is important to recognize that global change drivers are unlikely to have additive effects on organismal phenospaces. Instead disparate drivers may synergistically alter phenotypes or even counteract each other. In the later case, selection regimes may be altered without an apparent change in organismal phenotype

- *Solution 5* : Compare populations of species that exist across wide environmental gradients (ex. *Populus* sp., Red-tailed hawk, mosquitofish, Appalachian brown butterfly). Certain taxa with ranges spanning multiple environments will be key to understanding how variable links between genotypes and phenotypes are. We can start by measuring genetic, phenotypic, microbiome, behavior, endocrinology and physiological variation. Once these patterns are established, we can define the extent to which genotypic and phenotypic relationships are environmentally dependent by conducting reciprocal transplants across natural environmental gradients with the same target species (above) as a way to capture plastic responses to the environment.

Organismal plasticity allows species to cope with adverse conditions. Understanding this plasticity versus genetically encoded responses is key because it may fundamentally change genotypic and phenotypic relationships. For example, plastic organisms may appear to shift phenospace but since this shift is not heritable, multi-generational phenotypic change will not occur. This will cause us to overestimate organismal capacity to cope with global change. Alternatively plastic responses may provide the mechanism that links different adaptive peaks and eventually leads to genetic changes. Yet, it is important to recognize that plasticity alone may limit adaptive capacity, but there may be selection for plasticity as an adaptive strategy (Kingslover & Buckley 2017). But plasticity alone will not help all species (Duputie et al. 2015).

The role of genetic vs plastic change may vary across species that differ in their generation time. For example, species with shorter generation time may be more impeded by plasticity whereas those with longer generation times may benefit from plasticity buying time to respond to rapid change. If anthropogenic change is rapid (pollutant contamination), adaptation via selection on standing genetic variation might not act quickly enough to prevent population decline or collapse

(Bürger & Lynch, 1995). Phenotypic plasticity creates the potential for rapid acclimation to these novel conditions within a single generation. Across longer time scales, phenotypic plasticity may promote evolutionary innovation and adaptation by exposing otherwise cryptic genetic variation to selection (Diamond & Martin 2016). For example, phenotypic plasticity can allow populations to persist until constitutive variants of the trait arise for selection to act upon (i.e. genetic assimilation; Waddington 1953). For these reasons, plasticity likely contributes to allowing natural populations to persist when faced with rapid anthropogenic change (Snell-Rood et al. 2018). Although research has demonstrated the potential role of phenotypic plasticity in evolutionary responses to environmental change, understanding the role of plasticity in facilitating the evolution of wild populations to novel environments is still not well understood (Braendle & Flatt 2006).

Barrier 6: Determining which traits should be prioritized to understand organismal response to environmental change. Understanding which of the many traits that compose phenospace are most important for allowing species to cope with changing conditions is a challenge. The number of potential candidate traits is great, and the effort required to map genotypic and phenotypic variation in each is substantial. One route to addressing this challenge is to examine the degree of convergence across different species of traits that aid in responding to environmental change (e.g. traits related to homeostasis, movement, energetics, or cognitive abilities). Focusing on these traits in well-studied species may allow more efficient prediction of evolutionary response across other species.

- *Solution 6a:* Using comparative method can help identify trait combinations that allow species to adapt to rapid environmental change (Figure 2). Many of the species identified in Solution 4 would be prime for comparison. These include species belonging to long-lived lineages, and those those that belong to speciose adaptive radiations. Comparisons between these species and related species that are from recent or species-poor lineages may be especially fruitful in identifying key traits or combinations of traits. Likewise, comparisons between species that have successfully established in novel habitats and those that have failed to do so despite ample opportunity should also be fruitful in identifying key traits that determine winners and losers in the face of anthropogenic change (Sol et al. 2002). Finally, comparisons within species between environmentally-stressed versus non-stressed populations (Bendis & Relyea 2014) , or within invading species between expanding or established populations (Wright et al. 2010) could also identify key traits. Once these traits are identified, modelling approaches could be used to predict changes in other species (Auerbach & Bongard 2014).
- *Solution 6b:* Once key traits are identified, it may be possible to engineer these traits into new population or species, with broadly beneficial effects. For example, Bendis & Relyea (2016) generated communities with pesticide susceptible vs. pesticide tolerant populations of *Daphnia pulex*, exposed the communities to pesticides, then tracked community level responses. Following exposure to pesticides, communities with pesticide-susceptible *Daphnia pulex* populations, experienced a reduction *Daphnia pulex* abundances which led to a bloom of the phytoplankton on which they fed. In contrast, for communities with pesticide-tolerant *Daphnia pulex* populations, did not detect a reduction in *Daphnia* abundance nor a subsequent phytoplankton bloom. Thus, selection for populations that are tolerant to anthropogenic environmental change buffered the entire community from experiencing phytoplankton blooms

(Bendis & Relyea 2016). This example suggests that creating or engineering novel combinations of traits may be useful not only for prioritizing and understanding evolutionary and ecological responses to rapid environmental change but for buffering entire ecosystems from this change. It is important to note that there may be costs associated with evolving traits associated with environmental change that may lead to modifications on ecological interactions or even limit the ability for populations to perform their important ecosystem services.

What might be broader impacts?

When humans disrupt the environment, we have an ethical obligation to conserve the species we're disrupting. Developing a phenospace-driven framework placed within a comparative evolutionary context is the first step to fulfilling this obligation. If we can predict winners and losers of global change, we will be able to improve predictions of organismal resilience to anthropogenic change, engineer organisms to provide ecosystem services under future, altered environmental conditions, and design targeted conservation and preservation strategies. If organismal response traits to global change are linked to effect traits that feedback to global change (e.g., fire tolerant species producing high loads of flammable litter; Suding et al. 2008) then developing a process-based prediction of species assemblages of the future will also forecast ecosystem functions and global change itself. Therefore, our phenospace framework links underlying genes to phenotypes, to community assemblages and ecosystem function, and global change itself in a cyclical framework (Figure 4).

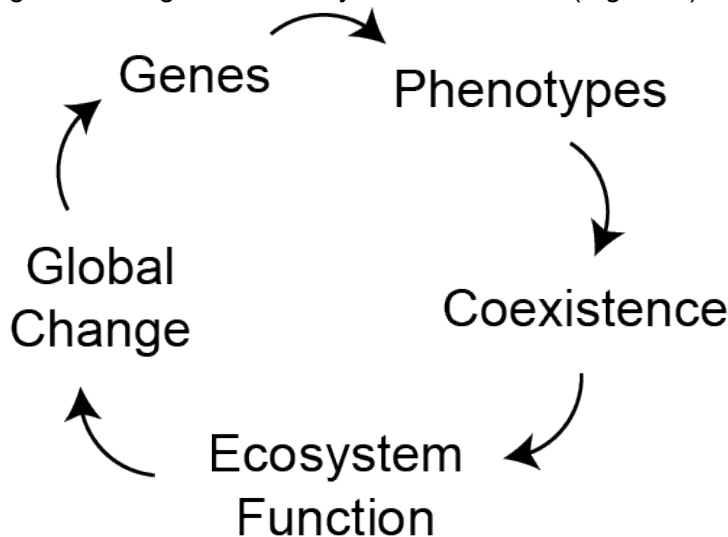


Figure 4. Genotypes predict phenotypes which then predict community level organismal coexistences. If response of species is related to effects on the environment, then community response to global change predicts ecosystem function, which can feedback to global change itself.

How does it reintegrate biology?

Our vision broadens the gene to ecosystem perspective. Frequently response to anthropogenic change is from physiological and conservation biology perspective. Using more integrated approach will aid in greater ability to manage and respond to anthropogenic change. Our proposed vision applies general principles across scales (time, biological organization and space).

What disciplines might be needed?

Physical integration of field and genetic labs would aid in our understanding of organismal capacity to respond to anthropogenic change.

Intended audience of the paper

This paper will be of interest to conservation biologists, those who study Biodiversity, and Environmental scientists.

Citations

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