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Understanding Organismal Capacity to Respond to Anthropogenic Change: Barriers and Solutions

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Synopsis Global environmental changes induced by human activities are forcing organisms to respond at an unprecedented pace. At present we have only a limited understanding of why some species possess the capacity to respond to these changes while others do not. We introduce the concept of multidimensional phenospace as an organizing construct to understanding organismal evolutionary responses to environmental change. We then describe five barriers that currently challenge our ability to understand these responses: (1) Understanding the parameters of environmental change and their fitness effects, (2) Mapping and integrating phenotypic and genotypic variation, (3) Understanding whether changes in phenospace are heritable, (4) Predicting consistency of genotype to phenotype patterns across space and time, and (5) Determining which traits should be prioritized to understand organismal response to environmental change. For each we suggest one or more solutions that would help us surmount the barrier and improve our ability to predict, and eventually manipulate, organismal capacity to respond to anthropogenic change. Additionally, we provide examples of target species that could be useful to examine interactions between phenotypic plasticity and adaptive evolution in changing phenospace.

Introduction

Human activities are altering ecosystems across the planet at an unprecedented pace (Ellis and Ramankutty 2008; Sutherland et al. 2013; Aronson et al. 2014; Goudie 2018). The rapidity and scope of these changes challenge the ability of many species to cope, resulting in their decline, extirpation, and sometimes extinction (Parmesan 2006; Burkhead 2012; Beketov et al. 2013; Ceballos et al. 2015). Some species, however, are resilient to these changes while still others thrive in the altered or novel landscapes created by humans (Barnum et al. 2017; Marques et al. 2019). At present, we have limited ability to predict which species will be winners and which will be losers in the face of anthropogenic environmental change (McDonnell and Hahs 2013). This limitation highlights a fundamental gap in our understanding of what factors determine the capacity of species to adapt and acclimate to changes in the environment, and how these factors differ among species (Smith et al. 2009).

Here, we first introduce the concept of multidimensional 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

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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.

Multidimensional phenospace

The central concept of evolutionary capacity, or the lack of it, can be considered in terms of multi-dimensional phenospace in which different dimensions represent the extent of possible variation in a particular phenotypic trait. As these phenotypic traits reflect underlying genetic variation and environmental variation, the evolutionary capacity of a species is related to how these traits vary across space and generations (i.e., heritability). Organismal phenospace is analogous to niche space where dimensions are environmental conditions modified by biotic interactions as defined by Hutchinson (1957), except here the focus is on the fundamental breadth of organismal traits and the realized breadth of organismal traits across a population in a given abiotic and biotic environment. These traits can be morphological, physiological, life history, 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. First, what determines the boundaries of the phenospace that a species occupies? Are there limits determined by selection gradients such that values at the edge of a species distribution are sufficiently disfavored to be rarely occupied? Or do these limits represent hard constraints to a species' ability to adapt? Second, what is represented by the empty space between species distribution? Does this space represent trait value combinations that have low fitness values under present conditions? Or does it represent evolutionary unstable combinations of trait values that simply cannot exist due to physical or other constraints? Alternatively, might it represent trait values that may confer high fitness but simply have not been achieved due to the stochastic nature of evolution?

Such phenospace maps represent a single point in time. Over time, populations may expand or move their phenospace as they adapt to changing environmental conditions. With changing environments, some trait combinations may become disfavored or completely inviable. Some species may have the capacity to adapt to new conditions by evolving different trait value combinations (via processes such as selection on constitutive traits, phenotypic plasticity, or genetic accommodation; Fig. 1b- Species 1), either alone (Carlson et al. 2014; McDermott 2019) or in combination with beneficial symbionts (Mueller et al. 2020). Other species may not have this evolutionary capacity and may go extinct (Fig. 1b- Species 2). Evolutionary constraints on trait combinations along phylogenetic lineages (Fig. 2) may inform which trait combinations are stable or unstable and therefore which species will persist under environmental change. However, our ability to link genotypic trait variation over evolutionary time with phenotypic traits, and to understand how these traits predispose organismal ability to respond to environmental change, remains one of the grand challenges in organismal biology (Schwenk et al. 2009).

We see five key barriers that currently challenge our ability to understand why some species 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 environmental change stressors and how these parameters vary across ecosystems. Globally, increases in atmospheric CO_2 (Blunden et al. 2018), and temperature are common (Masson-Delmotte et al. 2018) but the magnitude of these increases is not equal everywhere. For example, some arctic and alpine ecosystems are warming at much faster rates than other biomes (Beer et al. 2020; Williamson et al. 2020), due to surface changes in albedo and adjacent warming of oceans. Defining the environmental change context across ecosystems is fundamental to understanding how different abiotic conditions will alter organismal fitness. As stressors impact fitness, either directly or through combined stress impacts, there will be varying levels of consequences through phenospace. Environmental stressors will impact individual fitness differently through phenospace depending on the combination of traits within the population. For example, drought can directly impact individual fitness within a population, but the combined stress of drought and forage loss will have different fitness consequences for those same individuals.

Solution 1: Data from remote sensing and ecological observation networks provide the global coverage necessary to address this problem (Li et al. 2018). We have the ability to downscale climate data using the different climate change emission scenarios that are more appropriate to the spatial scale of ecological studies (e.g., Multivariate Adaptive Constructed Analogs

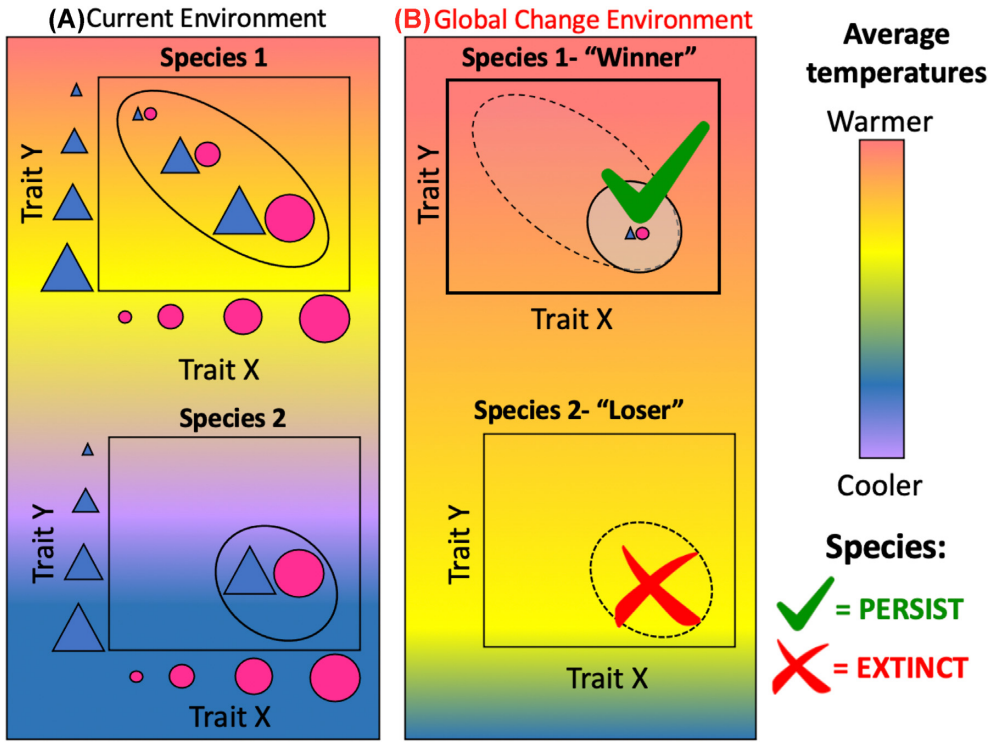


Fig. 1 (A) Hypothetical phenospace of two species (1 and 2) for two traits (X and Y) under current conditions. Larger values for both traits (represented by larger shape icons on axes) are more adaptive at lower temperatures (represented by cooler background colors) while smaller trait values are more adaptive at higher temperatures. **(B)** Hypothetical shift in phenospace for Species 1 (winners) in response to human-induced environmental change (represented by an increase in warm colors) vs. extinction of Species 2 (losers) due to inability to shift phenospace in an adaptive manner. Shifts in phenospace may occur via selection on constitutive traits, phenotypic plasticity, or selection on plasticity (i.e. genetic accommodation). Current position in phenospace may predict viability under anticipated global environmental change.

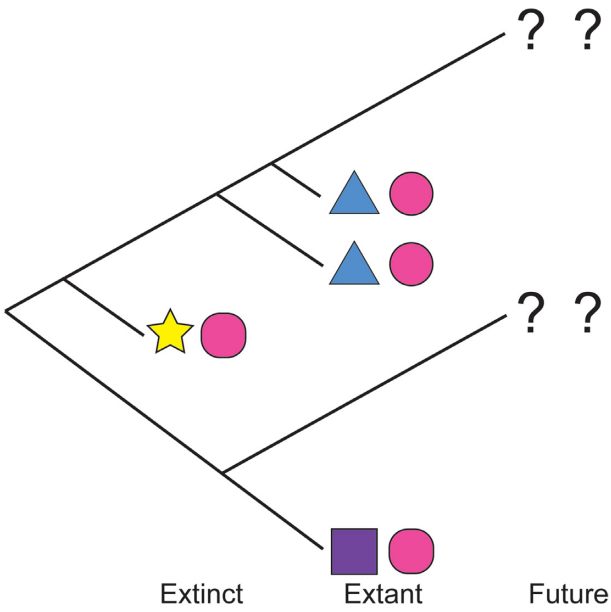


Fig. 2 Trait combinations vary among species both in the present and past. Accounting for both forms of this variation along evolutionary history may help predict which trait combinations are possible and viable under current and future environmental conditions.

(MACA) downscale climate method for the contiguous USA (within 4 km resolution); see also Abatzoglou and Brown (2012) for comparison of models). In polar and alpine systems, coordinated MODIS flyover data and ground-truthed snow cover and sea ice data allow us to collect fine grain data on environmental conditions and how they change over time (Flanner et al. 2011). Across other locations, long term ecological networks, such as NEON and the LTER sites, collect environmental data, such as temperature (DeAngelis et al. 2015; Diamond et al. 2016) nitrogen (N) deposition (Magill et al. 2004), and drought (Avolio et al. 2019), and pair it with observations of organismal fitness and global change. Moreover, coordinated networks of nitrogen addition (e.g., NutNet) and drought (e.g., Drought Net) impose similar climate change treatments across hundreds of sites globally and therefore can compare fitness outcomes across species ranges. Together these datasets 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 phenoscape.

Remote sensing combined with ecological data will allow for ecological modelling. Models can be used to understand complex ecological processes and predict how real ecosystems will possibly change (Saucède et al. 2017; Smith et al. 2017; Choi et al. 2019). For example, new species interactions may form in changing communities and the structure of these biotic interactions may directly relate to the resilience of species and ecosystems. In addition, trophic interaction studies can help predict species vulnerability to environmental changes. Coupling insights gained from trophic niche ecology, phenotypic distribution, remote sensing, and species distribution modelling represents a promising approach to predict the potential responses of species to future habitat changes (Saucède et al. 2017; Smith et al. 2017; Bestion et al. 2019; Choi et al. 2019; Lei et al. 2019).

Barrier 2: Mapping and integrating phenotypic and genotypic variation

Measuring existing phenotypic and genotypic variation across a species' range provides insights into the amount of standing variation that might contribute to the ability of an species to respond to changing environments. To date, we have accumulated a wide range of genotypic and phenotypic measures across disciplines, taxa, and ecosystems (Pélissié et al. 2018; Parejo et al. 2020; Wang et al. 2020). We can use tools and knowledge from quantitative genetics to model phenotypic and genotypic variation although this remains a challenge in natural populations, even with improving technology and quantitative approaches. Integrating these data will include measures from field observations, empirical data collection, models, museum collections and long-term datasets. Collectively, these existing resources could allow us to place organisms in their phenospace and to track, and eventually even predict, how phenospaces change as the environment changes. Data garnered from museum specimens and compared to living and changing populations may allow us to model past changes that affect phenospace in populations (Pélissié et al. 2018; Parejo et al. 2020; Wang et al. 2020). However, at present these data sets are dispersed across disciplines and repositories and not always widely accessible to the broader research community. An additional issue is that the datasets are often not inter-compatible, limiting the extent to which they can be integrated to map multidimensional phenospace. Some fields of science have been working on fitness across genotypes (Aw et al. 2018; Fragata et al. 2019) and building upon the knowledge gained will create great strides in understanding and mapping variation across spatial and temporal scales.

Once phenotypic variation is mapped, the next important step in predicting response to change is linking phenotypic variation to underlying genotypic variation. Doing so will allow us to explore the genetic basis underlying adaptive responses in organisms that exhibit a capacity to cope with changing conditions (or winners; Fig. 1). Similarly, if new adaptive (or non-adaptive) changes appear, we can link those back to their genetic basis and begin to understand the process of selection. It can be as simple as some individuals in the population migrating, while others do not, creating opportunities for the environment to impact individuals within the population (Collins et al. 2013; Hogan et al. 2014). It might also be possible to use this information to help transform species that do not exhibit the capacity to cope from losers to winners (see create/engineer traits Solution 5).

Solution 2

Improving access to, and integration among, existing datasets on phenotypic variation could provide data to explore past and present levels of phenotypic variation in populations. While this data integration is still an aspirational goal for most taxa, some integration across genotypes and phenotypes of microorganisms is starting to occur. For example, coordinated datasets of georeferenced and time-referenced DNA sequences along with subsequent transcriptomes, metabolomes and ultimately morphotype data (e.g., Global Fungi for fungi (Větrovský et al. 2020), Mycoportal (Miller and Bates 2017) and *Aiptasia* symbosis resource (https://www.aiptasia-resource.org/for-researchers/& https://www.protocols.io/workspaces/aiptasiasymbiodiniaceae-model-system/publications)) provide the first key steps of linking genotypes and phenotypes across landscapes. While the sequencing revolution is making this goal more tangible for microorganisms, similar integrated data portals for other parts of the tree of life are a more distant, but nonetheless important, goal. Once more of these are available, we will be able to explore the phenospace that an organism occupied in the near past and where it sits presently. If that species is a "winner" in successfully responding to environmental change then we may gain insights by hindcasting the adaptive process that results in winners that could then inform conservation of other less successful species. Modeling may also help us understand constraints to phenotypic responses to rapid change. The ongoing revolution in genotyping technologies is making the collection of these datasets increasingly feasible. Genotyping of existing sample collections such as those in museums is particularly exciting as it has the potential to link phenotype to

genotype across both space and time. Furthermore, computational improvements of spatial statistics will allow us to pair fitness landscapes with environmental gradients throughout a species range, thereby improving our understanding of how the fitness landscape changes across abiotic gradients (Fig. 1). Particular insight regarding the genetic factors associated with capacity to cope with new environments may come from comparing patterns from invasive species and other species that are "winning" under anthropogenic change and with those from displaced native species or others that might be considered losers.

Barrier 3: Understanding whether changes in phenospace are heritable

Microevolution of traits can play a role in response to rapid environmental change (reviewed by Reznick et al. (2019)). In addition, phenotypic plasticity (both within and transgenerational: (Bradshaw 1965; West-Eberhard 2003; Ghalambor et al. 2007; Lande 2015; Kelly 2019; Donelan et al. 2020), and epigenetic processes such as methylation or alternative splicing may also aid in generating adaptive phenotypes (Bossdorf et al. 2008; Day and Bonduriansky 2011; Robertson and Richards 2015; McNew et al. 2017). These different processes can differentially impact how individuals respond to changing environments, and whether these changes can be transmitted to future generations. For example, phenotypically-plastic individuals may shift in phenospace in response to changing conditions within their own lifespan, but if this shift (or the ability to shift) is not heritable, multi-generational phenotypic change will not occur. This could potentially lead to an overestimation of organismal capacity to cope with environmental change, and furthermore, suggests that plasticity may impose a limit on adaptive capacity and evolution (Kingsolver and Buckley 2017). Nonetheless not all plasticity is adaptive (Ghalambor et al. 2007). Alternatively, heritable forms of plasticity across generations may provide the mechanism linking different adaptive peaks and eventually leading to genetic changes that promote organismal capacity to adapt to environmental change (e.g., the Baldwin effect; West-Eberhard 2003; Badyaev 2009).

While research in the areas of phenotypic plasticity and epigenetics has grown at a tremendous rate (Theme issue Fox et al. 2019b), our next steps need to focus on understanding how unexpressed genetic potential (also referred to as "cryptic variation") contributes to responses to environmental change. Given the rich history of phenotypic plasticity (Fox et al. 2019a; Moczek et al. 2011) and epigenetic research across a diversity of disciplines (Hawes et al. 2018), we are at an ideal time for reintegrating efforts across fields of biology to examine the contribution of cryptic variation to creating winning phenotypes (e.g., Miner et al. 2005; Crispo 2008; Levis and Pfennig 2020). Doing so may help us to gain a better understanding of the processes that results in species responding and adapting to environmental change, or failing to adapt.

Solution 3

One solution to understanding the role of cryptic variation in determining a species' ability to cope with rapid environmental change 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 responses or constraints to change. It could also allow better estimation of the importance of heritable and non-heritable change in phenospace. Focusing on these species can provide key insights from different perspectives (evolutionary history and multiple scales). Identifying tractable study species that allow us to explore evolutionary and ecological capacity of species to respond to anthropogenic change will help us to understand those aspects of phenospace use and combinations of traits that enhance the ability to respond or constraints to change. In Box 1, we highlight potential target species that can provide key insights into how cryptic variation contributes to responses to change from different perspectives (i.e., evolutionary history and multiple scales). These include species from long-standing lineages that have already persisted through evolutionary change, hybrid or polyploid species that have high levels of genetic variation, and invasive species that have already demonstrated an ability to cope with anthropogenic change. None of these potential target species currently represent enough data to integrate genotypes and phenotypes across landscapes (e.g., as suggested in Solution 2), but they do provide a springboard for starting these efforts. Additional insights could be gained from examining evolutionary radiations of species in extreme environments. Integrating insights from these various target systems would help address the barrier of how cryptic variation contributes to an organism's ability to respond to change.

The role of genetic vs. plastic change may vary across species with differing lifespans (Fusco and Minelli 2010). Indeed, species with long lifespans relative to the rate of environmental fluctuations should be more plastic than species that are short-lived relative to the rate of environmental fluctuations (Ratikainen and Kokko 2019). These patterns may be especially relevant in

Box 1. Examples of potential target species to examine interactions between phenotypic plasticity and adaptive evolution in changing phenospace.

Key insights to study	Target species 1	Benefits 1	Target species 2	Benefits 2
Long lineage to track phenospace through evolutionary time	Horseshoe crabs (*Limulus polyphemus)*	Provide a good fossil record that is useful to track their phenospace use through evolutionary time (Kin and Błażejowski 2014)	Mycorrhizal fungi or ancient plant lineages	Quicker generation time that would allow one to more rapidly measure the response of these organisms, in the present, to rapid environmental change (Valiente-Banuet et al. 2006; Compant et al. 2010; Chanda et al. 2020)
Hybrid or polyploid species because they have greater genetic variation that aids rapid response to change	Recent hybrids—red lionfish (*Pterois miles* and *Pterois russelii)*	Hybrid vigor can provide genetic rescue rapidly such as with recent hybrids (Burford Reiskind et al. 2019)	Ancient hybrids—ynogenetic Amazon molly, *Poecilia formosa (*Alberici da Barbiano et al. 2013*)*	Ancient species will have both past and current data to fully explore how phenospace use changes through time
Invasive species and those with rapidly expanding ranges, as well as those species responding to these novel species can provide more recent insights into how species respond to rapid environmental change	Mosquitofish (*Gambusia affinis/holbrooki)*, gudgeon (*Gobio gobio*), house sparrows (*Passer domesticus)*, monk parakeet (*Myiopsitta monachus*), brown anoles (*Anolis sagrei*), rats (*Rattus rattus),* mice *(Mus musculus),* crayfish (*Procambarus clarkii*), fruit flies *(Drosophila subobscura*), dandelions (*Taraxacum officinale*), springtails (*Pogonognathellus flavescens)*, and alligator weed (*Alternanthera philoxeroides*)	Comparisons between invasive populations and the native range, with a species such as mosquitofish, that have been introduced worldwide (Pyke 2005), 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.	Australian black snake (*Pseudechis porphyriacus*) response to cane toads (*Rhinella marina*), mosquitos (*Aedes aegypti)* response to invasive *A. albopictus*	Rapid response to an invasive species may provide insights into how species can change rapidly (Phillips and Shine 2006; Burford Reiskind et al. 2018).
Convergent pairs or groups of species that may aid in understanding convergent mechanisms to explore how species cope with rapid change	Clades of pupfish (*Cyprinodon* spp.) from Death Valley	Pupfish show varying phenotypic differences (Lema 2014) which provides useful insights into phenospace use over time and traits that increase their ability to respond or constraints to change. Comparing related pairs of declining versus coping species could also provide insights into historical constraints and possible solutions to these constraints		
Species with large spatial ranges across multiple habitats may aid in understanding how species cope with variation along a gradient.	Red tailed hawks (*Buteo jamaicensis*), peregrine falcon (*Falco peregrinus*), racoon (*Procyon lotor*); tiger mosquito (*Aedes albopictus*) and yellow fever mosquito (*A. aegypti*); rockfish (*Sebastes spp*); and monkey flower (*Mimulus spp*)	Comparing individuals throughout range to understand how habitat and environment select for variation within a species, and how this variation is distributed across the range.		

understanding which species persist when faced with rapid anthropogenic change (pollutant contamination). For example, phenotypic plasticity can create 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 and Martin 2016). Thus, 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). Similarly, larger population sizes with more plasticity may persist longer which could provide time for evolutionary rescue of those populations which in turn could give rise to new beneficial mutations (Scheiner et al. 2020). 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, it can also prevent evolutionary change by slowing the response to natural selection (Price et al. 2003; Kelly 2019). Nonetheless, understanding the role of plasticity in facilitating the evolution of wild populations to novel environments is still not well understood (Braendle and Flatt 2006).

Barrier 4: Predicting consistency of genotype to phenotype patterns across space and time

Links among genotypes and phenotypes are 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 across both space and time. For instance, over time, shifts in abiotic and biotic landscapes due to global change can result in selection for different adaptive strategies (Pigliucci et al. 2006; Scheiner et al. 2020), such as selection for existing adaptive constitutive traits or selection for the ability to induce adaptive traits (phenotypic plasticity). These strategies can result in differential effects on the relationship between genotype and phenotypes. For example, selection on adaptive constitutive traits can result in a reduction in both genotypic and phenotypic variation (Fig. 3, Scenario 1). In contrast, selection on phenotypic plasticity may decouple this relationship by potentially having no effect on genotypic variation but reducing phenotypic variation (Fig. 3, Scenario 2).

Understanding the abiotic and biotic scenarios that facilitate these different outcomes is important as they may be associated with differential costs that influence phenospace and thus responses as well as persistence in the face of environmental change. Additionally, it is important to recognize that environmental change drivers across time are unlikely to have additive effects on organismal phenospaces (Meyer-Grünefeldt et al. 2015; Zaragoza-Trello et al. 2021). Instead, disparate drivers may synergistically alter phenotypes or even counteract each other. In the latter case, selection regimes may be altered without an apparent change in phenospace.

Similarly, shifts in genotype to phenotype patterns may also be initiated by abiotic and biotic variation across space. For example, edge populations face different abiotic and biotic conditions relative to central populations. Notably, in invasion scenarios, populations at the leading edge of expansion are expected to exhibit phenotypic traits that facilitate dispersal and survival in novel environments (i.e., behavioral plasticity; Wright et al. 2010: Fig. 4; Gruber et al. 2017). Thus, edge and central populations vary in phenospace due to environmental variability stress from abiotic and biotic conditions that may differentially influence the ability for these populations to persist in the face of global change (Fig. 4). Similarly, populations facing different disturbance regimes can respond via different mechanisms. For example, pest populations exposed to multiple low concentrations of pesticides (pulse) as opposed to a single high concentration (press) may develop insecticide tolerance albeit via different mechanisms (i.e., target site resistance vs. metabolic resistance; David et al. 2013). Collectively, as environmental change continues to threaten natural populations, understanding how abiotic and biotic variation across space and time influence genotype to phenotype relationships is critical to predicting future patterns of species persistence in the face of environmental change. Despite this recognition, our current understanding of phenotype-genotype relationships remains limited with equivocal conclusions that could be resolved with an integrative approach.

Solution 4

Coordinated approaches that integrate theoretical, modeling, and empirical efforts to collect reliable and repeatable measures of the abiotic and biotic landscape across broad spatial and temporal scales across organisms are paramount to making generalizable predictions about the genotype–phenotype relationship in the face of environmental change (Fig. 5). One approach to explore the consistency of genotype and phenotype across space and time would require comparison of populations of species that exist across wide environmental gradients (e.g., *Populus* sp., red-tailed hawk (*Buteo jamaicensis*), and mosquitofish (*Gambusia affinis*), Appalachian brown butterfly (*Satyrodes appalachia*), wood frogs (*Lithobates sylvaticus*), *Daphnia* spp., and

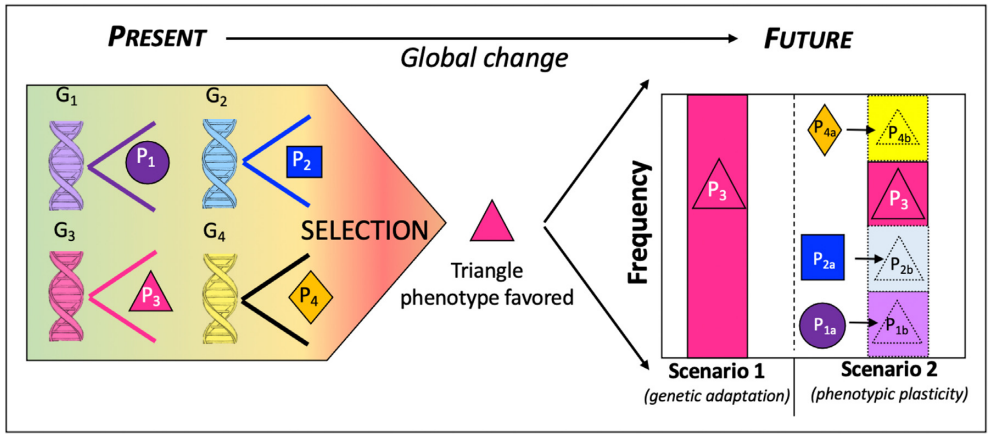


Fig. 3 Proposed effects of global change on genotype-phenotype relationships across time. Scenario 1 represents global change enacting selection on adaptive constitutive traits leading to a reduction in genotypic variation (indicated with "G") and phenotypic variation (Indicated by "P"). Scenario 2 represents global change enacting selection on adaptive phenotypes that are expressed constitutive traits and via phenotypic plasticity resulting in no reduction in genotypic variation but a reduction in phenotypic variation.

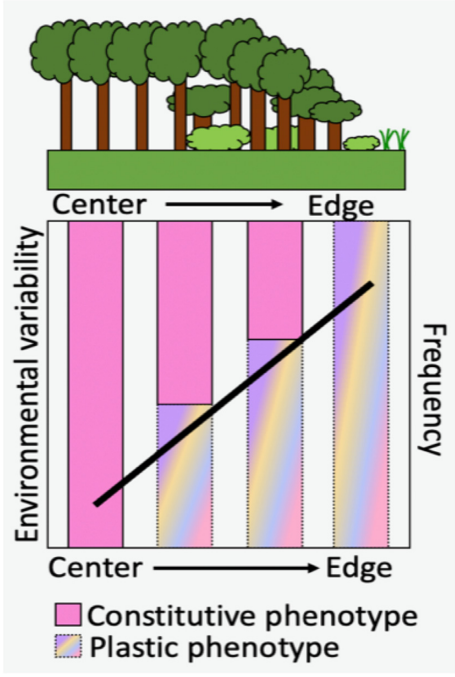


Fig. 4 Proposed effects of environmental change on genotype-phenotype relationships across space. Environmental variability increases from center to edge habitats. In this scenario, selection is predicted to favor constitutive traits in center populations and plasticity in edge populations, resulting in variation in phenoscapes from center to edge populations.

three-spined stickleback (*Gasterosteus aculeatus*); see Solution 2). Another is to examine invasive species as detailed in Box 1. We can start by measuring standing genetic variation and the resulting phenospace. Once these patterns are established, we can define the extent to which genotypic and phenotypic relationships are plastic by conducting reciprocal transplants or common garden experiments across natural environmental gradients with the same target species (above) as a way to capture plastic responses to the environment. These results can then be used to further refine models and theory for predicting how the genotype-phenotype relationship will vary over time and space.

Barrier 5: 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. There are several approaches that can be used to address this problem. One approach is to use phenotypic distribution modeling to identify responses to changing environments (Smith et al. 2017). Another route is to examine the degree of phenotypic convergence of traits across species 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 or target species may allow more efficient prediction of evolutionary response across other species and how they can be used to identify organismal response to change.

Solution 5

During times of change, species may cluster around different locations in phenospace (Doebeli et al. 2007). The emergence of such phenotype patterns through the ecosystem is a potential tool to understand capacity for adaptation and survival during changes in the abiotic and biotic environments (Doebeli et al. 2007).

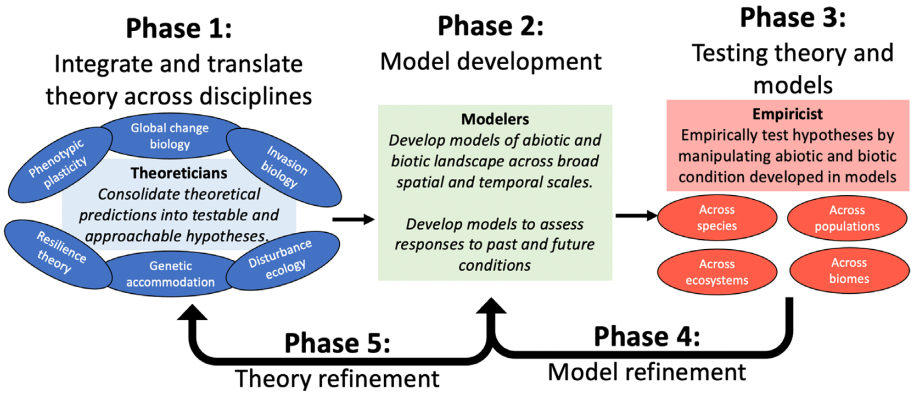


Fig. 5 An iterative five-phase proposed schematic for coordinating approaches that integrate expertise from diverse biological disciplines, approaches, and organization levels that can be used to predict genotype to phenotype patterns.

For example, a study by Lozano-Jaramillo et al. (2019) used phenotypic distribution to predict livestock performance. Species distribution models that account for phenotypic adaptations (Garzon et al. 2019) can be combined with methods from (Lozano-Jaramillo et al. 2019) to predict species response to changing environments. Using phenotypic convergence as a comparative method (Harvey and Pagel 1991) can also help identify trait combinations that allow species to adapt to rapid environmental change (Fig. 2). Many of the species identified in Box 1 would be ideal study systems as comparative data portals are constructed (Solution 2). These include species belonging to long-lived lineages, and those that belong to speciose adaptive radiations (DeWitt 2016). 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 (Hassan et al. 2018). 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). Invasive species may also be a useful target to identify specific phenotypic traits for survival. Finally, comparisons within species between anthropogenically-stressed vs. non-stressed populations (Bendis and 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 and Bongard 2014).

Once key traits are identified, it may be possible to create desired trait combinations via artificial selection or genetic engineering and drive them into new populations or species, with broadly beneficial effects. For example, selection for populations of *Daphnia* that are tolerant to anthropogenic environmental change can buffer an entire community from experiencing phytoplankton blooms (Bendis and Relyea 2016). Creating 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. Alternatively, genetic engineering using CRISPR-Cas9 or other gene editing methods is underway to address conservation questions such as re-introduction of the American chestnut (Newhouse et al. 2014) and eradication of rodents on islands (Campbell et al. 2015), although questions remain concerning how to drive these modifications into populations and the feasibility of scaling such approaches across ecosystems (Campbell et al. 2015). It is important to note that there may be costs associated with traits evolving with environmental change that may lead to modifications on ecological interactions or even limit the ability for populations to perform their important ecosystem services. The efficacy and ethical considerations of these approaches will need to be evaluated with stakeholder input if there is any hope of success (e.g., Merkle et al. 2007; Campbell et al. 2015; Barnhill-Dilling and Delborne 2019).

The broader impacts of understanding organismal capacity to change

The ideas laid out in this paper are ambitious and intensive. Addressing them will require the integration of multiple fields of ecology, evolution, and genetics as well as interdisciplinary collaboration between theoreticians, modelers, empiricists, and data scientists (Fig. 5). Is an effort of this magnitude and cost of sufficient importance to be a focus for limited funds? We believe the answer is an unequivocal "Yes." As humans increasingly disrupt the environment, we have both an ethical obligation and an enlightened self-need to understand the cascading effects of this disruption.

Developing a phenospace-driven framework placed within a comparative evolutionary context is a critical step to fulfilling this obligation. If we can predict winners and losers of environmental change, we will be able to improve predictions of organismal resilience to anthropogenic change, alter habitats to help losers, engineer organisms to provide ecosystem services under future altered environmental conditions, and design targeted conservation and preservation strategies. If organismal response traits to environmental change are linked to the affected traits that feedback to environmental change itself, then developing a process-based prediction of species assemblages of the future will also forecast ecosystem functions. Therefore, our phenospace framework links underlying genes to phenotypes, to community assemblages and ecosystem function, and environmental change in a cyclical framework.

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