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Adaptive Species Framework for Modeling Evolutionary Responses of Animals Under Environmental Stress

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Key Words

Phenotypic plasticity, Genetic adaptation, Environmental stress, Evolutionary response, Adaptive capacity, Reaction norms, Animal behavior.

Abstract

As environmental change proceeds at an ever-quickening rate, understanding whether an environmentally impacted animal population is utilizing phenotypic plasticity, genetic adaptation, or some combination of both has become of paramount importance. The vast majority of evolutionary adaptation research to date has conceptualized plastic and genetic adaptive responses as independent modes of adaptation, providing little in the way of predictive guidance on how the balance of plasticity and genetics might change with accumulating environmental stress. Here, the study introduce an Adaptive Species Framework-a conceptual modeling approach to analyze how animal populations respond to environmental stress. Our framework conceptualizes plasticity and genetic adaptation as intrinsically linked, mutually functioning and interactive responses, the relative balance of which varies through time, as indicated by measures at trait, transcriptional, and behavioral levels. This framework integrates contemporary themes from plasticity- in- evolution, genomic responses to climate change, loss of transcriptional plasticity following adaptation in a marine copepod, genomic reaction norms as predictors of plastic and adaptive responses, animal behavior in the study of multi-stressor scenarios, behavior and stress-related phenotypes in urban animals, and Genomic and modelling in aided migrations to assess population adaptability. While this framework is presented without multi- generational field or laboratory data, it provides a coherent structure from which predictions of when an animal species might shift from a plastic-driven response toward genetic adaptation in the face of ongoing or increased environmental stress can be made - thus informing and supporting more robust conservation and management plans for animal wildlife.

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Introduction

When environmental levels of stress, whether increasing temperatures, habitat destruction or changes in the availability of resources, are sustained, animals respond to stress by modifying the way that express the traits through phenotypic plasticity, and by altering the distribution of traits over generations through selection. Studies on the role of plasticity in adaptive evolution have demonstrated that the direction of the trend of environmental change, the nature of the environmental change (directional or fluctuating change), and the rate of change (slow or fast) that an adaptive process encounter can determine whether plasticity will be advantageous or disadvantageous for longer-term genetic adaptation (Vinton et al., 2022). Studies in the understanding of response to climate change in the era of genomics have shown that genetic evidence can now detect adaptive response not only with greater certainty than observed plastic response, but also with much higher resolution (Lancaster et al., 2022). However, the challenge of incorporating this genetic evidence with observed plastic response into a broader understanding of adaptive response for a species remains a work in progress. The loss of transcriptional plasticity after adaptation to global change conditions in a marine copepod has been recorded, and populations can experience a measurable shift away from plastic gene expression responses towards more fixed, genetically adapted expression patterns after prolonged exposure to stressful conditions, thus providing direct evidence of the temporal switch between plastic and genetically adapted expression patterns within a single population (Brennan et al., 2022). When using genomic reaction norms to predict plastic and adaptive responses to climate change, it has also been discovered that reaction norm approaches can be used to differentiate between populations that are likely to be plastic versus adaptive in the future, depending on the genetic architecture of the population's trait response (Oomen & Hutchings, 2022). Taken together, these studies highlight a lack of integration of approaches that could help to resolve the following common gap: Plasticity research, genomic climate response research, and reaction norm modelling have all made tremendous progress, but there is no consistent framework to track the change over time in the extent to which a population is depending on plastic or adaptive mechanisms, which is becoming increasingly important to better predict when a population is nearing the limits of its adaptive capacity.

This paper has three key contributions. First, it suggests a framework structure that follows plastic and genetic adaptive responses together and not separately so as to observe the changing dependence of a population on the different mechanisms as it experiences stress over successive generations. Second, it combines transcriptional and behavioral data with measures of the trait, all based on the premise that changes in the plasticity of gene expression can represent changes in the adaptive strategy before reflected in the evident phenotypic traits. Third, it adapts the concept of adaptive response modelling to include the behavioral aspect of stress response; behavior changes may follow or precede physiological and genetic adaptation.

Section II discusses the limitations of previous evolutionary adaptation research, based on recent investigation of multi-stressor behavioral integration, urban bird stress phenotypes, and genomics in assisted migration.Section III, presents the development of the proposed framework for stress-driven trait modeling. In Section IV, simulated adaptation trends are discussed, and the framework is compared to the existing evolutionary adaptation research. The paper is concluded in Section V, and directions for future validations are given.

Shortcomings of Prior Evolutionary Adaptation Studies

Multiple environmental stressor studies on evolutionary adaptation have tended to ignore behavioral stress responses, even though commonly the very first line of response to an environmental change, before measurable physiological and/or genetic changes, and which influence the level of stress exposure an individual will actually encounter (Lopez et al., 2023). However, work investigating whether behavior and/or stress-related phenotypes are adaptive, or whether a response to stress but without a fitness benefit, has shown that not all observed behavior or phenotypic change under stress is adaptive, and that previous studies may have been assuming more adaptive capacity than is actually present in the populations studied Caizergues et al., (2022). Genomics applications for assisted migration planning in the context of climate change have been used in research, with evidence showing that genomic information about the adaptive potential of a population can be a valuable tool for making practical decisions about assisted migration, such as where to move it, but there are fewer empirical studies in practice compared to the theoretical framework that exists (Chen et al., 2022).

The recent literature identified a common set of deficiencies in previous studies of evolutionary adaptations. Multi-stressor behavioral research has identified that while behavior is important in determining the actual stress exposure that an individual might be subjected to, it is often not considered in adaptation studies, which might present an inaccurate picture of the actual selective pressure on a population. Urban bird studies demonstrate that phenotypic change under stress is not necessarily an adaptive benefit, and, for modelling purposes, needs to be separated from adaptive changes from non-adaptive changes that are stress responses. In combination, these results suggest that a model of evolutionary responses to stress should explicitly account for behavioral response, not as an add-on, but as an integral component; should include a way to separate the adaptive from the non-adaptive trait shifts; and should be designed to link the outputs of the model to practical conservation and management solutions.

Framework Construction for Stress-Driven Trait Modeling

Baseline Trait and Plasticity Characterization

The framework starts by defining the distribution of traits in a population and the extent to which the population has the potential for plasticity in these traits under its present environment, on the basis of measurements of traits and, where available, on the basis of the transcription profile of gene expression plasticity. The plastic response of a population can be influenced by the nature of environmental change (how, what, and when), and this baseline characterization is thus a reference point against which future changes in plastic versus genetic contribution to the expression of the trait can be evaluated.

Plastic-to-Genetic Transition Tracking

The framework builds on the baseline characterization and monitors shifts in a trait response from plasticity to genetic response with successive generations of environmental stress. The tracking component relies specifically on evidence that under chronic stress conditions, the capacity for transcriptional plasticity can decrease, and that it is important to use measures of transcriptional plasticity as well as trait heritability to identify transitions to a more genetically constrained plastic or more genetically adapted state. Within this component, reaction norm evidence allows differentiation between populations with a flexible genetic architecture and those with a more rigid one, indicative of a genetic fixation.

Behavioral and Adaptive Benefit Assessment

This last construction element brings in behavioral response indicators as well as trait and transcriptional evidence, filling a gap in previous studies where behavior is not included in adaptation modeling, but is actually a driver of stress exposure. This module also incorporates an adaptive benefit assessment step: comparing the observed trait and behavioral changes with fitness-relevant outcomes (e.g., reproductive success or survival), to enable differentiation between true adaptational responses to stress and stress-induced responses that do not have a clear fitness value, a concern raised in urban bird research that not all observed changes in phenotype under stress are adaptive.

Simulated Adaptation Trends and Result Discussion

Anticipated Adaptation Trends

The expected patterns for the Adaptive Species Framework are based on patterns found in related studies on evolutionary adaptation, since the framework has not yet been applied to multi-generational field or laboratory data. The possibility of marine copepod populations modeled under extended periods of stress to exhibit a measurable shift from trait plasticity to a genetically-based response through successive generations is consistent with the plastic-to-genetic transition tracking component of the framework, and is supported by the presence of decreased transcriptional plasticity after sustained adaptation. Additionally, the framework implies that, in addition to this baseline characterization, populations with genetic architecture that is more flexible with respect to the reaction norms should exhibit less or slower fixation transitions compared to populations with more constrained genetic architecture, which should be reflected in genomic reaction norm research.

Comparison with Existing Adaptation Research

The proposed framework is likely to provide a more comprehensive understanding of the evolution of the population's adaptive strategy over time because it will monitor the changing balance between evolutionary adaptation and plasticity, rather than study them separately. The use of behavioral response is anticipated to better reflect the first signs of stress response as indicated by evidence that behavior can often precede measurable physiological and/or genetic response, as compared with the use of traits alone in trait-based adaptation studies. The adaptive benefit assessment component of the framework also is likely to be more conservative and evidence-based in distinguishing between adaptive and non-adaptive responses to a stress, as all observed trait changes under stress are currently considered adaptive.

Implications and Limitations

The capacity of the framework to identify when a population is moving from a plasticity-dominated to a genetically-dominated response has direct implications for conservation planning as it may mean that populations that are still most dependent on plasticity have more flexibility to respond to further environmental change than populations that are most dependent on genetic change. The main drawback of the framework is that it has yet to be tested with multi-generational data, and its accuracy will only be determined if enough transcriptional, trait and behavioral data have been gathered and are comparable across multiple generations of the same species. This data is present for relatively few species. Reliable fitness-relevant measures, including reproductive success, are also important to the adaptive benefit assessment of the framework, but can be challenging to collect for large-scale or long-lived species on the time scales required to see genetic adaptation.

Conclusion

This paper has proposed a conceptual model of the evolutionary "Adaptive Species Framework" that reflects the dynamic equilibrium between phenotypic plasticity and genetic adaptation across the various levels of the traits, transcripts and behaviors. The framework provides a structured basis for predicting when a population's adaptive capacity is changing from plasticity-dominated to genetically-based response by filling gaps in existing research that exclude behavior and its capacity to influence adaptation, the complexities of distinguishing adaptive from non-adaptive trait shifts, and the disconnect between the potential of genomic capacity and applied conservation practice. Future research to validate the framework with multi-generational field or lab data for various taxa and stressor types is also important and the incorporation of greater genomic data to further support the adaptive benefit assessment is an important direction for future research.

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