# Title

Digest: Herbivory and water availability interact to shape the adaptive landscape in the perennial forb, *Boechera stricta*

# Abstract

How do water regime and herbivory shape phenotypic variation in plants along environmental gradients? Using a multifactorial field common garden approach, Jameel et al. (2024) showed that water availability and herbivore abundance influence the expression of foliar and reproductive traits in the perennial forb *Boechera stricta*. The concordance between phenotypic plasticity, phenotypic clines, and the direction of selection demonstrates the adaptive nature of plasticity in ecologically-relevant traits. Furthermore, the experimental manipulations highlight which agents of selection drive the evolution of these traits.

# Main text

Plant phenotypes often exhibit clinal variation among populations across latitudes and elevations, reflecting adaptation to abiotic and biotic conditions that vary along these environmental gradients (Halbritter et al. 2018). This phenotypic variation can arise from plasticity, evolutionary responses to selection, or a combination of both. Among various abiotic and biotic factors, water availability and herbivory are two key drivers shaping plant traits (Díaz et al. 2007, Metz et al. 2020). These two factors often co-vary across environmental gradients and can interact with each other, rendering it challenging to disentangle their effects on trait expression.

To tease apart how water availability and herbivory influence phenotypic variation in plants and to dissect the contributions of plasticity and genetic adaptation,

Jameel et al. (2024) conducted a field common garden experiment using accessions of the perennial forb *Boechera stricta* sourced from natural populations distributed across an elevational gradient. They manipulated water availability and the abundance of the dominant generalist grasshopper herbivore and measured several key foliar and reproductive traits and fitness components over three years. They then tested the effects of source elevation and experimental treatments on these traits to assess plasticity and local adaptation, and examined the magnitude and direction of natural selection under manipulated conditions.

Their results provide evidence that water availability and herbivory influence trait expression in *B. stricta*. Water supplementation induced higher specific leaf areas, which aligns with the trait values of populations at high elevations and with the elevational gradient in water availability, as aridity declines with elevation. Moreover, under water restriction, individuals with lower specific leaf areas produced more seeds, indicating that water availability imposes selection on this trait and suggesting that plasticity in this trait is adaptive. Herbivore resistance decreased with source elevation regardless of experimental treatments in two of the three study years, consistent with the prediction that individuals should evolve greater resistance against higher herbivory pressure at lower elevations. Regarding reproductive traits, high elevation accessions flowered earlier than low elevation accessions under water supplementation but not under water restriction and herbivore addition, suggesting context dependency of clines in flowering phenology. Water restriction and herbivore removal induced shorter flowering duration, which could confer a fitness advantage to *B. stricta* as individuals with shorter flowering duration also produced more seeds under this treatment combination. Interestingly, not all studied traits exhibited plastic responses to water availability and herbivory. For instance, plant height at flowering did not differ between water or herbivory treatments. This highlights the need to consider various traits to capture a more complete picture of phenotypic variation in plants.

Jameel et al. (2024) demonstrate that abiotic and biotic contexts can jointly shape phenotypic variation in plants across environments via plasticity and evolutionary responses to selection. Their findings echo another study on the milkweed plant *Asclepias fascicularis* across an aridity gradient showing plasticity in leaf traits in response to water and herbivory treatments (Diethelm et al. 2024). Importantly, the work by Jameel et al. (2024) has implications for climate change impacts on natural plant populations. For example, increased herbivory and drought conditions under climate change could exert novel selection that reshapes the evolution of high-elevation populations. On the other hand, phenotypic plasticity can buffer against rapid environmental change and aid in population persistence (Franks et al. 2014). Further research on how abiotic and biotic conditions influence phenotypic variation along environmental gradients will help understand climate change impacts on plant populations and inform conservation management.

# References

Díaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Milchunas, C. Skarpe, G. Rusch, M. Sternberg, and I. Noy‐Meir. 2007. Plant trait responses to grazing–a global synthesis. Global Change Biology **13**:313-341.

Diethelm, A. C., M. Reichelt, and E. G. Pringle. 2024. Herbivores disrupt clinal variation in plant responses to water limitation. Journal of Ecology **112**:338-347.

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary Applications **7**:123-139.

Halbritter, A. H., S. Fior, I. Keller, R. Billeter, P. J. Edwards, R. Holderegger, S. Karrenberg,

A. R. Pluess, A. Widmer, and J. M. Alexander. 2018. Trait differentiation and

adaptation of plants along elevation gradients. Journal of Evolutionary Biology **31**:784-800.

Jameel, M. I., L. Duncan, K. Mooney, and J. T. Anderson. 2024. Herbivory and water availability interact to shape the adaptive landscape in the perennial forb, Boechera stricta. Evolution:qpae186.

Metz, J., C. Lampei, L. Bäumler, H. Bocherens, H. Dittberner, L. Henneberg, J. de Meaux, and K. Tielbörger. 2020. Rapid adaptive evolution to drought in a subset of plant traits in a large‐scale climate change experiment. Ecology Letters **23**:1643-1653.