Title

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

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Abstract

- 6 How do water regime and herbivory shape phenotypic variation in plants along
- 7 environmental gradients? Using a field common garden approach, Jameel et al. (2024)
- 8 showed that water availability and herbivore abundance influence the expression of foliar and
- 9 reproductive traits in the perennial forb *Boechera stricta*. The concordance between plastic
- trait responses, phenotypic variation along an elevational gradient, and direction of selection
- demonstrates the adaptive nature of plasticity in this system.

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Main text

- 14 Plant phenotypes often exhibit variation among populations across latitudes and elevations,
- reflecting adaptation to abiotic and biotic conditions that vary along these large-scale
- environmental gradients (Halbritter et al. 2018). Such 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
- 20 environmental gradients and can interact with each other, rendering it challenging to
- 21 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, in this study,

Jameel et al. (2024) conducted field common garden experiments using the perennial forb

Boechera stricta sourced from an elevational gradient. They manipulated water availability

and the abundance of the dominant grasshopper herbivore and measured several key foliar

and reproductive traits over three years. They then tested the effects of source elevation and

experimental treatments on these traits to infer the role of plasticity and local adaptation.

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Their results provide evidence that water availability and herbivory influence trait expression in B. stricta. Water supplementation induced higher specific leaf areas, aligning with the trait values of populations at high elevations (which are wetter compared low elevations). This suggests that plastic response to water regime can assist in local adaptation. Moreover, under water restriction, individuals with lower specific leaf areas produced larger seed sets, indicating selection by water availability. Plant 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, flowering time advanced with source elevation under water supplementation but not water restriction, suggesting context dependency of trait expression. 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 greater seed sets 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.

Overall, Jameel et al. (2024) demonstrate that abiotic and biotic contexts can jointly shape phenotypic variation in plants across environments via plastic trait shifts 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 plant populations. For example, increased herbivory and drought conditions under climate change can generate novel selection patterns that reshape 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.

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References

- 60 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

69	adaptation of plants along elevation gradients. Journal of Evolutionary Biology
70	31 :784-800.
71	Jameel, M. I., L. Duncan, K. Mooney, and J. T. Anderson. 2024. Herbivory and water
72	availability interact to shape the adaptive landscape in the perennial forb, Boechera
73	stricta. Evolution:qpae186.
74	Metz, J., C. Lampei, L. Bäumler, H. Bocherens, H. Dittberner, L. Henneberg, J. de Meaux,
75	and K. Tielbörger. 2020. Rapid adaptive evolution to drought in a subset of plant traits
76	in a large-scale climate change experiment. Ecology Letters 23:1643-1653.
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