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Digest: Evolution of plasticity and its potential role in the decline of specialists

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How does plasticity evolve over relatively short timescales? Through a series of common garden and reciprocal transplant experiments, Walter et al. found distinct patterns of variation in the phenotype and gene expression for two closely related Sicilian daisy species of the genus *Senecio* across an elevational gradient. This suggests that adaptive divergence may produce interspecific differences in both the magnitude and direction of plasticity. The nonadaptive nature of the plasticity found in *Senecio aethnensis* has important implications for conservation efforts and evolutionary modeling.

Despite the importance and omnipresence of genetic and phenotypic variation, their evolution remains poorly understood. This is especially true in the case of phenotypic plasticity, which describes the ability of a genotype to produce different phenotypes in response to ecological or developmental cues (Nijhout 2003). The flexibility of the one-to-many map between genotype and phenotype allows the organism to develop distinct morphological and ecological traits in response to variation in the environment. Although plasticity will be adaptive for environments where the plastic responses maintain high fitness, it may fail to be so in a novel or highly stochastic environment, which suggests that the relationship between adaptiveness and plasticity is variable and more complex than a simple linear relationship (Pfennig 2021). In this study, Walter et al. (2022) confirmed that adaptive divergence can lead to differences in plasticity over a comparatively short timescale (∼150,000 years) and analyzed the adaptiveness of these changes in plasticity.

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Walter et al. (2022) studied the evolution of phenotypic plasticity in two ecologically divergent but genetically similar Sicilian daisy species from Mt. Etna, *Senecio chrysanthemifolius*, native to disturbed habitats 400–1000 m above sea level, and *Senecio aethnensis*, endemic to lava flows 2000–2600 m above sea level. The authors conducted a common garden experiment using 34 individuals of *S. chrysanthemifolius* and 41 individuals of *S. aethnensis*. They found higher levels of intrinsic water use efficiency and leaf complexity in *S. chrysanthemifolius*, and higher leaf chlorophyll and flavonol content in *S. aethnensis*. The first two traits reflect an adaptation to a warmer environment with greater fluctuations in temperature, whereas the last two indicate a need for defense against high UV levels.

In 2017 and 2019, Walter et al. performed two reciprocal transplant experiments in which clones of multiple genotypes from both species were transplanted into four sites with altitudes of 500, 1000, 1500, and 2000 m. A plastic response is said to be adaptive if the transplanted species develops phenotypes resembling those of the native species (e.g., if *S. chrysanthemifolius* converges toward *S. aethnensis* phenotypically when transplanted at higher elevations). Using changes in leaf morphology, investment, pigment content, and chlorophyll fluorescence as proxies for univariate phenotypic plasticity, the authors found distinct trends of variation in the average phenotype from both species

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Table 1. Contrasting plastic responses from *Senecio chrysanthemifolius* and *Senecio aethnensis*. Walter et al. (2022) found distinct patterns of plasticity in multiple traits of the two species, including leaf complexity, leaf indentation, specific leaf area (SLA), photosynthetic performance, and flavonol content. A minus sign indicates a reduction in the corresponding trait at higher elevations (e.g., both species showed a decrease in leaf area in higher altitudes); a plus sign indicates an increase in the measured value of the corresponding trait at higher elevations; and a zero indicates no significant change across elevations (which suggests a low level of plasticity). For leaf indentation, different patterns of variation were observed in *S. chrysanthemifolius* from the 2017 and 2019 experiments, but both differed from the pattern observed in *S. aethnensis*. As the elevation rises, both species exhibited an initial increase in chlorophyll content followed by a subsequent decrease.

	Leaf Area	Leaf Complexity	Leaf Indentation	SLA	Photosynthetic Performance	Chlorophyll Content	Flavonol Content
Senecio chrysanthemifolius	–	–	0 or +	+, –	0	–, +	–
Senecio aethnensis	–	0	–	–	–	–, +	+

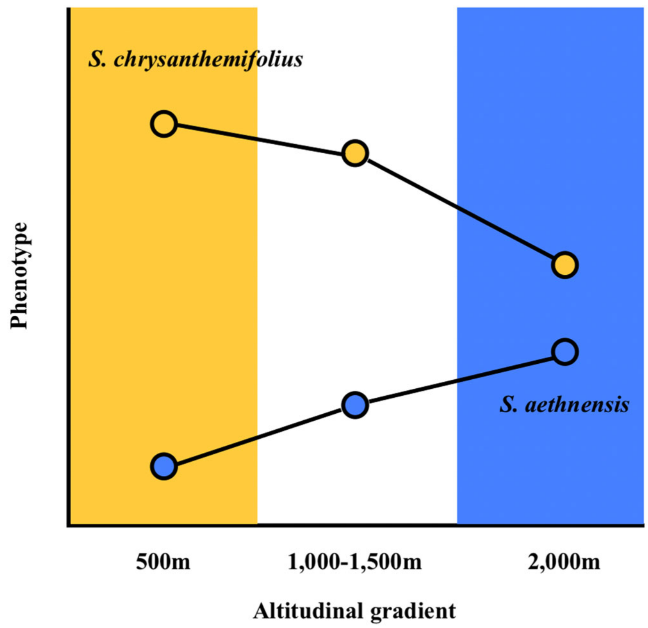

Figure 1. Adaptive versus nonadaptive plasticity. This plot contrasts the opposing trends of phenotypic changes in *Senecio chrysanthemifolius* and *Senecio aethnensis* using fig. 1b from Walter et al. (2022). The plasticity in *S. chrysanthemifolius* is mostly adaptive, as it moves the phenotype closer to that of *S. aethnensis* at higher elevations. By contrast, the plasticity of *S. aethnensis* shifts the phenotype away from that of *S. chrysanthemifolius* at lower elevations and is therefore likely nonadaptive.

and showed that such differences are trait dependent, both in terms of magnitude and direction (Table 1). An analysis of RNA extracted from young leaves showed that *S. chrysanthemifolius* over- and underexpressed more genes than *S. aethnensis*, demonstrating different levels of plasticity at the level of gene expression.

Differences of phenotypic plasticity in plants have been observed as a response to many different environmental factors, such as vegetation shade (Dudley and Schmitt 1996) and flow velocity for aquatic species (Puijalon and Bornette 2004). Nevertheless, much remains to be understood about the developmental process by which distinct phenotypes are produced (Gilbert and Epel 2015). Among the large number of genes that showed consistent differences in expression between *S. chrysanthemifolius* and *S. aethnensis*, many were not enriched for specific functions, which calls for further investigations into how environmental variations affect gene expression and thus the ultimate phenotype.

To establish the primary role of adaptive divergence rather than genetic drift in causing the observed interspecific differences in plasticity, the authors cite the two species' physiological differences under common garden conditions and their different patterns of plasticity in multiple traits. Based on the increased

	Identify specialization
✓	Use of environment is observed
✓	Niche breadth of each species is measured independent of number of observations available
✓	Specialization is not inferred from higher taxa
	Niche breadth is quantified across multiple axes
	Specialization is measured on more than a binary scale
✓	An individual of the generalist species does not depend on multiple habitat types

	Identify decline
✓	Decline is measured within a given habitat and not averaged across all known habitats

	Link specialization & decline
✓	Specialization is inferred independent of decline
	Study covers entire range of species

Figure 2. Criteria for identifying and linking specialization and decline, as outlined by Colles et al. (2009, p. 851). Check marks to the left of each criterion indicate that the experiment performed by Walter et al. (2022) met this criterion.

decline of *S. aethnensis* relative to *S. chrysanthemifolius* at all elevations except its native 2000 m, the authors concluded that plasticity was mostly adaptive in *S. chrysanthemifolius*, which occupies a comparatively wide range of environments, but often nonadaptive in *S. aethnensis*, whose habitat is much more restricted (Fig. 1). By fulfilling most criteria for studies relating specialization to population decline (Fig. 2; Colles et al. 2009), this study contributes to our knowledge of factors that may influence the long-held (Simpson 1944) and frequently validated finding that specialized taxa face extinction at a greater frequency than more generalized taxa (Julliard et al. 2003; Liow 2004).

Although the authors have framed plasticity as a consequence of adaptive divergence, they acknowledge the view that differences in plasticity can also reinforce adaptive divergence. Other studies have suggested that phenotypic plasticity may initiate developmental bias by generating variation in certain directions, thus shaping a species' evolutionary trajectory (Schwander and Leimar 2011; Parsons et al. 2020). Phylogenetic analyses covering a clade's extended history may shed light on this "adaptation-first or plasticity-first" question, the answer to which, of course, need not be a complete dichotomy.

The findings of Walter et al. (2022) also have important implications for conservation. The maladaptive plastic response of the specialist *S. aethnensis* relative to that of the generalist *S. chrysanthemifolius* implies that *S. aethnensis* will require rapid evolution to adjust to novel environmental conditions caused by selective pressures such as climate change. Understanding if and how the genetic network underlying plasticity allows for such rapid evolution will help identify species with high potential extinction risks under the growing anthropogenic impact on their habitat (Julliard et al. 2003; Diamond and Martin 2016).

Viewed from a different perspective, the impact of these results also extends to more theoretical subfields of biology. As statistical methods grow more sophisticated and computing tools more powerful, evolutionary biology has seen a trend toward leveraging refined simulations and complex models to provide a more holistic conception of evolutionary dynamics. In particular, multivariate evolutionary models that attempt to account for how phenotypic traits covary and are constrained differently across taxa (e.g., Rolian 2019) are becoming increasingly common in the "evolvability" literature. These models often rely on assumptions about how plasticity and constraint themselves evolve many of which have yet to be experimentally validated (e.g., when organisms evolve convergent phenotypes, their respective phenotypic plasticities begin to resemble each other as well). By demonstrating that differences in plasticity can indeed evolve rapidly and that the adaptive quality of plastic responses can differ between closely related taxa, the work of Walter et al. (2022) helps provide a valuable theoretical foundation for developing more accurate dynamic evolutionary modeling.

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