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VARIATIONS ON A THEME—THE ECOLOGY AND EVOLUTION OF WITHIN-PLANT DIVERSITY

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Biologists engage in a love–hate relation with variation. On one hand, interspecific diversity and differences among conspecifics motivate most biological hypotheses. On the other hand, variation that is peripheral to a hypothesis is typically dismissed as noise that confounds understanding. However, there is a fine line between love and hate, which is crossed repeatedly in one direction during the development of biology, as variation that was once ignored as mundane is recognized as interesting and so comes to stimulate its own hypotheses. In his recent book on variation within individual plants, Carlos Herrera strives to lead readers across this line, making the case that by influencing plant interactions with animals components of such variation can be adaptive and so warrant broader attention.

As unitary organisms, we biologists tend to view the limited variation within our own bodies, such as between the sides of our faces, and those of other unitary organisms either as inconsequential or negatively as a sign of developmental instability (e.g., Møller 2006). This perspective is reinforced by recognition that a body's cells share the same genome, so that stochastic within-individual variation cannot be transmitted to offspring. Even if somatic mutation creates genetic variation within a body, its transmission is unlikely because of the independence of somatic and germinative cell lines within unitary organisms.

In contrast, modular organisms, such as vascular plants, corals, and bryozoans grow by the reiterated production of somatic components, each of which has the capacity to make reproductive organs. This characteristic body plan creates opportunities for variation among reiterated organs within individuals that are not possible for unitary organisms. Such variation is readily observed by overlaying leaves from the nearest house or garden plant or ordering the grapes within a bunch from smallest to largest. Furthermore, to the extent that systematic patterns of phenotypic variation among organs are genetically determined, they represent traits that can be subject to selection. Thus, at least some aspects of the variation within modular organisms could represent adaptations to specific environments, including interactions with herbivores and agents of pollen and fruit dispersal. In his book, Herrera builds on an extensive, scholarly review of literature from Theophrastus to 2007 (supported by 78 pages of references) to argue that within-individual variation and its ecological and evolutionary implications deserve much more attention than they have received to date.

After a largely historical introduction, Herrera develops his argument in four sections encompassing nine chapters. In the first section, Herrera devotes a quarter of his overall text to convincing doubting readers that the traits of leaves, flowers, fruits, and seeds often vary extensively within plants. He achieves this objective through the weight of evidence drawn primarily from the ecological and agronomic literature. In this section, Herrera establishes that virtually all above-ground traits vary within plants (Chapter 2:

below-ground traits are not considered), that this variation can be extensive and often represents the major component of trait variation within populations (Chapter 3), and that much within-individual variation occurs systematically, rather than stochastically, during plants' lives and over their bodies (Chapter 4). This section certainly achieves its objective of illustrating that within-plant variation is pervasive and, in part, nonrandom, although these points could have been made much more concisely and one wonders about the insights that await meta-analysis of the compiled information.

The second main section examines the proximate causes of within-individual variation and its logical implication. In Chapter 5, Herrera attributes most variation among a plant's modules to phenotypic plasticity rather than to mutation, depicting genetic mosaics as "little more than a biological oddity" (p. 131). He then explores the causes and nature of plasticity (Chapter 6), demonstrating that systematic influences associated with internal gradients, such as hormone fluxes and source–sink relations, and contrasting external conditions, including those created by interacting animals, typically account for more variation than stochasticity, which he attributes to developmental instability. This section closes with Herrera championing the "Haldane–Roy conjecture" (Haldane 1957; Roy 1959) that within-plant variation is as much an individual's property as its mean (Chapter 7). In support of this conjecture, Herrera reviews published evidence of genetically determined phenotypic differences among plants in the extent and nature (variance, skewness, kurtosis) of organ variability.

In the third section, Herrera considers the ecological implications of within-plant variation for interacting animals (Chapter 8) and for plants themselves (Chapter 9). For animals, within-plant variation creates opportunities for selective foraging and imposes costs, both of which can alter their interactions with plants. Probably all mobile consumers respond to environmental variation in food availability, so it should not be surprising that herbivores (including seed predators), and foraging pollinators and fruit dispersers detect and respond to within-plant variability, even if such behavior has been studied much less than among-plant selectivity. The foraging costs of variability that Herrera identifies are manifold, including intensification of competition between selective herbivores with limited mobility, the time and energy spent searching for high-quality organs, and the less-intuitive effects of Jensen's (1906) inequality. The latter effect occurs inevitably whenever the output of a process (e.g., foraging return) varies nonlinearly with the input (e.g., nectar volume per flower), which causes the mean output of variable inputs to differ from the output expected from the mean input. Curiously, despite devoting six pages to the implications of Jensen's inequality for foraging animals, Herrera ignores its implications when considering the consequences of variation for plants (see Harder and Aizen 2010 for examples). Instead, he focuses on more direct influences, such as the opportunities to exploit environmental gradients, interact with a greater diversity of pollinators and engage in bet hedging during seed dispersal. Nevertheless, this section clearly demonstrates that within-plant variation influences plant performance, negatively and positively, so that variation differences among plants should commonly contribute to fitness diversity within populations.

The final section (Chapter 10 and Epilogue) draws Herrera's argument to an incisive conclusion with his demonstration of the evolutionary consequences of within-plant variation. To this point, Herrera has relied on compilation of existing literature to build his argument, using his own unpublished data as a supplement, rather than to expose new perspectives. However, in Chapter 10 he unveils novel findings that are sure to bring within-individual variation into mainstream analysis of the evolution of modular organisms. Specifically, Herrera contrasts the results of 10 pairs of phenotypic-selection analyses using Lande and Arnold's (1983) approach, in which a fitness component is regressed on either each plant's trait mean alone or both its mean and variance. Only half of the analyses that considered trait means alone detected significant selection, which is a common result for phenotypic-selection studies (Kingsolver et al. 2001; Geber and Griffen 2003; Harder and Johnson 2009). In contrast, all 10 analyses that also considered within-plant trait variance detected significant influences on fitness, with significant variance effects in nine of these cases. Interestingly, the partial regression coefficients for the mean and variance had opposite signs in nine of the 10 examples (significant for both in four cases). A mundane explanation of these results (not mentioned by Herrera) could be that inclusion of within-plant variance in these regressions simply accounted for uncertainty in estimating a plant's trait mean (recall that the standard error of the mean equals $\sqrt{s^2/n}$); however, my own simulations reject this possibility. Instead, Herrera's results suggest that phenotypic selection acts directly on within-plant variation and possibly more often than on the mean traits that currently occupy center stage in ecological and evolutionary studies. With this conclusion in hand, Herrera returns to the review format to summarize the limited theoretical and empirical literature concerning within-individual variation as an adaptation, before closing with six predictions about the magnitude of adaptive within-plant variation in different situations and a brief epilogue. (The analogy Herrera draws in the epilogue between modular organisms and social-insect colonies is less applicable than he claims, because the latter are comprised of genetically heterogeneous individuals and so do not exhibit "within-genotype phenotypic variance" as he claims.)

Overall, Herrera's book evokes mixed impressions, which are encapsulated in his final sentences. Herrera has convincingly demonstrated that ". . . there is little doubt that within-plant variation in organ traits is a biological phenomenon whose multifarious implications render it worthy of study in itself" (pp. 342–343).

In his detailed, clearly presented review, Herrera has provided a scholarly reference that, by drawing together relevant literature from disparate fields from agronomy to animal behavior, lays a solid foundation for such study. And yet the conclusion that "(o)nly time ... will eventually tell if, in addition to being interesting, the phenomenon is also important" (p. 343) is unnecessarily tentative and reflects a generally cautious approach that pervades this book. This attitude is evident in Herrera's decisions: not to adopt "a hypothesis-driven stance" but instead to "leave adaptive and evolutionary considerations for the closing chapter" (p. viii); to focus consideration of functional aspects of variation on "plant-animal interactions, as this is the field in ecology with which I am most familiar" (p. viii); to employ "rather crude comparisons" (g. 39); and to provide only limited direction for future analysis, even claiming that despite the apparent relevance of "current theories conferring a central role to phenotypic plasticity in differentiation of adaptive strategies, and ultimately macroevolutionary diversification ... (i)t seems ... somewhat speculative at present to pursue this line of reasoning further" (p. 338). Such prudence is expected for a journal article, but the added opportunity to stimulate and provoke afforded by writing a book has been only partially realized.

Among the topics that Herrera has not considered is the extent to which the nature of some traits imposes unavoidable, and possibly misleading, variation, as illustrated by two examples. First, consider the coefficient of variation, $CV = 100s/\bar{Y}$, which, following common practice, Herrera uses to summarize within-plant variability relative to a plant's trait mean. For multidimensional traits, such as areas and volumes (and hence masses), the *CV* always exceeds those of the linear dimensions of which they are composed as a mathematical necessity (see Appendix 1 of Lynch and Walsh [1998] for the mean and variance of a product). Therefore, account must be taken of this association before the *CV*s for traits that represent different numbers of dimensions can be compared directly. Second, consider the subdivision of R resources to produce discrete organs, for which there is a single optimal size, m. If $n = R/m$ is not an integer and a partial organ is useless, how should the residual resources best be allocated? The solution is to produce either n' organs of size $R/n > m$, or $n' + 1$ organs of size $R/(n + 1) < m$, whichever maximizes overall fitness (Ebert 1994: n' is the largest integer less than n). Given this allocation, variable resource availability generates a particular variation pattern in both organ size and number, and size variation declines with increasing organ number, even though there is a single optimal organ size. Such patterns could manifest as, for example, variation in leaf size among a plant's branches, flower size among inflorescences, and ovule size among flowers. These examples illustrate that inherent features of some traits contribute to within-plant variation. Such effects should be identified and isolated before comparing variation among traits or attributing the remaining variation to developmental instability or direct function.

Although Herrera appreciates, for example, that "the characterization of leaf traits for individual plants is far from trivial, and ecologists and statisticians alike have long struggled to design optimal sampling strategies" (p. 44), he offers no suggestions for study design and devotes limited attention to appropriate approaches for analyzing within-plant variation. Such issues are not simply technical, because some approaches can expose insights that others obscure or even misrepresent. A key aspect of the analysis of variation concerns the distribution of trait variation. For normally distributed, continuous traits the partitioning of variance among hierarchical components (e.g., among plants, among branches, among leaves) is relatively straightforward, because normality applies at all levels and appropriate techniques are well-developed (see Lynch and Walsh 1998). In contrast, the normal distribution is inappropriate for discrete traits (e.g., petal number, carpel number, ovule number, seeds per fruit: note that Herrera uses "discrete" in reference to categorical traits) and many continuous traits (e.g., proportions), although the means of such traits will tend to be normally distributed as sample size per plant increases, according to the central-limit theorem. Such distributional heterogeneity complicates variance partitioning even when the appropriate distributions can be identified (Goldstein et al. 2002) and appropriate computer techniques are not readily available. Importantly, use of methods that assume incorrect sampling distributions can lead to inaccurate variance partitioning, including the relative magnitude of systematic influences (e.g., organ position) and stochastic developmental instability. Related problems arise also in regression analysis of, for example, the causes of within-plant variation, its influence on plant interactions with animals, and phenotypic selection (see Richards 2008). Thus, before undertaking analyses of within-plant variation of the type advocated by Herrera, careful attention should be paid to relevant aspects of sampling design and eventual statistical analysis.

By choosing to consider functional aspects of within-plant variation primarily in the context of interactions with animals Herrera has left many topics unexplored. The "multiplicity in unity" theme highlighted in the book's title is particularly relevant from an ecological perspective, as variation diversifies a plant's interactions with all aspects of its environment. Herrera's review clearly demonstrates that variation can enhance the benefits of interacting with mutualists and reduce the costs of interacting with antagonists. Does this imply that species that experience limited herbivory or have abiotically dispersed pollen and/or seeds exhibit less within-plant variation, or that a smaller component of their variation is distributed nonrandomly? To what extent and in what ways does resource availability, including competition between plants, affect within-plant variability (see Geritz 1995 for theory related to seed-size variation)? Within-individual variation may provide a mechanism by which modular organisms accommodate temporal environmental stochasticity given their inability to move to more hospitable sites. If so, do annual species, which experience less environmental stochasticity during their short lives, require or exhibit less variation that perennials? For similar reasons do the leaves of "deciduous" species exhibit less variation within plants than those of "evergreen" species? Does the production of single structures (e.g., single flower, uniovulate ovary) reflect the benefits of large size (i.e., the extreme in the size-number trade-off) or of no variation in specific environments? Readers interested in these and many other questions unrelated to plant–animal interactions will have to use Herrera's book as a general stimulus to explore their own interests, rather than as a guide to specific open questions.

Evolutionarily, a "unified diversification" perspective on within-plant variation is more relevant than multiplicity in unity, because fitness is a characteristic of the individual, rather than of its components. This is clearly represented by the pervasive role of Jensen's inequality in governing the influence of variation in vegetative and/or reproductive function on overall fitness when performance varies nonlinearly with input. A corollary of Jensen's inequality is that within-plant variation does not affect mean performance when fitness varies linearly with input, so that the simple existence of such variation provides no evidence of its adaptive value. More importantly, Jensen's inequality implies that the phenotype of modular organisms includes not only the distribution of variation in their organs, as Herrera emphasizes, but also the functions that relate the traits of individual organs to their fitness contributions. Such functions, or more accurately the biological processes they represent, likely help unify diversified organisms, even though, as Herrera reviews in Chapter 6, individual modules often operate somewhat independently. As a result, these processes probably represent prime targets of selection and so should be included among the topics deserving special attention in the analysis of modular organisms.

The preceding paragraphs demonstrate that Herrera has not exhausted the topic of variation within plants, let alone modular organisms as a whole. Nevertheless, he has surely succeeded in his main goal to reveal that "a feature that was either unnoticed or taken as a nuisance turns into an opportunity for framing new questions" (p. 339). The foundation that he has provided greatly promotes the necessary integration of within-individual variation in analyses of the ecology and evolution of modular organisms and should be read by all students of this topic.

LITERATURE CITED

Ebert, D. 1994. Fractional resource allocation into few eggs: *Daphnia* as an example. Ecology 75:568–571.

Geber, M. A., and L. R. Griffen. 2003. Inheritance and natural selection on functional traits. Int. J. Plant Sci. 164:S21–S42.

Geritz, S. A. H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. Am. Nat. 146:685–707.

Goldstein H., W. Browne, and J. Rasbash. 2002. Partitioning variation in multilevel models. Understand. Stat. 1:233–231.

Haldane, J. B. S. 1957. Karl Pearson, 1857–1957. Biometrika 44:303–313.

Harder, L. D., and M. A. Aizen. 2010. Floral adaptation and diversification under pollen limitation. Phil. Trans. R. Soc. Lond. B 365:529–543.

Harder, L. D., and S. D. Johnson. 2009. Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. New Phytol. 183:530–545.

Jensen, J. L. W. V. 1906. Sur les fonctions convexes et les inégalités entre les valeurs moyennes. Acta Math. 30:175–193.

Kingsolver J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gilbert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. Am. Nat. 157:245–261.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1201–1226.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates Inc., Sunderland, MA.

Møller, A. P. 2006. A review of developmental instability, parasitism and disease infection, genetics and evolution. Infect. Gen. Evol. 6:133–140.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. J. Appl. Ecol. 45:218–227.

Roy, S. K. 1959. Regulation of morphogenesis in an oleaceous tree, *Nyctanthes arbor-tristis*. Nature 183:1410–1411.

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