

cultivated relatives, there are good reasons for caution because the situation may change. Some populations are not yet in equilibrium and gene frequencies may go to fixation, potentially resulting in a decrease or no change in diversity relative to pre-introgression levels.

A picture emerges of processes (inter-specific hybridization, introgression, persistence of immigrant alleles) and occasional consequences (evolutionary change, ecological and agricultural harm) that, while clearly not ubiquitous, still cannot be considered unusual on the basis of the evidence in hand. That this can at times have substantial consequences is well illustrated by the story that Ellstrand weaves throughout the book (chapters 1, 6, and 10) of hybridization between wild sea beets (*Beta vulgaris* subspecies *maritima*) and the interbreeding progenitor and weed of cultivated beets (*Beta vulgaris* subspecies *vulgaris*). This is the scientifically documented melodrama of what both researchers and practitioners considered to be an unlikely long-distance romance, including the substantial harm caused by the progeny of those encounters, and how their story was uncovered.

Overall, *Dangerous Liaisons?* provides a valuable evaluation and discussion of our knowledge of gene flow in plants and the implications for transgene movement into wild crop relatives, with great relevance for transgene flow into FVs as well. Ellstrand manages to infuse his discussion and explanations with both thoughtful caution—walking the fine line between the polarized sides of the transgene discussion by not venturing beyond what the data support or dismissing what lack of data cannot preclude—and the excitement of surprising new insights and the changes they demand of us. Visual presentations of the data and ideas discussed would have been a nice addition to the book (it contains only six figures and 13 tables). The book's accessible and informal style make it a pleasure to read, but that informality also makes the book's abrupt end without even a summary paragraph a bit of a surprise—why did our friendly companion in understanding plant gene

flow leave us without even a parting thought?

In Mexico and elsewhere, the discussion of transgenes and their flow into wild relatives of maize and Mexican FVs continues, including the current debate about lifting the 1998 moratorium on planting transgenic varieties for research purposes. The circumstances in Mexico raise questions concerning gene flow and containment that demand rethinking on the part of biologists and policymakers. For example, what will be the impact on genetic diversity in FVs, given what is known about their genetic structure in contrast to that of MVs (modern varieties) (see pp. 141, 181)? Lack of monitoring for primary or secondary ecological impacts is a concern in wild plant populations (p. 183), but who will monitor traditional agricultural systems for such impacts? Management of gene flow may be sought through linking transgenes to tandem constructs tailored to lower fitness in environments outside of industrial agricultural fields (p. 201), but how might those affect performance in the low-resource agricultural systems ubiquitous in Mexico and the “third world”? These are just some of the myriad questions about transgenes that will benefit from the understanding of gene flow and the approach to investigating it demonstrated by *Dangerous Liaisons?*

At one point in his discussion, Ellstrand comments that “thinking about impacts [of GE crops] involves thinking out of the box” (p. 164), and this book, as well as his own research on hybridization between cultivated and wild plants and the potential significance in the case of transgenes, opens the door for us to do just that.

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GETTING RIGOROUS ABOUT DEVELOPMENTAL INSTABILITY

Developmental Instability: Causes and Consequences. Michal Polak, ed. Oxford University Press, New York, 2003. 488 pp., illus. (ISBN 0195143450).

The term “developmental instability” (DI) refers to the inherent degree of variability or “noisiness” of biological development. DI cannot be observed directly, but its occurrence is signaled by the phenotypic variability of comparable structures whose development took place under presumably identical internal (genetic) and external (environmental) conditions. The greater the divergence of such structures from one another, the greater the inferred degree of DI.

The phenomenon of DI was first identified and defined a century ago, in work on plants, by the eminent biometrician Karl Pearson. Forty to 50 years later, its investigation received impetus from some critical work and thinking by a small group of biologists, in particular C. H. Waddington, Kenneth Mather, and John H. Thoday. Nevertheless, it remained a rather neglected subject until the mid to late 1980s, when it experienced a surge of interest, becoming a fashionable subject in the 1990s. Yet despite this long history of attention and analysis, the precise significance of DI in the biology of complex organisms and for its investigators has remained frustratingly elusive. Perhaps the only point of universal agreement is that the phenomenon of DI is of interest and significance.

The particular focus of attention for the past 20 years or so has been the proposition that there should be an inverse relationship between DI and fitness; the greater the DI, the less fit the animal or plant will be. Another related

idea, associated initially with Therese Markow and Anders Pape Moller, in particular, is that the visible morphological asymmetries that develop as a result of DI serve as scorable indicators of (poor) fitness, and these asymmetries reduce the probability of successful mating. In effect, this hypothesis links DI to another idea that was becoming fashionable in the 1980s after a similarly long period of neglect, namely, Darwin's idea of sexual selection. The idea has a corollary: If the effects of DI are signaled to potential mates, as this hypothesis suggests, then there should be selection for "good genes" that reduce DI in general and the corresponding visible asymmetries produced by it.

Crucial to testing this hypothesis is the way in which one measures DI, since it cannot be detected directly by simple observation. The necessity of comparing structures with identical genotypes means that for sexually reproducing organisms, one has to compare identical structures arising within the same individual. For individual animals, the simplest measure is deviations from perfectly symmetrical left and right structures, such deviations being termed "fluctuating asymmetry" (FA). The critical assumptions in using FA as a surrogate for DI are that the left and right sides of the developing animal experience identical environments during development and that they are wholly independent of each other. Estimates of the variance of difference within a population, in principle, yield estimates of FA and, hence, the degree of underlying developmental instability. One problem with FA as a measure of DI, however, is that it has only one degree of freedom. To measure variances accurately under these conditions requires accurate measurement both of (often) small differences and of large sample sizes. For plants, measures of departures from symmetry are easier because one can compare multiple structures, such as flowers, leaves, or seeds, that should in principle be identical in the absence of DI.

The multi-author volume under review here, edited by Michal Polak (University of Cincinnati), examines the subject in depth. It has two broad aims.

The first is to provide a picture of what one can currently conclude about DI in terms of its genetic and biological bases, its significance in development, and its importance for evolution. The second, and no less important, aim is to examine the methodological problems inherent in the quantitative assessment of DI in actual populations and to arrive at some degree of consensus on the best analytical approaches.

The book consists of 24 chapters. The list of contributors includes all, or nearly all, of the best-known figures in the field, plus many of the field's key younger scientists. The chapters are grouped into five sets devoted to (1) the developmental origins of DI (six chapters), (2) the genetic foundations of DI (five chapters), (3) the fitness consequences of DI (five chapters), (4) the statistical tools used to measure DI (three chapters), and (5) studies on environmental stress and its applications (five chapters). Partitioning the subject in this way is both sensible and

helpful but, as one might expect, there are overlaps in discussion between the different sections. For instance, some discussion of the genetic foundations of DI (section 2) creeps into several of the chapters on development (section 1), while it is impossible to discuss the genetic causes of DI (section 2) without first discussing some aspects of the developmental processes themselves.

Space does not permit a detailed accounting of the individual chapters, but it seems safe to predict that, regardless of one's particular area of interest in DI, the reader will find much of interest. For this reviewer, the key chapters were the first two and the final one. The former deal with developmental perspectives on the sources of DI and were written, respectively, by H. F. Nijhout and G. Davidowitz and by Christian Peter Klingenberg. The final chapter in the book, also by Klingenberg, deals with the uses of FA to ascertain the degree of dependence between developmental

modules, a novel and interesting application of the ideas. I also found the historical perspective written by Charles M. Woolf and Therese A. Markow on the differing historical views that informed the concept of “developmental homeostasis” quite valuable. For the statistically minded reader, on the other hand, several of the chapters in sections 3 (fitness consequences) and 4 (statistical tools) will undoubtedly have the strongest appeal. (Correspondingly, for the relatively statistically unsophisticated, those chapters will surely be hard going.) Finally, for those readers who principally want to find out about the uses of FA as a measure of “stressors” in the environment, the chapters in the final section will be of strongest interest.

Despite the inevitable differences of perspective presented in a multiauthor book, one gets the sense that there is growing agreement about certain issues. For example, it becomes evident at least halfway through the book that there is a consensus that much of the work carried out in the 1980s and 1990s, which initially supported the sexual selection connection, was not robust. Several of the chapters (in sections 3 and 4) grapple with the methodological, analytic, and statistical problems that may have led to a premature acceptance of the idea that FA is an important signaler in sexual selection. (And there are some interesting discussions of just why the earlier work seemed to provide such initial strong support for the idea.)

A second area of general, if not complete, agreement is that the FA estimates for different traits are usually not highly correlated. Just why this might be so is explicable in terms of a hypothesis published several years ago (Christian Peter Klingenberg and H. Frederik Nijhout, “Genetics of Fluctuating Asymmetry: A Developmental Model of Developmental Instability, *Evolution* 53 [1999]: 358–375). This model predicts that there are no general “FA genes” but that the FA for any trait is based on the specific genetic foundations of that trait. If this is the case, then the “good genes” hypothesis of sexual selection—involving the use of FA by animals as a signaling device for the possession of such genes—is in trouble.

Indeed, one gets the sense that as the tests for FA have become more rigorous with time, there has been declining support for this hypothesis.

Altogether, the book is a pleasure to read. The individual chapters are well written and the book as a whole has clearly been well edited. It is also handsomely produced, with good clear print, decent figures, and very few typographical errors. It is, of course, impossible to predict what its shelf life will be. New findings of interest continue to arise. For instance, a new analysis (James R. Kellner and Ross A. Alford, “The Ontogeny of Fluctuating Asymmetry,” *American Naturalist* 161 [2003]: 931–947) suggests that during development, FA becomes less pronounced, indicating that left and right sides *do* communicate in some manner during development to achieve a degree of developmental matching. If confirmed, this finding undermines a key assumption in the use of FA as a measure of DI. As other new findings are made, some are bound to require reevaluation of current ideas, rendering some of the material here obsolete. Yet my guess is that a fair number of the chapters will continue to be of value 5 to 10 years from now, and a few of them, such as the historical perspective that Woolf and Markow provide, will remain of interest even longer. For anyone working on developmental instability or related subjects, this book is to be highly commended. It is an invaluable resource for the field and may be such for some time to come.

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