

BOOK REVIEW

Integration: How complex traits are put together

Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes

Edited by M Pigliucci and K Preston
Oxford University Press, New York, USA; 2004. 443pp.
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Reviewed by CP Klingenberg

For a long time, morphological integration has been a research subject that has been curiously endemic to America and, more particularly, to the Midwest. The concept was originally developed by Olson and Miller (1958) in Chicago, and the researchers who have been responsible for the revival of this research topic in the 1980s and 1990s have had ties to the region (particularly Chicago, Wisconsin, Michigan). Other researchers who have published on the subject mostly have been North American either by birth or at least by training. Outside of North America, the subject was relatively little known. I was particularly struck by this difference during my postdoctoral training, when I borrowed Olson and Miller's book, in its original edition, from the libraries at Duke University (USA) and at the University of Cambridge (England): the Duke copy was in tatters, whereas the one at Cambridge was still in mint condition. I am sure that this difference is not just because British students are somehow more effective at keeping their sandwiches away from the library books. However, globalization is now sweeping through this field as well, and morphological integration is no longer a peculiar case of conceptual endemism, but is coalescing with other ideas to become a unifying perspective in evolutionary biology. The book on *Phenotypic Integration* edited by Pigliucci and Preston is likely to make a significant contribution to this trend.

The editors have assembled a roster of contributors who represent all of the main conceptual directions and empirical research methods in the field. The chapters of the book therefore provide a great diversity of viewpoints, and at times it can be a challenge for the reader to integrate them into a coherent picture of the field. The theme of integration has a long tradition in biological research as it is related to earlier concepts such as allometry and reaction norms. Many of the chapters in the book take up these historical connections, but also point out new directions to establish novel links with ideas from evolutionary developmental biology, genomics, and other new fields. In particular, the concept of modularity, which is tightly connected to integration, is present throughout the book.

The book starts with a series of chapters evaluating integration as an adaptation and as a constraint on evolution. These chapters, making up about a third of the book, are mainly reviews of case studies that examined the different aspects of integration in a variety of study

systems. These examples illustrate the complexity in many real evolutionary systems, where multiple players interact, for instance, flowers and their pollinators (Armbruster *et al*) or males and females in the evolution of sexual ornaments (Badyaev), or where the modular structure of the organisms produces a hierarchy of levels of variation as in plants (Preston and Ackerly). The final two chapters in this first section use a quantitative genetic perspective to examine the role of integration as a constraint and adaptation (Merilä and Björklund) and to explore the relative roles of such constraints and of stabilizing selection as explanations of the observed stasis of traits at a macroevolutionary time scale (Hansen and Houle).

The environment is a prime determinant for phenotypic traits and their integration, and, accordingly, the focus of the second section is on the role of plasticity. A chapter by Pigliucci discusses the use of model systems (and specifically, *Arabidopsis*) in research on integration and phenotypic plasticity, combined with a critique of *P*-values in statistical significance testing. The following chapter contains a discussion of plastic responses to predators and their ecological and evolutionary consequences (Relyea). Clearly, the examples presented by these two chapters do not cover the spectrum of environmental effects on organisms and their integration, but they whet the reader's appetite to learn more on this subject.

The third part consists of three chapters that examine specific aspects of the genetics and molecular biology of integration. Murren and Kover review QTL methods for mapping genes affecting phenotypic traits and discuss the analysis of integration. The second chapter discusses the possible developmental mechanisms that produce the covariation of traits, outlines a morphometric approach to study them empirically, and outlines their implications for evolution (Klingenberg). The effects of mutation have long been identified as a critical factor for understanding long-term evolution, and have recently been addressed by experiments using mutagenesis (Pigliucci). Yet, this chapter illustrates yet again the complexity of genetic and developmental systems, as it turns out that the mutational effects depend on the genetic background, among other factors. Altogether, the three chapters in this section are outlines of new possibilities rather than summaries of fully established research programmes – the rapid progress of the techniques in these fields suggests that many exciting results will soon emerge.

A further section of the book is highlighting some macroevolutionary aspects of integration. Eble gives a general review of the concepts from the perspective of a palaeobiologist. A discussion of heterochrony and life history theory makes the point that organismal integration concerns the development of morphological structures as well as the reproductive and ecological parameters (Zelditch and Moscarella). Ackermann and Cheverud review the literature on integration in primates and demonstrate how reasoning about integration can be used in the reconstruction of fossil shapes and to interpret patterns of diversification.

The book concludes with a section on methodological and theoretical issues of integration. A review of methods for the analysis of multivariate data in a phylogenetic context (Steppan) provides a fundamental basis for the comparative study of integration. This topic is further examined by some results from theoretical and empirical studies on the evolution of additive genetic covariance matrices (Roff). Wolf *et al* provide a theoretical discussion on the evolution of traits and their integration using the concept of developmental landscapes, the functions that map different developmental factors (genes, environment) to the phenotype of interest. The theoretical discussion of the notion of constraint by Schwenk and Wagner emphasizes that constraint is best considered relative to selection, besides the pairs of mutability *versus* stability and of externalism *versus* internalism. Griffiths and Gray round off the section by a discussion of developmental systems theory, an approach advanced particularly by philosophers of biology, and its relation to evolutionary developmental biology.

The book contains a great diversity of viewpoints, different conceptual frameworks and empirical approaches. It clearly demonstrates that phenotypic integration has come a long way from being an idea prevalent mainly in the American Midwest. But, just as it happens when local businesses develop into companies of a world-wide scale, globalization of concepts can occur with a loss of focus. Readers therefore may ask, what precisely is phenotypic integration? And is there anything in evolutionary biology that is not encompassed by it? As indicated by the subtitle of the book,

Studying the Ecology and Evolution of Complex Phenotypes, the editors indeed have a very inclusive view of the concept. They have favoured breadth and diversity over a rigid delimitation of the topic. As a result, the book is a quite general collection of essays on the evolution of complex traits with an emphasis on the recurring topics of integration, modularity, and constraint.

Reading the book provided me with many opportunities to discover ideas and facts that were new to me, even though I have worked in the area of morphological integration for some time. I think this volume will provide stimulating reading for most students, teachers and researchers in a variety of biological disciplines. For evolutionary geneticists, in particular, the theoretical reviews and the many case studies concerning the manifold interactions between genotypes and environments will be an inspiration for teaching as well as research.

References

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CP Klingenberg
School of Biological Sciences, University of Manchester,
3.614 Stopford Building, Oxford Road,
Manchester, M13 9PT, UK
E-mail: cpk@man.ac.uk