Everything flows and nothing stays

The Biology of Streams and Rivers

by P.S. Giller and B. Malmqvist

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River ecologists live in exciting times. First, we have new tools to use, ranging from satellite imagery to molecular techniques, that enable us to ask profoundly important questions at vastly divergent scales. Second, we work in habitats that lend themselves to experiments (in microcosms, but also in replicated tributaries in real rivers) to investigate current hypotheses linking organismal ecology, biodiversity and ecosystem functioning. Third, in a time of high concern about sustainability of human resource use, we work in systems that are not only of undeniable importance in their own right (use of water and instream resources), but are also barometers of the state of their catchment areas (integrating atmospheric pollution, climate change, land-use impacts, etc.).

Giller and Malmqvist provide glimpses of this excitement; for example, by describing a molecular biology study of patterns of movement and colonization by stream larvae and their (terrestrial) adults, and by devoting their final chapter to human impacts. But, because this is more than (or less than?) a book about ecology, the authors are preoccupied in the first five chapters with describing the essential nuts and bolts of river habitats and their occupants. Commentators, including Giller and Malmqvist, have recently begun quoting an ancient authority, Heraclitus (*c.* 540–480 BC), who remarked that 'you can't step twice into the same river.' I think that they mean to emphasize the extreme variability within and between rivers, although Heraclitus probably had in mind the continuously moving water (the title of this review is another of his not-entirely-apposite aphorisms). A river's narrow, linear form, its unidirectional flow and its intimate connection with groundwater, naturally lead river ecologists to emphasize linkages in three spatial dimensions: horizontally from upstream to downstream, laterally from land to water and vertically with the sediments beneath the stream. The hyporheic zone (the saturated interstitial spaces beneath the streambed) is a key site of exchange of water and dissolved resources between the river channel and the adjoining groundwater aquifer and could also be important as a refuge or nursery area for benthic invertebrates, fish eggs and larvae. The fourth dimension, time, also has a special place in river ecological research because of profound variations in discharge, both predictable and unpredictable (the medium provides special opportunities to study disturbance ecology[1]).

The Biology of Streams and Rivers generally deals well with the hierarchical nature of river ecosystems and with three of the dimensions, but for me the authors' treatment of the hyporheos rather skimmed the surface. The need to view rivers within their landscape forces river ecologists to be holistic and multidisciplinary in approach[2], combining the biological study of individual, population, community and ecosystem processes with the physical study of hydrology, geology, geochemistry, geomorphology and hydraulics[3,4]. Giller and Malmqvist emphasize the relevance of a range of disciplines to river ecology and, in three later chapters, they provide fairly comprehensive treatments of ecosystem processes and community dynamics. They seem to assume that their readers have a thorough grasp of ecological principles when they mention, in passing and without definition or explanation, topics such as dominance and founder control, exploitation competition, guilds and the microbial loop. This needs correcting in later editions of the book. Rivers, headwaters within rivers, and reaches within headwaters all possess elements of islandness and metapopulation dynamics. They provide admirable systems for studying the processes of speciation, colonization and extinction. In this context, Giller and Malmqvist quote the example of a chironomid species, *Orthocladius calvus*, which was unknown before it colonized newly established artificial stream channels in southern England[5]. It reached massive densities within a few weeks, then disappeared and apparently has not been seen since. This seems to be one of ecology's most dramatic illustrations of 'r-selection' and perhaps a unique case of a species that, indeed, did not step into the same river twice!

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An alternative evolutionary synthesis

Phenotypic Evolution: A Reaction Norm Perspective

by C.D. Schlichting and M. Pigliucci

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One of the most important conceptual breakthroughs of contemporary evolutionary biology has been the widespread recognition of the prominent role of internal, or structural, features of organisms in mediating a wide range of fundamental phenomena, including the origin of morphological novelty, the integrated evolution of complex characters, and even the differential success and diversification of lineages. Although relevant internal features can range from sheer physical attributes and the mechanical properties of biomaterials to functional (physiological) relationships, arguably the most prominent focus of current research is development. *Phenotypic Evolution* is the latest in a spate of single- and double-authored volumes[1–4] that attempt to address the inadequacy of the neodarwinian synthesis *vis-à-vis* the role of development[5,6], by promoting more prominent incorporation of developmental approaches into the current evolutionary paradigm.

The particular twist offered by Schlichting and Pigliucci is to promote the idea of the developmental reaction norm (DRN) as an important conceptual organizing principle for unraveling the many remaining mysteries of phenotypic evolution. The DRN has three key components: changes in ontogenetic trajectories, correlations among characters, and responses to different environmental conditions. It is inextricably linked to the environment and environmental variation, and Schlichting and Pigliucci unabashedly attribute inspiration for their ideas to the pioneering studies of ecogeographic variation by Clausen, Keck and Hiesey, as well as to the concepts of stabilizing selection and genetic assimilation as originally formulated by Schmalhausen, the great Russian morphologist, and Waddington, the British embryologist, among others. Their treatment comprises ten chapters. The first five present an introduction and background to the problem, along with overviews of the three key components of the DRN. The last half of the book applies 'reaction norm thinking to problems in phenotypic evolution'. I enjoyed parts of the first section, especially the historical recapitulation; it's always rewarding to discover the depth, breadth and complexity of the ideas of our early intellectual heroes. How many people working in 'evo-devo' today, for example, know that J.M. Baldwin, who was among the first darwinians to propose a plausible mechanism for the evolution of phenotypic novelties (the 'Baldwin effect'), published a book entitled *Development and Evolution* in 1902?

Phenotypic Evolution, however, is not simply a summary of facts or an attempted 'state of the art' review. Instead, it explicitly promotes a research program for addressing an array of topics, ranging from organismal integration and constraints to the mechanisms of constructing the genetic architecture, to modes of evolutionary change and the origin of evolutionary novelties. The authors appropriately emphasize the role and ability of the environment to elicit phenotypic change, as well as the intrinsic capacity of existing developmental systems to produce novel features following a minor genetic or environmental perturbation. This message is too often lost, or at least minimized, in the frequent attention paid to dramatic phenotypic effects produced in gene-knockout experiments or overexpression studies. Their discussion of hidden variability also nicely presages the recent exciting report of this phenomenon following perturbation of heat-shock protein Hsp90 in *Drosophila*[7]. Finally, it is refreshing to see genetic assimilation resurrected as an important mechanism in the origin and stabilization of novel phenotypes – 'it is the most likely mode of evolutionary change for many characters' – although I wish that this theme had been developed further.

Most authors of books in the field of evolution and development come from backgrounds in either paleobiology (or some other 'macroevolutionary' discipline) on the one hand, or molecular, cell and developmental biology on the other. In this light, the population- and quantitative-genetics perspective offered by Schlichting and Pigliucci is both valuable and welcome. It allows them, for example, to address a series of topics that receive little or no notice in other treatments; these include adaptation, phenotypic plasticity, heritability, environmental effects and heterogeneity, and genetic correlations. Nevertheless, this perspective does appear to come at a cost. For instance, as one who has come to regard allometry as principally a morphological or physiological concept, I was surprised (and somewhat chagrined) to see allometry (Chapter 4) defined much more broadly to encompass 'the relationships among *any* phenotypic characteristics.' Similarly, I was disappointed to see the treatments of two essential topics – constraints (Chapter 6) and phenotypic integration (Chapter 7) – focus so heavily on genetic correlations and/or covariance matrices, seemingly at the expense of other key aspects. Such a standardized, generic approach risks eliminating the dynamism of developmental and functional systems, the valuable idiosyncratic properties of specific characters and character complexes, and the potentially important role of other biological processes, all of which could contribute significantly to our understanding of constraints and integration.

Phenotypic Evolution takes a different approach to the study of the relationship between development and evolution from that currently employed by many of its main practitioners. In many respects, it is a broader approach; for example, Schlichting and Pigliucci are not just interested in how novel phenotypes arise, but also in how they come to be established in populations and integrated into existing functional and developmental systems. Such an approach ultimately must prevail if modern biology is to achieve a truly synthetic understanding of evolution.

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Despairing optimism

Feeding the Ten Billion: Plants and Population Growth

by L.T. Evans

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In 1798, Thomas Robert Malthus, the first economist, wrote an essay about the interaction between human population growth and agricultural production. At that time, the world's population numbered less than one billion and the majority were chronically hungry. Malthus's pessimistic essay, claiming that humans would always reproduce up to the constraints set by hunger, provoked much further debate.

Today's six billion people are, on the whole, vastly better fed, healthier, better educated and materially more prosperous. Enough food is currently produced to feed about ten billion people an adequate vegetarian diet. Approximately 40% of cereal grains are fed to domestic animals, and about three-quarters of a billion people (one person in eight) are believed to be chronically hungry.

The 1998 median projection of the United Nations Population Division foresees a world population of 8.9 billion in 2050. Population sizes of eight or ten billion are probably equally plausible. The added billions will live mostly in the poorest regions of today. The number to be added depends on individual and political choices now and in coming decades. Most economists and agricultural scientists agree that the rich regions will continue to be able to feed themselves. The great unanswered question – one that keeps Malthus's concerns vivid – is how well the rapidly growing populations of the presently poor countries will eat and live.

Feeding the Ten Billion: Plants and Population Growth aims 'to understand how the evolution of agriculture has both shaped and been shaped by the course of world population growth'. Evans, a distinguished plant physiologist and a former President of the Australian Academy of Sciences, achieves this aim by describing the past interactions of population and agriculture. He writes with authority, subtlety, accuracy, clarity, a marvelous richness of detail and a very engaging human touch. Evans has read widely, and good literature has shaped his perceptions and style. Separate chapters describe the progress of food production as the population grew to five million, 50 million, half a billion, and each successive billion up to the present six billion. His 227 pages of text are armed with 228 excellent references.

Evans shows that up to 1960, when the population was three billion, humans increased the area of arable land in proportion