

PREFACE

Towards the marriage of theory and data

Theoretical biology is a subject with a rich history, tracing back certainly to demographers such as Graunt [1], and also drawing inspiration from perhaps the most important biological theoretician of all, Darwin [2]. Although Darwin did not deal in mathematics, his use of deductive reasoning to provide a conceptual framework for an otherwise confusing body of observations, and to make testable predictions, is the model for what theoretical biology should be.

Quantitative approaches to biological problems have been around for a while, among demographers such as Graunt, as well as among others such as Verhulst [3] and Quetelet [4,5], who addressed Malthus's [6] challenges of population regulation. However, in the first part of the twentieth century, the subject was elevated to a new level: in ecological systems by the sophisticated mathematical contributions of Volterra [7] and Lotka [8]; in population genetics by Wright [9–11], Fisher [12,13] and Haldane [14,15]; and in epidemiology by Ross [16] and by Kermack & McKendrick [17]

No course in ecology is complete without a discussion of the equations of Volterra and Lotka, describing the dynamics of interacting species; despite their reliance on mathematical techniques that may be unfamiliar to some ecologists, their essential elements can be translated into terms that all can understand, and led early on to close links to experimental work, such as the studies of Gause [18], Park [19] and Utida [20].

The legacy of Volterra and Lotka has not been universally positive, although this is certainly not their fault. The attractive simplicity of the model equations proved irresistible to mathematicians eager to add bells and whistles, with little concern for biological relevance, and to explore their tortured implications in painful detail. This has produced a large literature, harmless except for its effect on perceptions of the field of mathematical biology, and its obfuscation of the cryptic nuggets that sometimes lie within.

I was influenced early in my career by the distinguished probabilist Mark Kac [21], who wrote that the great contributions of physicists to biology had been carried out by physicists who had become biologists; that perceptive insight would be even more valid today. In interdisciplinary work, the standards for

success must rest in whether the problem of interest has been solved, or at least illuminated, not in the elegance of the methods. This Theme Issue and the meeting from which it arose are dedicated to that principle, and in particular to the importance of confronting theory with data.

When I first entered theoretical biology in the 1960s and 1970s, the most exciting things for me to read were wide-spectrum volumes, such as Waddington's [22–25] *Towards a Theoretical Biology*, which brought together broad thinkers from biology and other disciplines to look for commonalities across systems in such phenomena as pattern formation, periodicities and bifurcations. Abstract mathematical work, such as Rene Thom's theory of catastrophes, attracted wide interest for a while because of the perceived potential, unrealized, to provide a unifying framework for similar phenomena in diverse applications. Theoretical biologists eagerly swarmed to meetings such as the Gordon Conferences in Theoretical Biology and Biomathematics to share insights, and commiserate with one another about how unappreciated they were among biologists. Lecture notes volumes appeared that individually had little focus because of their wide scope, but nonetheless were scooped up and read avidly by mathematicians and physicists seeking points of entry into biology. More focused monographs began to attract attention also from mathematically inclined biologists seeking new insights into their own fields, as well as from mathematicians and physical scientists interested in digging deeper into the biological details.

The situation has changed dramatically in the decades since. I rarely see many of the colleagues I used to see regularly, because I attend more specialized meetings in ecology and evolutionary biology, whereas they attend meetings in their particular areas of application. This is a good thing, because it means we have all taken Kac's recommendations to heart—explicitly or implicitly—by becoming biologists and taking possession of the problems on which we work. My graduate students and postdoctoral fellows find jobs in ecology and evolutionary biology departments rather than mathematics departments, and this changes the standards by which they judge their own work: instead of valuing mathematical elegance above all, they rather place the greatest emphasis on what they have contributed to the solution or at least understanding of

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a problem. Theories for them no longer float in the abstract, but are confronted with data. That is the rationale for the excellent collection of papers that appear in this Theme Issue, and I think is emblematic of the maturation of a discipline. All of the papers in this issue in one way or another deal with the interplay of models with data, from the work by Stollenwerk *et al.* [26] on the treatment of parameter estimation to Petrovskii & Petrovskaya's [27] review of computational challenges in ecology.

I do not mean to imply that those early years of theoretical biology were misguided. Lotka and Volterra laid the foundations for the application of dynamical systems theory to a range of problems, Galton and Fisher helped launch the field of statistics, and theories of pattern formation and collective phenomena continue to inspire novel approaches to understanding such phenomena as diverse as embryogenesis, the normal functioning and pathologies of the nervous system, and vegetation patterning. Indeed, several papers in this issue illustrate the continuing challenges of understanding collective phenomena, from bacteria and amoebae to fish and birds to collective decision-making in human societies. My prediction is that the next decade will include an expansion of interest in these issues, on the more general problem of the organization and robustness of complex adaptive systems from individuals to the biosphere and the interlinked global socio-economic system. In all such systems, macroscopic patterns emerge from the interactions among large numbers of individual agents, and the challenge is to develop a statistical mechanics for such systems, connecting the microscopic and the macroscopic.

Collective decision-making, in which individuals share information intentionally or accidentally, is one of the most exciting areas of research in behavioural ecology and behavioural economics, uniting the two disciplines in a rich framework with implications for our potential to solve humanity's problems. We live in global commons in which no individual is an island, and in which the decisions one makes can affect everyone. Preserving our common resources for all to enjoy—now and in future generations—of course not only raises issues of ethics but also raises very practical issues about how agreements can be reached and sustained. Cooperation is a well-studied, albeit not completely understood, phenomenon in biology; and indeed, extreme forms of cooperation, such as eusociality, so puzzled Darwin that he delayed publication of *On the Origin of Species* for 20 years. There is much that we can learn for the achievement of cooperation in dealing with our global problems from how natural and cultural selection have resolved conflicts and produced consensus and cooperation. Hence, animal aggregation is of interest not only in and of itself, but also as a model for how consensus can be formed in human societies and in other animal species. The former topic is the focus of Grunbaum's [28] elegant treatment of ecological patchiness in this issue, and the latter topic is beautifully summarized in Condradt's [29] authoritative review of models of collective decision-making.

Animal aggregation and consensus formation raise challenges both familiar and novel. How does one

scale from the microscopic to the macroscopic, retaining enough detail but not too much? How are conflicts resolved between the interests of individuals and those of the groups to which they belong? Can aggregations operate as single integrated multi-cellular units, each part contributing to the welfare of the whole? This is a rich and rapidly developing area of research.

This Theme Issue represents a welcome confirmation of the development of theoretical ecology into an integral part of the science of ecology, and the evolution of ecology itself into a discipline with a firm quantitative structure.

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