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Editors

Dispersal, Individual Movement and Spatial Ecology

A Mathematical Perspective

Springer

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Foreword

The study of biological populations is one of the oldest and most successful areas in mathematical biology, dating back at least a century to the work of Vito Volterra, the Italian mathematician equally famous for his contributions to the theory of integral equations. Indeed, there are examples even earlier of the use of mathematics in population biology, especially in demography and population growth; even Fibonacci dabbled in this subject largely to illustrate how the sequence of numbers that bears his name could arise easily in a population model. But Volterra's foray into mathematical ecology was an event of significance, because it demonstrated not only how sophisticated mathematics could contribute to biology but also that serious attention to biology could stimulate advances in mathematics. Both aspects are illustrated in this volume, which provides further evidence of the irresistible appeal of population problems for mathematicians.

Volterra's investigations focused on the dynamics of well-mixed populations and did not consider the spatial dimension, though his contributions to integral equations would certainly have put him in a position to advance the subject of spatial population biology. The first major efforts in that direction actually came from population genetics, where Fisher, Haldane and Wright all made major contributions in the 1930s and later. Fisher, in particular, was the first to note that the asymptotic speed of propagation of an advantageous allele would be twice the square root of the product of the intrinsic rate of increase and the diffusion coefficient, a result profound enough once again to attract leading mathematicians to provide formal analysis [10]. Indeed, attention to that rich problem has continued to be of interest to mathematicians [2, 4, 7], including those in this volume.

In ecology, the landmark paper was undoubtedly Skellam's 1951 treatise [18], which developed a broader framework for the consideration of spread, including those in response to climate change, and furthermore addressed the problem of critical patch size for persistence. These topics have remained of continuing interest for more than half a century, both for practical reasons [1] and because of their inherent mathematical richness. Skellam's framework allowed easily for the consideration of long-distance transport and was followed by papers such as Mollison's [12] and later work [15, 20] that explicitly dealt further with long-distance movements.

The consideration of spatial clines [9] and more general patterns [11], in addition to the problems mentioned earlier, has spawned a rich mathematical literature and one that has close contact with the biology [5, 13, 16, 17].

As this volume provides evidence, problems in dispersal, movement and spatial ecology continue to attract the attention of serious mathematicians and continue to grow in ecological importance [19]. On the biological side, we have seen the birth of a new sub-discipline called movement ecology [14]; and from many directions, interest in anomalous diffusion has grown [3, 21]. Conservation biology has raised many new problems, including those associated with the design of nature reserves, and the fascinating subject of collective motion has attracted the attention of biologists, mathematicians and physicists alike [6, 21]. Substantive mathematical problems remain, like the problem of scaling from the microscopic to the macroscopic, marrying the Lagrangian and Eulerian perspectives [8]. All of these issues are evident in the broad scope of the papers in this volume.

This collection is a welcome addition to the literature, illustrating once again the mathematical richness that underlies the movement problems as well as the ecological importance.

Princeton, New Jersey — Simon Levin
May 26, 2012

References

1. D.A. Andow, P.M. Kareiva, S.A. Levin, A. Okubo, Spread of invading organisms. Landscape Ecol. **4**(2/3), 177–188 (1990)
2. D.G. Aronson, H.F. Weinberger, Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In *Partial Differential Equations and Related Topics*, vol 446, ed. by J.A. Goldstein (Springer, Berlin, 1975), pp. 5–49
3. F. Bartumeus, P. Fernandez, M.G.E. da Luz, J. Catalan, R.V. Sole, S.A. Levin, Superdiffusion and encounter rates in diluted, low dimensional worlds. Eur. Phys. J. Spec. Top. **157**, 157–166 (2008). doi: Doi 10.1140/Epjst/E2008-00638-6
4. M. Bramson, *Convergence of Solutions of the Kolmogorov Equation to Travelling Waves*. Paper presented at the (Mem. Am. Math. Soc., Providence, Rhode Island, 1983)
5. R.S. Cantrell, C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations* (Wiley, Chichester, West Sussex, England; Hoboken, NJ, 2003)
6. I.D. Couzin, J. Krause, N.R. Franks, S.A. Levin, Effective leadership and decision making in animal groups on the move. Nature **433**, 513–516 (2005)
7. P.C. Fife, J.B. McLeod, The approach of solutions of nonlinear diffusion equations to travelling wave solutions. Arch. For Rat. Mech. Anal. **65**, 335–361 (1977)
8. G. Flierl, D. Grünbaum, S. Levin, D. Olson, From individuals to aggregations: the interplay between behavior and physics. J. Theor. Biol. **196**, 397–454 (1999)
9. J.B.S. Haldane, The theory of cline. J. Genet. **48**, 227–284 (1948)
10. A.N. Kolmogorov, I. Petrovsky, N. Piscounov, Etude de l'equation de la diffusion avec croissance de la quantite de matiere et son application a un problema biologique. Moscow University Bull. Ser. Internat. Sect. A **1**, 1–25 (1937)
11. S.A. Levin, Dispersion and population interactions. Am. Nat. **108**(960), 207–228 (1974)

12. D. Mollison, Spatial contact models for ecological and epidemic spread (with discussion). J. R. Stat. Soc. B **39**, 283–326 (1977)
13. J.D. Murray, *Mathematical Biology*, 2nd ed., vol. 19 (Springer, Heidelberg, 1990)
14. R. Nathan, Movement ecology. Special Feature Proc. Natl. Acad. Sci. **105**, 19050–19125 (2008)
15. M.G. Neubert, M. Kot, M.A. Lewis, Invasion speeds in fluctuating environments. Proc. R. Soc. Lond. B **267**, 1603–1610 (2000)
16. A. Okubo, S.A. Levin, *Diffusion and Ecological Problems: Modern Perspectives,* 2nd ed., vol. 14 (Springer, New York, 2001)
17. N. Shigesada, K. Kawasaki, *Biological Invasions: Theory and Practice* (Oxford University Press, Oxford, 1997)
18. J.G. Skellam, Random dispersal in theoretical populations. Biometrika **38**, 196–218 (1951)
19. D. Tilman, P. Kareiva, *Spatial Ecology* (Princeton University Press, Princeton, 1997)
20. F. van den Bosch, J. Metz, O. Diekmann, The velocity of spatial population expansion. J. Math. Biol. **28**(5), 529–565 (1990)
21. G.M. Viswanathan, M.G.E. da Luz, E.P. Raposo, H.E. Stanley, *The Physics of Foraging: An Introduction to Random Searches and Biological Encounters* (*Cambridge University Press*, *Cambridge*, 2011)

Preface

It has long been recognized that ecological dynamics is essentially spatial. Population aggregation that can be either self-organized or induced by heterogeneity in the environment is a commonly observed phenomenon. Spatial patterning has a variety of implications for biodiversity, harvesting, pest control, species extinction, and nature conservation. Dispersal is the process that results in a coupling between local populations and thus integrates them at a global level into an ecological entity. The properties of the entity can be very different from the properties of its parts. Thus it is important for us to know how to correctly interpret at the macroscopic level behavior at the local level if we are to determine how the entity behaves.

The approaches to study dispersal can differ greatly in terms of their focus and the level of detail involved. According to a commonly accepted definition, dispersal is the movement of organisms away from their parent source. The primary focus of dispersal is therefore on individual animal movement. Correspondingly, the focus of research is on individual movement paths and the most detailed description of dispersal should include all necessary information about the individual movement pattern.

However, this comprehensive description of dispersal is neither always possible nor always necessary. Once the state of the system is described by mean-field variables, e.g., by the population densities, information about individuals is lost. In fact, it is not required: Once the dispersal kernel is known, mathematical models are capable of grasping essential features of the population dynamics. Biological invasion is one example where application of population-level models has been particularly successful. One of the advantages of the population models is that they appear to be analytically more tractable than individual-based models allowing a fuller classification of different types of behavior in parameter space.

The most interesting part of the story is probably the bridge between the two "extremes." How can we derive the equations of the spatiotemporal population dynamics from the properties of the individual animal movement? Can we combine the benefits of the two approaches? What pattern of individual movement is behind a particular population dynamics model? One should recall here that population models are usually obtained from empirical or heuristic arguments rather than derived from first principles. Mathematical rigor is often lacking in this approach and, as a result, the empirical models may have hidden pitfalls and caveats that are difficult to identify. For example, implicitly assumptions may have been made that are erroneous or inconsistent with each other.

The structure of this book follows the general logic of dispersal studies outlined above. Part I (Chaps. 1–3) is concerned with individual animal movement. This subject has been increasingly controversial, sometimes even resulting in rather heated debates. Classical studies assumed that the individuals move around in a diffusive manner, i.e., a random walk process known as Brownian motion where the step length/size is described by a normal or exponential distribution effectively suppressing long steps. However, over the last two decades there has been increasing evidence that this might not always be the case. Indeed, field and laboratory data often show a rate of decay in the step size distribution which is much slower than exponential, e.g., as a power law. Correspondingly, stochastic processes such as Levy flights and/or Levy walks were introduced to take into account the long jumps in order to describe and analyze data on animal movement. However, the biological relevance of the Levy statistics still remains a controversial issue as it is not always clear whether it is a genuine pattern of the individual movement or an artifact of data collection and processing. The chapters in Part I contribute to this discussion and partially reflect this controversy by providing different points of view of the subject.

Part II (Chaps. 4–8) considers how the properties of individual movement can be scaled up to the population level. It starts with a review of mathematical models of self-organized population patterning with an emphasis on interaction and communication between the individuals (Chap. 4). Chapter 5 gives an overview of hybrid approaches that attempt to incorporate individual-based description to population-level models by considering movement of discrete objects (e.g., animals) in a continuous environment, chemotaxis being used as a paradigm. A different type of hybrid model is studied in Chap. 6 where foraging behavior is described as a space- and time-continuous process but transition between consequent generations (multiplication) is described as a time-discrete map.

The analysis of Chaps. 4–6 is mostly focused on self-organized behavior in a homogeneous and isotropic environment. This assumption is relaxed in Chaps. 7 and 8. In particular, Chap. 7 considers population models when individual movement is anisotropic, e.g., occurring in an environment with a directional bias. The population dynamics of wolves in a forest with seismic lines is used as an instructive example. Chapter 8 considers complex foraging behavior of zooplankton in a prey–predator (e.g., phyto-zooplankton) system in a vertically stratified water column. Interestingly, the behavioral response to stratification can result in a change of the predator function response, so that the Holling type II response assumed in local grazing gives way to type III after averaging over water column height.

Part III (Chaps. 9–13) considers dispersal and its implications on the level of populations and communities. One of the main objectives here is to understand how the population abundance, e.g., as quantified by the population density, changes in space and time because of the interplay between dispersal and the local population dynamics. The two phenomena that are essentially attributed to this interplay are biological invasion and population range shift (Chaps. 9 and 10). The properties of dispersal may affect the rate of species spread significantly. For instance, it is well known that fat-tailed dispersal can increase the invasion rate considerably. It therefore becomes important to develop analytical approaches which allow us to reveal the properties of the dispersal kernel (Chap. 9) and to better understand how the population behavior depends on the kernel used.

Another major issue is population dynamics on a fragmented habitat. Dispersal coupling results in the possibility of re-colonization of empty patches. Chapter 11 shows that the effect of re-colonization can be subtle and counterintuitive depending on how much detail of the food web is taken into account.

With the spatiotemporal complexity of dispersal in mind, perhaps it is not surprising that dispersal has not only ecological but also evolutionary implications. Chapter 12 considers interaction between the processes going on different temporal scales and concludes that dispersal coupled with non-local resource consumption can be a crucial factor resulting in speciation.

Finally, Chap. 13 considers the implication of dispersal—regarded here as diffusion—for the pest population size estimation commonly required in pest control programs. Somewhat counterintuitively, it shows that a pest with a lower diffusivity may be more difficult to monitor than a highly mobile one.

The idea of this book emerged and was eventually shaped into its final form during a series of meetings, in particular at the conference *Models in Population Dynamics and Ecology 2010* (Leicester, September 1–3, 2010) and the MBI Workshop: *Ecology and Control of Invasive Species* (Columbus, February 21–25, 2011). Obviously, considerable progress has been made over the last two decades in understanding all aspects of dispersal, as can be traced from the references provided with the chapters. Appreciation of the diversity of studies focused on or closely related to dispersal led to the feeling that an account of the state of the art in this field may be timely and useful. It is for the reader to decide whether this goal has been achieved and how comprehensive is the account. Whichever is the case, we hope that this book is going to be stimulating for future research.

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