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Esa Ranta, Per Lundberg and Veijo Kaitala
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1 · *Introduction*

> . . . there is nothing so practical as good theory.
>
> *Richard Feynman*

The scope of this book is almost as wide as it gets. It touches upon a range of topics in ecology and evolution found in many modern textbooks. Instead of going into considerable depth in any one topic, we have chosen to cover quite a few in order to show that the same basic (and well-known) tools are applicable to a wide variety of ecological and evolutionary problems in population biology. However, this is also a narrow-minded book in the sense that it is very "theoretical," i.e., full of mathematical expressions and computer simulation results. We believe ecology becomes a healthier science if it appreciates and acknowledges its strong quantitative and more rigorous nature. It is also narrow-minded in the sense that it reflects our own interests in population ecology without attempting to cover all aspects of the ecology of populations. Yet, the scope remains wide and possibly shallow. We believe that ecology and evolutionary biology have to become far more integrated than the fragmented and disparate impression they give today. We think that this can be done by going back to very simple first principles of births and deaths, immigration, and emigration. From those "simple" entities, we can derive virtually everything that plants and animals do in nature. To do so, however, requires a common thread of theory, the seeds of which at least we believe exist. Extensions of that theory will also be dealt with in this book. The second reason for a wide scope is to show how theory and data can be closely integrated, at least in some (rather important) areas of ecology, and that this integration often is useful for the application of the science of ecology. Although the scope is deliberately wide, there are obvious restrictions and biases involved in our endeavor. For example, plants play a smaller role than animals. In particular, large mammals and birds dominate the case stories and examples. The only excuse for this bias is that we are especially used to those organisms and the literature that covers their biology. We nevertheless think that there

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is a great deal of generality to be found in our approach. However, one can easily imagine a number of scientific problems with a rather limited selection of organisms as examples and templates for more theoretical considerations. Microorganisms and many plants are, of course, very different from most animals on a number of grounds (e.g., modular structure versus well-defined individuality, reproductive modes and life cycles, and mobility). Even so, and of course depending on exactly in which unit we choose to measure the presence of the organism, the basic and almost trivial relationship is

$$N(t+1) = N(t)(1 + b + i - d - e), \tag{1.1}$$

where N is the abundance of a population at time t, b and d are per capita births and deaths, respectively, while i and e are per capita immigration and emigration rates during one time interval. Our task as ecologists and evolutionary biologists is to figure out what determines b, i, d, and e, and the dynamical and evolutionary consequences of them.

Our point of departure is hence the simple *renewal function* above that maps the state of the population at one point in time to another. That is, we will – almost without exception – assume that it is possible to read off the state of the population at one point in time and do it again at some other point. The time interval between the observations is in principle arbitrary, but usually matches some natural biological interval, e.g., the sequence of reproductive events. By "state" of the population, we usually understand population size or density. This is of course a very restrictive definition that will be relaxed depending on circumstances. For example, in Chapters 6 and 12, age structure and sex are introduced making "state" more interesting and sophisticated.

Another reason why we have chosen a discrete time approach is that much of the available population and community data come in this form: population size, dispersal, or gene frequencies are measured in discrete time intervals. This does not mean that the time intervals in data are always biologically adequate; for example, many populations are measured once a year for practical rather than biological reasons. This potential mismatch between observation interval and biologically more meaningful sequences is an interesting empirical and applied problem in itself, probably deserving more attention than it usually gets. The format data come in also has implications for the (statistical) analysis of them. Most theory of stochastic processes (e.g., time series analysis, something we will make frequent use of throughout) is based on discrete (random) events. The correspondence between theory and data will consequently be both obvious and close.

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Generally, spatial processes will also be viewed as discrete processes. This usually comes less naturally. Although it is almost invariably true that the environment that natural organisms inhabit is heterogeneous, at least at some appropriate scale, the different parts of it are less obviously discrete entities. Much spatial ecology theory nevertheless ignores the fact that landscape or habitat elements really have poorly defined identities and borders. It turns out, however, that this is rarely a problem, both for practical and theoretical purposes. As shall be seen in later chapters (e.g., Chapters 3 and 4), the distinct patches or habitats assumed in the theoretical constructs and models are indeed fair representations of real landscapes when it comes to understanding population and community processes. Partly, this is because many spatial processes are in fact scale invariant in the spatial dimension (see, e.g., Chapter 5).

The way we most often express the renewal functions is hence in discrete time (difference) equations. In Chapter 2 we analyze the discrete time population processes in more detail. As a preamble, consider Box 1.1 for the general discrete time mapping. We also refer to more general textbooks, e.g., Edelstein-Keshet 1988, Roughgarden 1998 and Caswell 2001, for thorough treatments of such processes. Our intention is, however, that most of the material in this book is self-contained. We do not expect the reader to be especially dependent on additional information from other, more technical sources. For obvious reasons, however, many of the topics covered cannot be dealt with in great detail and depth. Therefore, we expect the reader to be familiar with the advanced undergraduate or graduate level of population and community ecology and the associated theoretical and mathematical (and statistical) tools. This does not mean that the somewhat less initiated reader should be left hanging in the air. We have tried to accommodate that by avoiding overly technical jargon, by letting some of the technical problems appear in boxes outside the main text, and by ample references to the literature where more in-depth treatments of technical matters are found (see also the Suggested reading list at the end of this chapter).

Fitness

The question often arises whether there is really any strong connection between classic population and community dynamics and evolutionary processes. The two branches of evolutionary ecology are often seen as separate which is very unfortunate and misleading. Of course they aren't. Consider the simple renewal processes

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Box 1.1 · *Discrete time mapping*

We are interested in finding out how the number of individuals (or some other adequate entity) is changing from one arbitrary point in time, t, to another, $t+1$. Note that the indexing is also arbitrary. Instead of mapping from time t to $t+1$, we can do it from $t-1$ to t (as long as we only deal with one (forward) time step at a time). Let the population size at time t be denoted by $N(t)$ and we then have

$$N(t+1) = f\,[N(t)],$$

where f is some yet unspecified function. Hence we assume that the population size at future times is dependent on the population size at previous times. Suppose the function f now takes the form

$$f\,[N(t)] = \frac{\lambda N(t)}{1+bN(t)}.$$

This is a monotonically increasing function of N determined by two parameters, λ and b. This is the *renewal function* for the population process (Box 2.1). Suppose now that there is a situation such that $N(t+1) = N(t)$. Denote that population density N^*, and we have

$$N^* = \frac{\lambda N^*}{1+bN^*}.$$

We can now solve this equation for N^* and, after some algebra, we have

$$N^* = \frac{\lambda - 1}{b}.$$

This is the equilibrium population size, i.e., the size at which there is no change from one time to another. That value of N can be illustrated by plotting the function f in the $N(t) - N(t+1)$ plane, and is the point where f is intersecting a straight line with slope 1 in the plane. The slope of f in that point is important because it determines the stability of the equilibrium (see, e.g., Edelstein-Keshet 1988, for a more rigorous and detailed treatment of both general discrete time mapping and its application in population biology).

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$$N(t+1) = RN(t), \tag{1.2}$$

where N is some relevant ecological quantity, e.g., population density, and R is some (positive) constant. The rate by which the population density (or size) changes is thus determined by R (cf. eq. 1.1). The exact nature of R is of instrumental importance in population ecology: why is R sometimes large, sometimes small for a given population, why does it vary among populations, and how are, for example, spatial structure and other species in the environment affecting its magnitude and variation? Expressed in this traditional population dynamics ways, R is rather unambiguous – it is (when log-transformed and given the symbol r) the finite rate of increase of the population. This is precisely why it appears as a measure of *fitness* (with identical meaning) in the Euler–Lotka equation (here in the discrete time version)

$$1 = \sum l_x m_x \mathrm{e}^{-rx}, \tag{1.3}$$

where l and m are age-specific (at age x) fecundity and survival, respectively. This is indeed the key equation in all evolutionary ecology. Murray (2001) argues rightly that it has the status of a "law" because it encompasses both evolutionary and ecological change. Evolutionary change in that a trait or strategy (see e.g., Cohen *et al.* 1999 for strategy definitions) that maximizes r in eq. 1.3 is the strategy that will be the evolutionarily most successful one, i.e., by definition having the highest fitness. Should r or R take on values such that eq. 1.3 is no longer satisfied, *ceteris paribus*, then that indicates a population increase or decline. Should we for some reason ignore age (or stage) structure or the entire strategy space (individual variation within the population), then all that is left is population change and we have recovered population dynamics. In the following, we will occasionally slide between the ecological and evolutionary domain, always trying to keep the Euler–Lotka theory in mind.

The heir of Euler–Lotka theory is what is sometimes referred to as adaptive dynamics (Dieckmann and Law 1996; Dieckmann 1997; Abrams 2001). It is a an even more explicit way of incorporating both ecological and evolutionary dynamics within the same theoretical framework. It is a means of characterizing the entire (or at least most of the relevant components) "feedback environment" of an organism (e.g., Heino *et al.* 1998). By doing so, both ecological change (change in

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abundance and distribution) and evolutionary change (the changes of traits or strategies in time and space) are explicit parts of the analysis. We have refrained from expanding our treatise to include this theoretical approach simply because the focus here is indeed on abundance and distribution, although we will break that rule in later chapters (e.g., in Chapter 11 and 12).

Ecology of populations

At the very beginning, we stated that this book has a very wide scope, but are now down to a much more narrow and limited one – classic "population dynamics." This is not as restricted as it may seem. It is in fact the study of populations – their distribution and abundance (Andrewartha and Birch 1954) – that is necessarily the core of ecology and evolutionary biology. It is of course true that the individual (or some appropriate similar concept), or even the gene, is the actual scale at which evolution seemingly operates such that those units are the ones that are selected. For both theoretical and practical purposes, however, it is the population level that is the relevant one for our study of the manifestation of evolutionary change; it is at this level that the manifestation of life itself takes place, namely the births and deaths of more than one individual (or gene). This collection of individuals is the population, however we choose to define it more precisely (Berryman 2002). Hence the interesting, measurable, and practical, e.g., in the application of ecology for management or conservation purposes, processes are apparent at this level. Conversely, this approach does not of course preclude the study of biology at all other levels of organization. Anything from molecular biology to ecosystem research will reveal and generate useful biological knowledge. The most obvious and relevant arena for all life is, however, the population – the scale at which molecular processes and vast ecosystems coalesce. Hence the approach taken in this book.

Theory and data in ecology

Ecology is an empirical science and is therefore ultimately data driven. But it is so only to the extent that we want to explain what is observable rather than there being an unambiguous truth in data. Data, or more correctly, any set of observations of pattern and processes in nature, only get their meaning when interpreted. Theory is what provides conceptual and analytical tools to do that. Strangely, this is rarely an attitude delivered in most undergraduate (or even graduate) teaching in ecology. We strongly advocate the fundamental role of theory not only in the loose and perhaps trivial sense, but as it is formulated in mathematical terms. This is because mathematics provides us with the most powerful analytical tools when things start becoming complicated (as in ecology!) and our intuitive capacity no longer keeps up with that complexity. Also, and perhaps most importantly, a strong theoretical and mathematical foundation of our activities makes them *useful* when we are asked to solve, e.g., conservation or management problems. Qualitative statements or suggestions may be a good start, but can neither replace nor be as operational as quantitative ones, albeit with perhaps disturbingly large confidence limits.

In the following, we are going to transgress the data–theory border as much as possible. That means we are going to be inspired by intriguing patterns we can observe, and by data that have not been satisfactorily explained. Likewise, it means that we are going to analyze old data in new ways, as well as hopefully inspire others to collect the data that theory may indicate are important or interesting. However, this is not a book on applied mathematics or statistics – that is not our intention or within reach of our competence. Instead, we will refer as much as possible to the literature that does a better technical or more rigorous mathematical or statistical job. Much of the data we use, or produce by simulations, are time series of population abundance, density, or some index of it. Such data do, of course, have obvious limitations; they are very "shallow" and are often uninformative. The time series approach is therefore both simplistic and also challenging. Much of the information about population change does indeed come in the form of time series so we do need the tools to analyze them. Time series data are also very inspiring for anyone interested in the demography–environment interaction, i.e., how environmental fluctuations, however generated, affect the mean and the variance of the population or community in question. They also force us to ask what a reasonable population model should look like and to what extent the "environment" should be included in the model or kept aside as "noise." Finally, time series data, and the problems emerging from them, are not confined only to the classic long-term data we recognize from the textbooks (e.g., the Canada lynx – snowshoe hare system in North America). In fact, most ecological research is done over time and whatever phenomenon one is interested in, be it the breeding biology of birds, host plant selection in insects or life history of fish, there is always a statistical problem of model selection and the handling of "noise," or "error" as it is called in the statistical literature. This takes our approach beyond the classic time series domain into all ecology where there is variation across time and space.

The interplay between theory and data becomes perhaps best illustrated in the process of model selection (Hilborn and Mangel 1997; Burnham and Andersson 1998). This goes beyond the standard practice of evaluating null and alternative hypotheses, often from a purely statistical rather than biological point of view. Instead, we may (and should) formulate biologically meaningful models (note the plural) and confront them with the data. This procedure challenges us to keep one foot in each camp at all times, and to think carefully about the biological problem at hand by forcing us to formulate hypotheses as biological models. This approach also becomes particularly intriguing when we are dealing with stochastic processes and when we have to decide what should be regarded as "noise" and what should be included in the biological process. The next chapter takes a closer look at that problem.

Suggested reading

This is a short list of suggested textbooks and general treatments of theoretical population and community ecology, mathematics, and statistics. Since we are covering neither all relevant theory nor all the analytical tools frequently used at sufficient depth, we refer to the more extensive treatments below. They can be used either as a preamble to the rest of this book, or as references whenever needed.

Burnham, K. P. and Anderson, D. R. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. New York: Springer-Verlag.
Caswell, H. 2001. *Matrix Population Models,* 2nd edn. Sunderland, Mass.: Sinauer.
Chatfield, C. 1999. *The Analysis of Time Series: An Introduction*, 5th edn. Boca Raton, Fla.: Chapman & Hall.
Chiang, A. 1984. *Fundamental Methods of Mathematical Economics*. Singapore: McGraw-Hill.
Edelstein-Keshet, L. 1988. *Mathematical Models in Biology*. New York: Random House.
Hilborn, R. and Mangel, M. 1997. *The Ecological Detective*. Princeton, N.J.: Princeton University Press.
Roughgarden, J. 1998. *Primer of Theoretical Ecology*. New York: Pentice Hall.
Royama, T. 1992. *Analytical Population Dynamics*. New York: Chapman and Hall.

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2 · *Population renewal*

Population renewal is about how births and deaths of individuals are translated into population level dynamics. Here, we are reviewing some basic concepts and models of population renewal, disregarding both spatial processes (immigration and emigration) as well as interactions with other populations. Those extensions will be addressed in subsequent chapters. We are also briefly reviewing some statistical building blocks necessary for understanding population dynamics as a stochastic process and not only a deterministic route to persistence or extinction. This includes primarily the time series approach to population dynamics. We conclude this chapter by highlighting some very important and disturbing problems when confronting models with data (and the reverse), especially when trying to disentangle the demographic skeleton from "noise."

There is really nothing more to population ecology than births and deaths. If the number of individuals born exceeds the number that dies, the population size increases; should deaths exceed births, the population size decreases. If that simple, how is it so difficult to predict the population size in the future, and to determine what limits – or even regulates – the distribution and abundance of organisms in natural systems? We could argue that it is because the models we inevitably need to perform the above exercises are not good enough. One could also say that the task is difficult because it is not so easy to measure things accurately in nature. It is even problematic to determine what a population really is. One common argument is also that there are so many factors influencing the number of births and deaths, i.e., the problem is so complex, that it will be impossible to solve.

All of the above is probably true, one way or another. In this chapter, we are going to have a closer look at the problem of understanding population renewal. We certainly agree that one of the challenges is to reduce measurement error of, for example, population size estimates. This is true for both the actual counting of individuals (or biomass, or some other relevant measure of population size), and the determination of

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what constitutes the population in question. The latter involves both relevant time scales over which the population process is measured, and the spatial delimitation. This issue is discussed in an intriguing and important note by Berryman (2002). Our concern in this chapter will, however, primarily be the model formulation problem. If we understand the problem, then we are able to formulate a useful model. This is, of course, not to say that this solves it all, but it would give us considerable mileage. Towards the end of this chapter, we are going to address an important theoretical problem that relates to this issue. How to move from the understanding of individual behaviors and performances to their manifestation at the population level, and how (if ever) we can understand the reverse process. That is, whether we can infer from population level data, e.g., a time series of abundance, what is happening beneath the surface in terms of births and deaths. Before doing that, we are going to prepare ourselves with the basic building blocks and tools for making models of the population renewal process.

Population growth rate

To begin with, we shall review some of the fundamental population growth processes. There is a rich literature that treats this issue in detail and at depth (e.g., May 1975; Emlen 1984; Edelstein-Keshet 1988; Yodzis 1989; Gotelli 1995; Hastings 1997; Roughgarden 1998). Two very useful accounts are Royama (1992) and Caswell (2001), dealing much with models and data, and structured populations, respectively. What is said in the following sections here is dealt with excellently by those two sources.

r, R and λ

Recall the basic renewal process outline in Chapter 1 (eq. 1.1)

$$N(t+1) = N(t)(1+b+i-d-e), \tag{2.1}$$

where b and d are per capita birth and death rates, respectively, and i and e the per capita immigration and emigration rates, respectively. For illustrative purposes, let us omit immigration and emigration from the population process. We then have

$$N(t+1) = N(t)(1+b-d). \tag{2.2}$$