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Edited by David Storch, Pablo A. Marquet and James H. Brown
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Scaling Biodiversity

We know that there are millions to tens of millions of plant and animal species, but we do not know enough to be able to describe the patterns and processes that characterize the distribution of species in space, time, and taxonomic groups. Given that in practical terms it is impossible to understand the intricacies of the relationships between all the organisms and the dynamics of populations and communities in all spatial and temporal scales, other approaches must be used. Scaling rules offer one possible framework, and this book offers a synthesis of the ways in which scaling theory can be applied to the analysis of biodiversity. *Scaling Biodiversity* presents new views on quantitative patterns of the biological diversity on Earth and the processes responsible for them. Written by a team of leading experts in ecology who present their most recent and innovative views, this book will provide readers with the state of the art in current ecology and biodiversity science.

DAVID STORCH is a researcher and university teacher at Charles University in Prague and former international Fellow of the Santa Fe Institute. He teaches courses on animal ecology, macroecology and community ecology.

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Foreword

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One of the appealing things about physics is the existence of invariance principles and conservation laws, which provide the basis for powerful simplicities and generalizations (if the laws of physics are the same at all times and places then, for example, momentum is conserved). Extending this, if we are presented with a set of equations describing how a physical system behaves – the Navier–Stokes equations describing fluid flow, for instance – then we can immediately set about recasting them in terms of appropriately dimensionless variables (coordinates of space and time rescaled against the system's characteristic lengths and time) and dimensionless combinations of other parameters (the Reynold's Number, which is essentially the ratio between inertial and viscous forces, for example). Such scaling laws then allow us to construct a small model of a racing yacht, or Formula I car, or airplane, and test its fluid dynamical behavior in an appropriately constructed testing tank or wind tunnel. On the back of an envelope, we can explain why the V-shaped waves break away from the bow of a ship in deep water at an angle of $\theta = 19.5^\circ$ ($\tan\theta = 1/2\sqrt{2}$), independent of the ship's speed, a result first established by Kelvin in 1887.

A particularly notable example of the use of dimensional arguments was given in the 1950s by G. I. Taylor, the leading fluid dynamicist involved in the Manhattan Project at Los Alamos (an appropriate example in the context of this book, perhaps, given the geographical proximity to Santa Fe). In an atomic explosion, there is an essentially instantaneous release of a large amount of energy, E, from what is effectively a point source. The subsequent spherical shock wave propagates into the surrounding air, of density ρ, with the pressure behind the early-stage wave front being vastly larger than the air pressure. It follows that the only physical factors determining the radius of the spherical shock wave front, R, are E, ρ, and the elapsed time, t. In terms of the basic scaling dimensions of mass, length and time (M, L, T), these three independent variables have dimensions $[E] = \mathrm{ML}^2\mathrm{T}^{-2}$, $[\rho] = \mathrm{ML}^{-3}$, $[t] = \mathrm{T}$; R has dimensions $[R] = \mathrm{L}$. To get the scaling relation between R (dimension L) and t (dimension T), we eliminate M among $[E]$, $[\rho]$ and $[t]$ to get $\mathrm{L}^5 \sim \mathrm{T}^2$. This implies $R \sim t^{2/5}$ or a straight line with slope 1 when $\ln R$ is plotted against $(2/5)\ln t$. Taylor used the data from a series of

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high-speed photographs of the fireball expanding over the test site in Nevada to verify this result, and then further used the *y*-axis intercept of this line to estimate $E \sim 10^{21}$ erg. He published this simple and elegant analysis in 1950, causing a furore among the military bureaucracy; although the film was not classified, the energy release figure was Top Secret (for a more detailed account, see Barenblatt, 1996).

These ideas have made their way into several areas of biology, mainly at the level of the physiology and behavior of individual organisms. D'Arcy Thompson's *On Growth and Form in Biology* (see particularly Bonner's 1961 abridged addition, with commentary) is one notable early example. Further developments and applications are surveyed by Berg (1983), Vogel (1988) and others. The first sentence in Berg's book begins "Biology in wet and dynamic". His book elaborates this theme, brilliantly drawing out the distinction between those organisms whose physical dimensions in relation to the medium through which they move are such that inertial forces dominate (e.g. airplanes, or us walking down the street) and those where the medium's viscosity dominates (e.g. bacteria propelled by rotating flagella). Here the scaling questions involve the above-mentioned dimensionless Reynold's Number, $\mathrm{Re} \sim \rho v L/\mu$, where ρ, v and μ are the density, relative velocity, and viscosity of the fluid, and L is the "characteristic length" (diameter of pipe or channel for internal flows; maximum length of a solid object – submarine or bacterium – moving with relative velocity v against the fluid). More broadly, it is fascinating to see how scaling laws can illuminate biological issues as varied as how prairie dogs ventilate their burrows, how tiny worms withstand high pressures, or why a mouse walks away when it falls down a mineshaft but we break and horses go splat.

Going beyond Berg's "Wet and dynamic", I particularly like the application of these ideas first made in 1680 by Giovanni Alfonso Borelli, and later independently presented by John Maynard Smith (1968), to show that, to a good approximation, the characteristic height to which an animal can jump (i.e. lift its center of gravity) is common to all, fleas to horses (around one meter). This result, sometimes called Borelli's Law, is derived as follows. The energy needed to lift an animal of mass m (which scales as L^3, where L is the animal's characteristic length scale) to a height h is mgh, where g is the acceleration due to gravity. This energy is provided by the animal's downward force on the ground, F, multiplied by the distance through which the force moves (the leg extension giving the uplift, which is of the order of L). The force F is limited by the mechanical strength of the limb, which scales as L^2. Hence we have $h = F\mathrm{L}/mg \sim \mathrm{L}^2 \times \mathrm{L}/\mathrm{L}^3$. That is, h is, to a rough approximation, independent of the animal's characteristic size. Obviously there are fluctuations around this characteristic height, set by particular adaptations to the animal's life history, but even so the rule holds remarkably well across the animal kingdom. This and other examples are to be found in Maynard Smith's wonderful little book on *Mathematical Ideas in Biology* (1968), whose cover is a schematic diagram illustrating the above calculation for a jumping mouse; the Russian edition has replaced this schematic diagram with a socialist-realist mouse!

The dynamics of the spread of an infectious disease within a host population also can, in simple limiting circumstances, be illuminated by dimensional analysis and scaling laws. Suppose we have an infection which is transmitted directly by contact between susceptibles (S) and infected/infectious (I) individuals, in a homogeneously mixed population. Individuals recover (R) from the infected/infectious phase after a characteristic interval D, thereafter being immune. If a few infected individuals are put into a wholly susceptible population, the resulting equations for this so-called SIR system can be put in dimensionless form, and the shape of the consequent epidemic curve is seen to have a form that depends only on the single dimensionless parameter, R_0, which measures the average number of secondary infections produced by an infected/infectious individual in the initial stages, when essentially everyone is susceptible. The total number ever infected as the epidemic sweeps through the population, I, is given by $I = 1 - \exp(-R_0 I)$; the fraction of the population who are infected/infectious at the peak of the epidemic is simply $y_M = 1 - (1 + \ln R_0)/R_0$ (Anderson & May, 1991, ch. 6). This dimensionless quantity R_0 is called the basic reproductive number, and it can among other things be used to assess the proportion of the population we need to vaccinate in order to protect against a possible epidemic (i.e. to drive the population's effective basic reproductive number below unity); this fraction is $1 - 1/R_0$. Although the shape of the epidemic curve depends only on R_0 in this simple limiting case, the timescale over which an epidemic unfolds – possibly eventually extinguishing itself, or possibly oscillating to settle at a state of endemic infection – involves other parameters (such as D and the rate at which new susceptibles enter the population by birth or migration). Interestingly, ecologists have long recognized the importance of what they call a population's "basic reproductive rate", R_0. When Roy Anderson and I first emphasized the central role played by R_0 in epidemiological theory, we underlined the basic relationship with ecologists by using their conventional terminology – "reproductive rate" – even though we recognized that R_0 was dimensionless, not having the dimension of 1/(time) which "rate" would strictly imply. Later epidemiological workers, incensed by such terminological inexactitude, have prevailed in establishing "basic reproductive number" as approved usage; ecological texts, however, remain unrepentant in their time-honored use of "reproductive rate".

More generally, of course, computationally sophisticated studies aimed at better understanding of HIV/AIDS, foot and mouth disease, SARS, avian H5N1 flu, and much else deal with heterogeneities in individual behavior and transmissibility, in guiding public health policy. The basic understanding provided by scaling relations, however, remains important (Keeling *et al.*, 2003; Keeling, 2005).

Efforts to apply such scaling considerations to observed patterns of biological diversity are, in general, more recent. The present volume, very much in the spirit of the Santa Fe Institute, outlines work on several different levels, beginning with the relation between spatial scale and numbers of species. Later chapters in this rich offering widen the scope to scaling relations involving taxonomic groupings, species–energy relations, latitudinal gradients in species numbers, and more. Some of the work closely parallels the physics-like scaling rules sketched above, while other chapters take a broader view of "power laws" and possible mechanisms causing them.

In my opinion, the complex and contingent workings of evolutionary processes, playing out in an ecological theater which itself undergoes environmental change, mean that we cannot generally expect to find the crisp scaling laws of physics in assemblies of species. But we can sometimes hope to come close, and – at very least – this book shows the quest itself is interesting and informative.

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Preface

This unusual book had an unusual origin. It resulted from a symposium entitled "Scaling Biodiversity" that took place in Prague, Czech Republic, on 19–22 October 2004. The goal of the symposium was to bring together a diverse group of scientists who are applying ideas, approaches, and methods of scaling to address major conceptual questions about biodiversity.

The symposium was cosponsored by the Santa Fe Institute and Center for Theoretical Study, Charles University in Prague and co-organized by David Storch of Charles University, Pablo Marquet of the Catholic University in Chile, James Brown of the University of New Mexico, and Geoffrey West of the Santa Fe Institute. This sponsorship and organizing committee says much about the origin and operation of the workshop, the identity of the invited contributors, and the contents of this book. All of the co-organizers and many of the participants have strong relationships with the Santa Fe Institute (SFI). Much of the funding for the symposium, the activities of the co-organizers that led up to it, and the preparation of this book came from the SFI International Programs. Founded in 1984, the Institute is an interdisciplinary research center in Santa Fe, New Mexico. It is widely regarded as the birthplace and leading center of modern "complexity science". It is a special place that attracts mathematicians and physicists, biologists and ecologists, economists and anthropologists, who are dedicated to working on big, challenging questions in the natural and social sciences. There is a heady atmosphere of intense interaction and collegial collaboration at the Institute, and it results in a special kind of SFI-style science.

The symposium and the resulting book are representative of this kind of science. The participating scientists represent a blend of card-carrying ecologists and interlopers from other disciplines, established scientists and new, young investigators, theoreticians and empiricists. Several of the participants have been affiliated with SFI. Geoffrey West and Murray Gell-Mann are members of the Resident Faculty, James Brown is a member of the External Faculty, David Storch, Pablo Marquet, and Beáta Oborny have been International Fellows, and Timothy Keitt, James Gillooly, Andrew Allen, John Harte, Andrew Clarke, Jessica Green, and Ethan White have

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all participated in Institute workshops or other activities. That said, however, the other participants in the symposium and authors of this book are fresh faces.

This book and the symposium that gave rise to it represent an initial effort to bring the perspective of scaling to address the challenging topic of biodiversity. Concepts of scaling relations, along with theoretical approaches and analytical methods for studying them, are well represented across the physical, biological, and social sciences. Classic examples of so-called "scaling laws" include the Maxwell–Boltzmann distribution of kinetic energies of gas molecules, the size distribution of heavenly bodies in physics, the three-fourths power scaling of metabolism with body mass, the relationship between body size and longevity, the Gutenberg–Richter distribution of earthquake magnitudes, the Horton–Strahler hierarchy of stream and river orders, the Zipf distribution of word frequencies in languages, and the Pareto distribution of incomes among households. Classic examples in the scaling of biodiversity include species–area and species–time relationships, trophic pyramids, and distributions of abundance, range size, and body size among species.

Indeed, over the last two centuries, and accelerating rapidly in recent years, major empirical patterns of biodiversity have become increasingly well documented: across landscapes and geographic space, ecological and evolutionary time, and organisms of different body sizes, functional groups and trophic levels, and phylogenetic lineages and taxonomic groups. Many of these patterns represent scaling relations with respect to space, time, body size, environmental temperature and productivity, and other variables. Still missing, however, is a theory of biodiversity that can provide a unified, synthetic explanation for these relationships. Indeed, there is no general consensus explanation for the quintessential pattern, the decrease in number of species and many other measures of biological diversity from the tropics toward the poles.

Neither the symposium nor the book reaches definitive conclusions. The contributions do, however, present a special perspective on the state of the science. They focus on scaling as a way to characterize empirical relationships and explore theoretical concepts across the many dimensions and enormous spectrum of biodiversity. They highlight some of the progress that has recently been made, and some of the promising lines of investigation that are currently being pursued. In particular, they showcase the contributions and promise of some of the more theoretical and quantitative approaches to biodiversity. The contributors are interested not only in documenting the patterns of biodiversity with increasing accuracy and detail, but also in understanding the ecological and evolutionary processes that generate and maintain these patterns. Perhaps most importantly, the symposium presentations and book chapters collectively articulate an optimistic vision of biodiversity research. Half a century ago, the eminent ecologist G. E. Hutchinson asked, "Why are there so many species of animals?" Twenty-first century science can see into the

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farthest reaches of the universe and rapidly sequence the genome of any organism. Hopefully it will soon be able to explain why there are so many species of organisms, and more in tropical rain forests and coral reefs than in arctic tundra and the abyssal plain.

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