CHAPTER TWENTY-ONE

Biodiversity power laws

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Introduction

The last ten years have been marked by important discoveries and scientific advances in our understanding of biodiversity. The emergence of new fields, such as bioinformatics, ecoinformatics, and computational ecology (Helly *et al.*, 1995; Spengler, 2000; Green *et al.*, 2005) has brought about an informational revolution by making available massive data sets on the composition, distribution and abundance of biodiversity from local to global scales and from genes to ecosystems. This has in turn changed biodiversity sciences, expanding the scale of analysis of ecological systems wherein biodiversity resides. While the 1970s and 1980s were marked by studies at local scales, the 1990s were marked by gaining access to regional, continental and global scale analyses. In parallel, and in part as a consequence of the above trend, there has been a shift from approaches that emphasize the highly variable and idiosyncratic nature of ecological systems to a view that emphasizes the action of first principles, natural laws and zeroth order approaches (the macroscopic approach hereafter).

The small-scale approach can be illustrated by a representative quotation from Diamond and Case (1986, p. x): "The answers to general ecological questions are rarely universal laws, like those of physics. Instead, the answers are conditional statements such as: for a community of species with properties A_1 and A_2 in habitat B and latitude C, limiting factors X_2 and X_5 are likely to predominate." Macroscopic approaches, in contrast, emphasize the existence of statistical patterns in the structure of communities that are thought to reflect the operation of general principles or natural laws. Prominent among these principles is the identification of scaling and power-law relationships with similar or related exponents, which as pointed out by West and Brown (2005) imply "the existence of powerful constraints at every level of biological organization. The self-similar power law scaling implies the existence of average, idealized biological systems, which represent a "0th order" baseline or

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point of departure for understanding the variation among real biological systems". These regularities underlie two related research programs in ecology: the first is macroecology (Brown & Maurer, 1989; Brown, 1995; Gaston & Blackburn, 2000; Marquet, 2002a; Storch & Gaston, 2004) and the second is the recently dubbed Metabolic Theory of Ecology (Brown *et al.*, 2004). The change in the conceptualization of ecological systems entailed by these approaches, as opposed to the idiosyncratic view expressed by Diamond and Case (1986), is apparent in the following excerpt (Brown *et al.*, 2004, p. 411): "Our own recent research is based on the premise that the general statistical patterns of macroecology are emergent phenomena of complex ecological systems that do indeed reflect the operation of universal law-like mechanisms." According to this view the law-like mechanisms are intrinsic to life itself and reflect the geometric, physical, chemical, and thermodynamic principles that affect the performance of living entities in different biotic and abiotic settings.

It is not at all unexpected that the macroscopic approach emphasizes the search for power laws and scaling relationships, for it is well known that these are quintessential to complex systems that emerge as statistical regularities not affected by the specific details of the interaction among system components (e.g. Stanley, 1995; Stanley *et al.*, 2000). Despite their potential importance, however, power-law distributions remain little explored in ecology, where most of the attention has been put into the analysis of simple scaling relationships, which although related, are fundamentally different, as we shall see below.

In general, relationships where some quantity can be expressed as some power of another according to the following functional form

$$y = \beta x^{\alpha} \tag{21.1}$$

are called power-law relationships. Power laws are well known to biologists in the form of bivariate relationships of power-law type called scaling relationships (e.g. Peters, 1983; Marquet, Navarrete & Castilla, 1990; Brown & West, 2000; Brown *et al.*, 2002; Chave & Levin, 2003) by which molecular, physiological, ecological, and life history attributes relate to some attribute of organisms raised to a power as in Eq. (21.1). Further, scaling in ecology has been usually associated with relationship where the independent variable is the size of an organism (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). I will call these "allometric scaling relationships" and will differentiate them from power laws that represent probability or frequency distributions, of the form $p(x) = Cx^{\alpha}$.

In this chapter, we will show that power laws are ubiquitous in ecological systems, and although they represent a challenge for understanding, at the same time they provide an interesting interdisciplinary research venue for identifying the general principles underlying biodiversity patterns and dynamics. We will start with a brief description of power laws and scaling relationships and the importance of extreme events (those occurring in the tail of probability distributions) and then provide a couple of selected examples on the existence of power laws in the abundance and population dynamics of species.

The power is in the tails

Power laws are closely related to fat-tail distributions. A distribution $P(x)$ is said to be a "fat-tailed" distribution if the probability associated with larger values of x contain a larger fraction of the probability mass or density than a Gaussian distribution or any other reference distribution with thin tails, typically a Gaussian or exponential (see Fig. 21.1). The importance of distributions with fat tails is that any distribution with "sufficiently fat tails" is a power-law distribution (J. D. Farmer and J. Geanakoplos, unpublished manuscript), although in a strict sense this is true for a particular class of non-Gaussian Lévy stable distributions only (see Mantegna & Stanley, 2000). In general, we can say that a random variable X follows a power-law distribution if

$$P[X > x] \sim x^{-\alpha} \text{ as } x \to \infty, \tag{21.2}$$

which is equivalent to say that it follows a power law above some threshold x. Following Newman (2005), a continuous random variable with power-law distribution will take a value in the interval $x + \mathrm{d}x$ with probability $p(x)\,\mathrm{d}x$ where

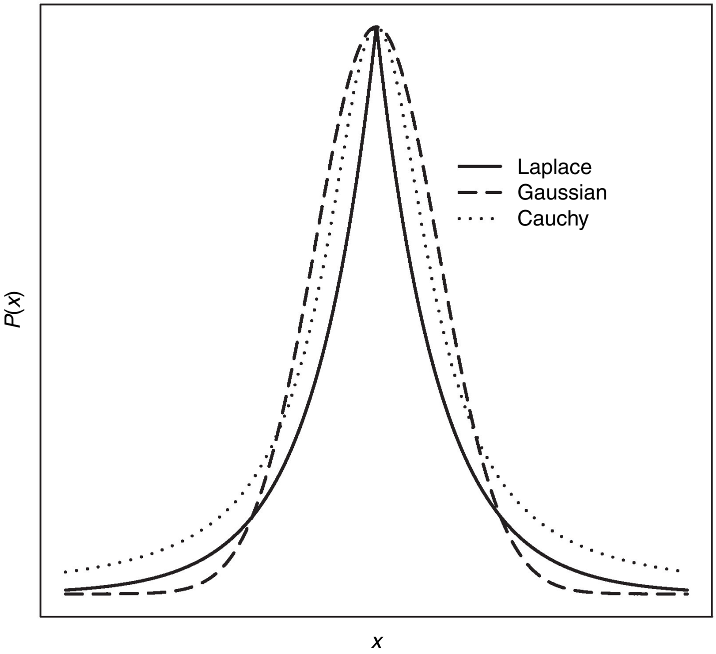

Figure 21.1 Gaussian, Laplace and Cauchy distributions showing the fat tail of the Cauchy, which is well described by a power law.

$$p(x) = Cx^{-(1+\alpha)}, \tag{21.3}$$

which holds for $\alpha > 0$ and above some lowest value $x_{\min}$. Interestingly, if $\alpha \leq 1$, the first central moment of the distribution, or its mean, is not finite (i.e. is undefined). Similarly, if $\alpha < 2$, the variance does not converge to any finite value but increases with the sample; a phenomenon commonly observed in ecological time series of abundance and dubbed the "more time more variation effect" (e.g. Pimm & Redfearn, 1988; Inchausti & Halley, 2003). Power laws are ubiquitous in physical and social systems, emerging in phenomena such as the frequency of earthquakes of different magnitudes (the Gutenberg–Richter Law), the distribution of income among individuals (Pareto's law), and the rank–frequency distribution of words in natural languages and city sizes (Zipf's law) (see Mantegna & Stanley, 2000; Sornette, 2004; Newman, 2005, for a discussion of these and other power laws).

Fat-tail distributions are becoming increasingly important in ecological research, especially in the analysis of plant and animal dispersal data (Kot, Lewis & van den Driessche, 1996; Viswanathan *et al.*, 1996, 1999; Clark *et al.*, 1999; Mårell, Ball & Hofgaard, 2002; Gautestad & Mysterud, 2005; Katul *et al.*, 2005; Borda-de-Água *et al.*, this volume). Considering the wild behavior of power-law distributions, their existence represents a challenge to ecologists fascinated with Gaussian distributions with central tendencies and finite variances, and who are therefore used to statistical tools based on them. Fortunately, theory and statistical methods to work with fat-tailed distributions are being developed (Samorodnitsky & Taqqu, 1994; Adler, Feldman & Taqqu, 1998).

There are two notions or characteristics associated with power-law relationships that single out their theoretical and empirical importance. The first is that power laws describe scale-invariant processes with no characteristic scale (e.g. Stanley *et al.*, 2000; Gisiger, 2001; Sornette, 2004), that is, they display invariance under scale change. This can be seen if we consider a scale transformation in x such that $x \to \lambda x$. Then $p(x) = \beta x^{\alpha} \to \beta\lambda^{\alpha}x^{\alpha} = \lambda^{\alpha}\, p(x)$; thus a change in the scale of the independent variable preserves the functional form of the original relationship. Scale invariance describes phenomena that are not associated with a particular or characteristic scale and are also known as scale-free or true on all scales; that is, they are self-similar and possess the same statistical properties at any scale (although scale invariance is not exactly equivalent to self-similarity; see Šizling & Storch, this volume). In practical terms this means that the same principles or processes are at work at each scale of analysis (Milne, 1998). The second is the notion of universality. This concept was introduced into physics in association with critical phenomena (e.g. Biney *et al.*, 1992) to describe the state and dynamics of systems as they approach a phase transition (such as water turning into ice or the onset of magnetization when temperature is changed or the transition between dynamical regimes through bifurcations in deterministic dynamical systems). Near phase transitions, systems are said to become critical and relevant quantities that describe their state (e.g. magnitude of fluctuations, correlation length) have power-law probability distributions with critical exponents (e.g. Stanley, 1971, 1995, 1999; Maris & Kadanoff, 1978; Solé *et al.*, 1996; Oborný *et al.*, this volume). Interestingly, it has been shown that systems which are completely different away from a critical point, show similar critical exponents and their macroscopic phases become indistinguishable at the critical point (e.g. Biney *et al.*, 1992). These nonarbitrary exponents are said to be universal and define disjoint classes (universality classes) into which different physical systems can be classified. A system can arrive at a critical state through changes in a variable external to it (e.g. temperature), but also as a result of its own internal dynamics, in which case we speak of self-organized criticality, a concept introduced by Bak, Tang and Wiesenfeld (1987). During the last decade or so, several empirical and theoretical investigations have suggested that biological systems in general, and ecological systems in particular, seem to operate near a critical state, which results in the ubiquity of power-law behavior in several descriptors of their dynamics (e.g. Miramontes, 1995; Bak, 1996; Keitt & Marquet, 1996; Rhodes, Jensen & Anderson, 1997; Ferrier & Cazelles, 1999; Solé *et al.*, 1999; Gisiger, 2001; Solé, Alonso & McKane, 2002; Roy, Pascual & Franc, 2003; Pascual & Guichard, 2005), and might even belong to the same universality class as other complex systems such as economic systems (Stanley *et al.*, 2000). Thus the analysis of power laws and scaling relationships can help us to identify general principles that apply across a wide range of scales and levels of organization, revealing the existence of universal principles within the seemingly idiosyncratic nature of ecological systems. However, it should be borne in mind that power laws might emerge as a consequence of several processes not necessarily related to critical points and phase transitions (Brock, 1999; Mitzenmacher, 2001; Allen, Li & Charnov, 2001; Sornette, 2004; Newman, 2005; Perline, 2005; Solow, 2005), so that whether ecological systems are maintained near a critical state or not is still an open question.

Power laws in ecological quantities

As reviewed by Marquet *et al.* (2005), power laws are common descriptors of several ecological quantities. They emerge for example in the size and duration of epidemic events (Rhodes & Anderson, 1996; Rhodes *et al.*, 1997), in patterns of abundance, distribution, and richness (e.g. Frontier, 1985; Banavar *et al.*, 1999; Harte, Kinzig & Green, 1999; Harte, Blackburn & Ostling, 2001; Marquet, 2002b; Labra, Abades & Marquet, 2005), in food web attributes (e.g. Garlaschelli, Caldarelli & Pietronero, 2003; Brose *et al.*, 2004), and in disturbances such as landslides and fire (Malamud *et al.*, 2004; Malamud, Millington & Perry, 2005; Moritz *et al.*, 2005). In the following paragraphs we will present and discuss some power laws associated with population abundance and dynamics.

Abundance

One of the characteristics of the frequency distribution of species abundance is the appearance of heavy tails, such that there is a nonnegligible probability of finding extreme values in abundance. These patterns have been usually modeled more or less accurately by means of lognormal distributions, or by fitting exponential functions in order to describe their tail behavior (Williamson, 1972; May, 1975; Dennis & Patil, 1998; Diserud & Engen, 2000; Halley & Inchausti, 2002; Marquet, Keymer & Cofre, 2003). However, recent theoretical developments have called attention to the possibility that they may also conform to a power-law form (Brown, Mehlman & Stevens, 1995; Ives & Klopper, 1997; Solé & Alonso, 1998; Sornette, 1998; McGill & Collins, 2003; Niwa, 2003; Labra *et al.*, 2005; Marquet *et al.*, 2005), which opens a different scheme of interpretation.

To illustrate the existence of power-law signatures in the distribution of abundances across space at a continental geographical scale we used the North American Breeding Bird Survey (hereafter BBS; Sauer, Hines & Fallon, 2005), which comprises several thousand routes of approximately 24.5 miles long each, sampled once a year during the breeding/nesting season (mainly June) across USA and southern Canada (Sauer *et al.*, 2005). We analyzed three different levels of description representing different ways of analyzing data: intraspecific, interspecific and no-specific. The first level was simply analyzed by constructing probability plots from local abundances measured at different locations in space for a single species. In the second approach, we used the total number of individuals per species measured at the continental level. Finally, we avoided using any taxonomic membership and constructed frequency distributions for the total number of individuals observed in different locations across the continent, irrespective of species identity. For all analyses we used BBS raw counts of individuals, only excluding routes that have remained inactive since 1982. Probability plots were done for every level of description and for years 1982 and 2002. These years were chosen in order to check the robustness of the pattern. In addition to power laws, we also fitted an exponential distribution, since it captures the rapid probability decay in the tails when no scale-free dynamics is present (Newman, 2005). In order to illustrate the intraspecific distribution of local abundances we used as focal species the American coot (*Fulica americana*), a social bird that lives in flocks. This species is a migratory bird found in freshwater lakes and ponds across USA and Canada in summer and in the southern portion of the USA in winter (Terres, 1980; Udvardy, 1994). It is important to keep in mind that the BBS data may suffer from strong biases regarding the effect of habitat complexity upon bird counts, which may affect the effective survey radius (Hurlbert, 2004), and observer quality (Sauer, Peterjohn & Link, 1994). If these were important we would expect significant deviations from a power-law relationship, as scale invariance would be violated. Such deviations may manifest themselves as regime shifts or cutoffs in the observed distributions.

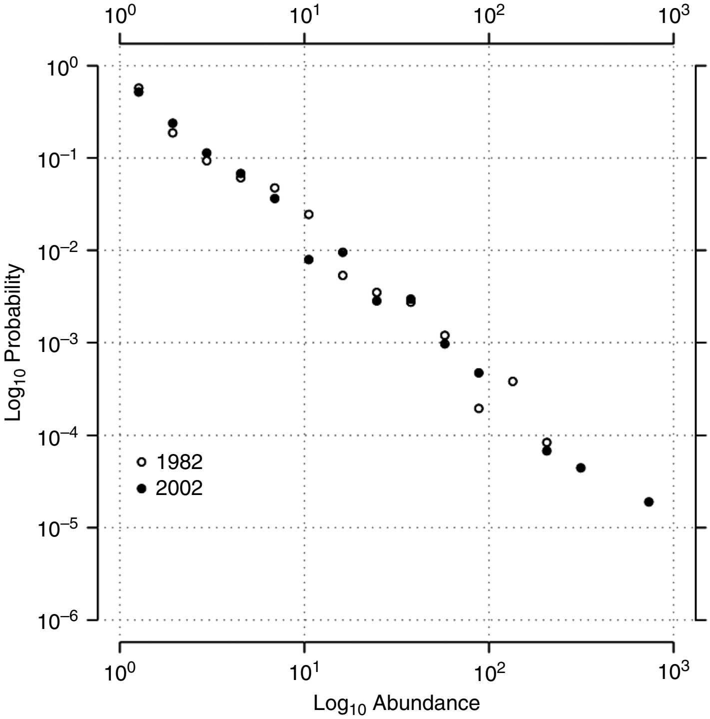

Figure 21.2 Empirical probability distribution for local abundances observed across USA for the American coot (intraspecific level of description).

Interspecific probability patterns were explored for a total of 534 and 595 species (years 1982 and 2002, respectively), summing all individuals counted per species across all routes in the USA. As in the intraspecific case, linear fits in log-log scale and exponential fitting were used to test for the presence of a power-law relationship. Finally we constructed empirical probability distributions for local abundances irrespective of taxonomic identity, by counting the total number of individuals observed in every route sampled across the USA. We fitted the models for years 1982 (1769 routes) and 2002 (2676 routes), but, as is clear in Fig. 21.3, only the right tail was used for the power law fit, given that a small "rollover" is present at low abundances.

The empirical probability distribution for the intraspecific case is shown in Fig. 21.2. Both the exponential and power-law distributions provided significantly good fits, but the power law explained a larger amount of variance than the exponential (Table 21.1). The power-law regime ranged over three orders of magnitude, with a consistent tail exponent of 1.85 for both years compared (Table 21.1). In general, the tail exponent value indicates the number of finite moments of the probability distribution, which in this case implies the existence of a mean but no bounded variance (e.g. Stanley, 1971; Newman, 2005). The lack of finite second and upper moments is indicative of a strong scale-free phenomenon, with a heavy tail towards high abundances. In practical terms,

Table 21.1 *Summary of power law fits*

Aggregation indicates the level of description analyzed. Tail index corresponds to the slope of the linear regression on log-log scale (standard error shown in brackets). PL R^2 is the explained variance for the power law fit and Exp R^2 for the exponential distribution fit; P-value < 0.05.

Aggregation	*Year*	*Power-law tail index*	*PL R^2*	*Exp R^2*
Intraspecific (Fig. 21.1)	1982	−1.85 [0.075]	0.97	0.69
	2002	−1.85 [0.045]	0.98	0.53
Interspecific (Fig. 21.2)	1982	−1.15 [0.031]	0.96	0.54
	2002	−1.11 [0.030]	0.96	0.56
No-specific (Fig. 21.3)	1982	−3.43 [0.350]	0.91	0.96
	2002	−3.78 [0.216]	0.96	0.73

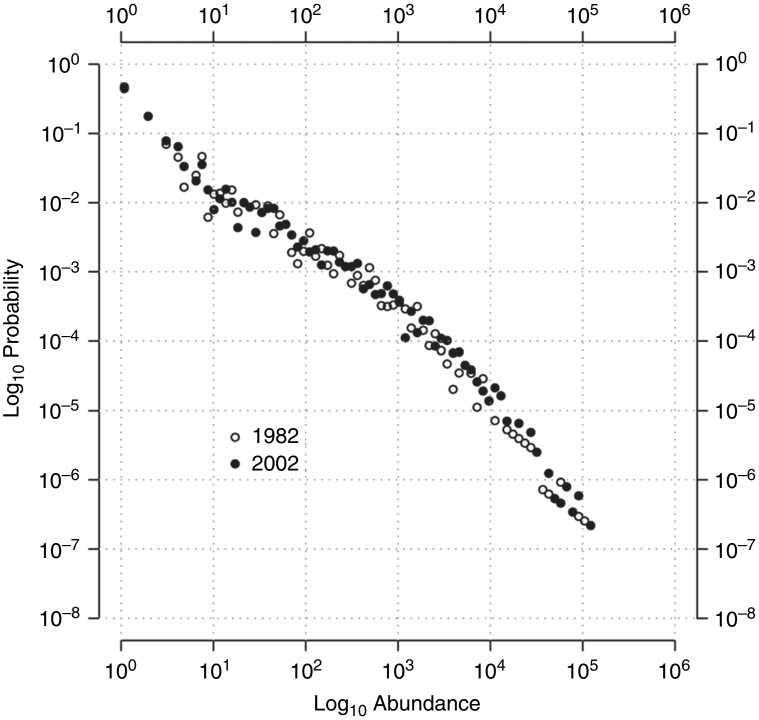

Figure 21.3 Empirical probability distribution for the total number of individuals per species across the USA (interspecific level of description).

a distribution with an infinite second moment indicates that no matter how much sample size is increased, variance will always keep on increasing (Stanley, 1971; Newman, 2005). A power-law probability distribution in local abundances captures valuable information about the internal structure of a species' geographical range: all abundance levels are present in inverse proportion to its

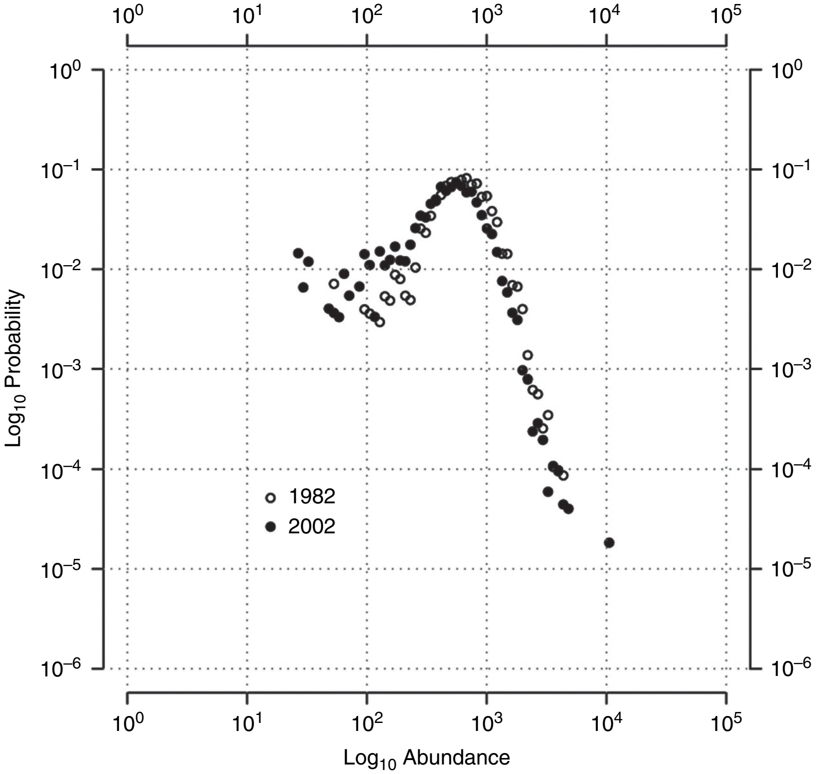

Figure 21.4 Empirical probability distribution for the total number of individuals observed across the USA irrespective of taxonomic membership (no-specific level of description).

size, similar to the well-known Gutenberg–Richter law for earthquakes (Gutenberg & Richter, 1944; Christensen *et al.*, 2002). Thus, abundances described at a geographical scale would be characterized by a few very abundant local spots and many less abundant sites (see Brown *et al.*, 1995) covering a large spectrum of local realizations and departing from what would be expected under a "normal" fast exponential decay (Newman, 2005; McGill & Collins, 2003).

In the interspecific case (Fig. 21.3), a power law ranging five orders of magnitude also characterized distributions better than exponentials, with tail exponents of 1.11 and 1.15 for years 1982 and 2002, respectively (Table 21.1). Accordingly, finite first but no second moment exists, thus a heavy right skew governs these distributions. For the no-specific case (Fig. 21.4) the probability distributions for the total number of individuals measured across the USA, irrespective of taxonomic identity, show a power-law decay covering almost two orders of magnitude but only for year 2002, after the small "rollover" at approximately 5000 individuals. The exponent is 3.78, indicating a fast decaying tail, but still differing from an exponential one (Table 21.1). For year 1982, however, the exponential distribution explained a larger amount of variance than the power law. A similar result has been reported for 2003 (Newman, 2005).

Our results illustrate the existence of power-law behavior in the spatial pattern of population abundance. Although the mechanisms underlying this behavior are not known, it is expected given the existence of power-law distributions in population growth rates and fluctuations (as we shall see below). Further, in the time domain, it has long been known that variance in population abundance in different taxa is not finite but increases with the length of the census period (the more time more variability effect; Pimm & Redfearn, 1988; Arino & Pimm, 1995; Cyr, 1997; Inchausti & Halley, 2001, 2002), as is expected if the temporal variance in abundance follows a power-law distribution. The consequences of this are far reaching. First, more variability in abundance means increased extinction risk (Leigh, 1981; Pimm, Jones & Diamond, 1988; Lande, 1993; Inchausti & Halley, 2003). And since the value of the power-law exponent is related to the exponent characterizing the relationship between variance and number of observations (Newman, 2005), it could be used as a measure of extinction risk given the observed correlation between variance in population abundance and time to pseudoextinction (Inchausti & Halley, 2003). Second, if indeed population abundance follows a power-law scaling with exponents <2 as shown here for the American coot, this raises a word of caution in making inferences using statistical methods based on distributions with finite means and variances. More interestingly, our results show that the level of description does affect the value of the scaling exponents, which tend to increase from intraspecific to the interspecific and no-specific level of analyses. The observed rollover and the fact that the power-law behavior may disappear at the no-specific level of description are difficult to explain. These might be a consequence of sample biases as pointed out above. This clearly requires further investigation.

Growth rates

Standard ecological wisdom asserts that population size is expected to follow a lognormal distribution, given that it is the product of a multiplicative renewal processes (e.g. MacArthur, 1960; Lawton, 1989; Blackburn, Lawton & Pimm, 1993; Halley & Inchausti, 2002; but see Williamson & Gaston, 2005). Furthermore, several single species population models give rise to normal or lognormal population abundance distributions (e.g. Keeling, 2000). If population abundances in different time intervals follow a lognormal distribution, it is expected that the ratio of successive abundances $N(t+1)/N(t)$ also has a lognormal distribution, and hence, the logarithm of such a ratio $r = \ln[N(t+1)/N(t)]$, should show a normal or Gaussian distribution. In other words, under an expectation of lognormal population abundances, population growth rates should exhibit a Gaussian probability distribution.

Keitt and collaborators (Keitt & Stanley, 1998; Keitt *et al.*, 2002), however, have shown that population growth rates of North American breeding birds show a power-law probability distribution. As seen in Fig. 21.5(a), this tent-shaped distribution is symmetric about a zero growth rate, with an equal probability of observing increases or decreases for the species studied. While these findings have been criticized, casting doubts on their generality, recent research shows that they are indeed general. Analysis of population growth rates of local ensembles of birds, small mammals and trees has shown that they share the same power law functional form (Labra, 2005), indicating that they do not depend on the geographic scale of analysis. As a further example, when all fish species found in a local community are considered (Magurran & Henderson, 2003), the same tent-shaped power law distribution of growth rates is once again observed (Fig. 21.5b). The fact that species with very different lifestyles, resource requirements, and phylogenetic history show such a consistent pattern is suggestive of a general set of processes giving rise to this power-law distribution.

The presence of scaling and universality in population growth rates has strong implications for understanding population dynamics in general. In physical systems, scaling is often found in the presence of "cooperative" behavior. In inanimate systems such as ferromagnets near a critical temperature point, scaling relationships arise because each particle interacts directly with a few neighboring particles, and as these neighboring particles interact with their neighbors, interactions can "propagate" long distances, thus resulting in power-law distributions (Stanley *et al.*, 2000). Similar results have been observed for the probability distributions of growth rates of companies, universities and countries' gross national product. In physics, such behavior is interpreted as evidence that the particular details of the interaction among the components of the system have no role in setting the system properties, which depends mostly on the dimensionality of the system. This strongly suggests that there may indeed exist universal principles that underlie the growth dynamics of complex adaptive systems involved in the acquisition, transformation and storage of information, materials and/or energy. Recently, Fu *et al.* (2005) have shown that the shape of the distribution of growth rates may be explained by a general stochastic model, which accounts for both the central part as well as the tails of the distributions observed in business and firms' growth rates. Interestingly, the shape of the business growth-rate distribution is due to the proportional growth in number and size of the constituent units of businesses of a given size. More importantly, this result is claimed to hold both in an open economy (with entry of new firms) as well as in a closed economy (with no entry of new firms). Whether similar mechanisms may hold in ecological systems poses a very interesting research question.

In the case of ecological communities, the scaling in population growth or fluctuation can be brought about either by the spatial dimension of spatial

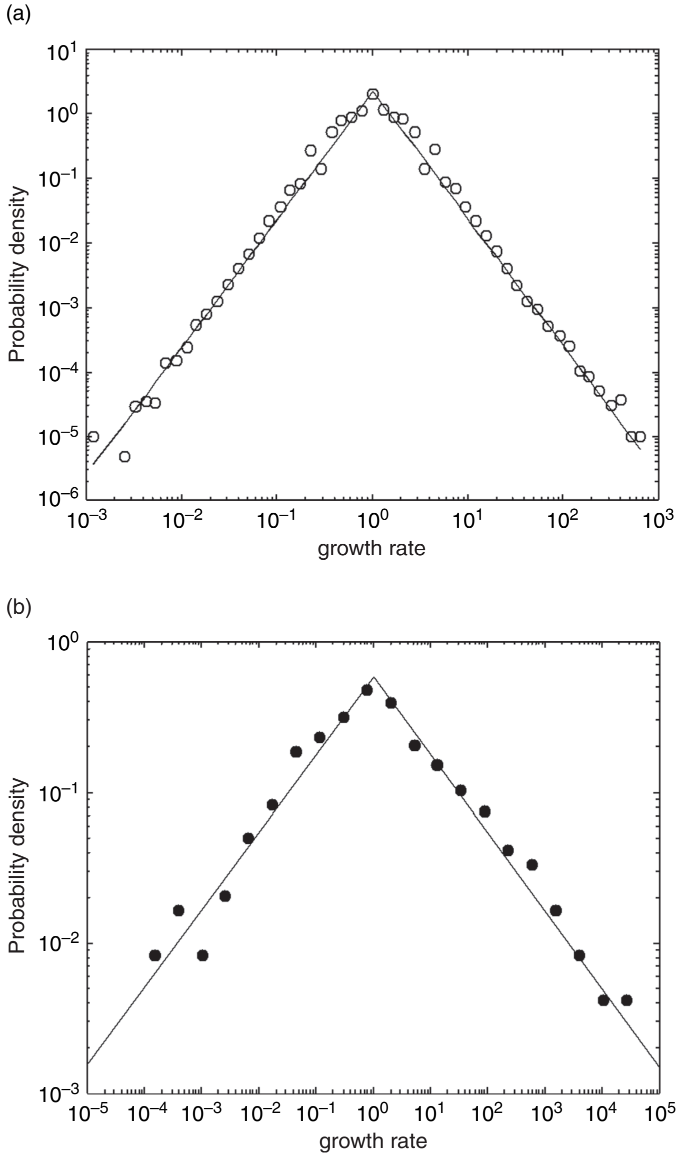

Figure 21.5 Probability distribution of population growth rates. (a) The distribution of population growth rates across all species in the North American Breeding Bird Survey data set over three decades. The growth rate $r(t)_s$ is calculated by log transforming the ratio of species abundances in successive years, i.e. $r(t)_s \equiv \log[N(t+1)/N(t)]$. Abundances are taken as the total number of individuals of a particular species counted within each survey route. Modified after Keitt and Stanley (1998). (b) The distribution of population growth rates across all fish species in the Hinkley point data set over two decades. The growth rate $r(t)_s$ is calculated by log transforming the ratio of species abundances in successive years, i.e. $r(t)_s \equiv \log[N(t+1)/N(t)]$. Abundances are taken as the monthly average number of individuals of a particular species counted within each year. Data were obtained from the Global Population Dynamics Database. In both cases the distribution of growth rates shows a scale invariant form, symmetric about $r_s = 0$, which indicates a balance in population increases and decreases for the species in the sample over the study period.

population structure, or more importantly, by the physical dimension of energy and material flows. In the first case, it can be argued that interactions in ecological systems may propagate through spatial metapopulation dynamics, with local populations interacting through colonization–extinction dynamics with nearby populations (see Oborny *et al.*, this volume; Kunin, this volume; Borda-de-Água *et al.*, this volume). By contrast, species present in an ecosystem interact directly with some (but not necessarily all) species, which may in turn interact with a second set of species, so that interactions can "propagate" through time and space from the individual to the population, community and ecosystems, and finally to the biosphere scale. The fundamental connectivity of the living makes the existence of power laws plausible.

The relationship between energy and material flows and the emergence of observed power laws in ecological systems can be further highlighted by an important implication, which although remarked by Keitt and Stanley (1998), has not been emphasized by previous authors. In addition to its tent-shaped form and the observed rescaling features, the observed distribution of growth rates is highly symmetrical about $r_s = 0$ in all cases considered (Fig. 21.5). This implies that exactly as many species are increasing in abundance as are decreasing over the 31-year period studied, be it over the whole ensemble, or when grouping by initial abundance bins (although it is not the case at the level of such ecological groups as forest or grassland birds; see Sauer *et al.*, 2005). This result strongly suggests that these species undergo a zero sum dynamics in population size, with demographic gains and losses by all the species balancing over the study period. This is not obvious, nor is it expected from previous theoretical explanations for the emergence of scaling laws in physical systems. The idea of the existence of zero sum dynamics in ecosystems under energy limitation can be dated back to the Red Queen Hypothesis, which predicts that any change in the control of trophic energy by a species is balanced by a net equal and opposite change in the amount of trophic energy controlled by all the other species in the community with which that species interact (Van Valen, 1976, 1977; Stenseth, 1979). In this formulation, trophic energy, defined as an individual's control of a constant amount of the energy available to a group of related species that compete for it, is a proxy for fitness. This implies that, in general, resource (energy) use by the species in a community is a zero-sum game (Hubbell, 1997, 2001; Bell, 2000), with a balance in the energy gained and lost by all the interacting species. In this regard, the Red Queen Hypothesis emphasizes that under a scenario of finite resources zero-sum dynamics must necessarily operate, as an expression of the first law of thermodynamics (Van Valen, 1976, 1977; also see open discussion in Van Valen, 1980).

It is important to note that these results have not been exempt from criticism in the literature, and we close this section by mentioning and discussing the main points made against the existence of power laws in the distribution of population growth rates. It has been argued that the tent-shaped distribution of population growth rates may be the end product of a mixture of lognormal distributions in population size (Allen *et al.*, 2001). This phenomenological explanation, however, does not account for the symmetrical nature of the distribution, nor does it provide a mechanism that accounts for its form and location. Another possible explanation of these results is that the distribution of growth rates in the community arises from a mixture of Gaussian population growth rate distributions for each of the species with different variances (Amaral *et al.*, 1998). This would require, nevertheless, that all the distributions of growth rates be centered with mean zero, so that all species must be, at all times, regulated around an equilibrium point, and hence it does not take into account the fact that in the observed data some species show marked trends in abundance, and thus species increases had to be balanced by decreases in other species.

Population fluctuations

Power laws in population fluctuations are well known and have been the focus of an increasing number of contributions in recent years, as a consequence of the availability of long time series in population dynamics, such as the Breeding Bird Survey (BBS) and the Global Population Dynamics Database (GPDD). Time series analyses of population fluctuations have shown that the amplitude of fluctuations (n) decreases, on average, as the inverse of the frequency (f) with which they occur or as "$1/f$ noise" or "pink noise" (e.g. Halley, 1996; Miramontes & Rohani, 1998; Inchausti & Halley, 2001; Storch, Gaston & Cepák, 2002; see review in Halley & Inchausti, 2004) such that the distribution of fluctuation sizes $D(n)$ is described by a power law of the form $D(n) \sim n^{-\alpha}$, with α close to 1, as expected under self-organized criticality (Bak, Tang & Wiesenfeld, 1987).

In addition to $1/f$ noise, one of ecology's most interesting patterns regarding population variablity is Taylor's power law (Taylor, 1961). It has been observed that for many species the variance in population abundance $s^2(N)$ is related to the mean of population abundance $<N>$ by a power law with a fractional exponent: $s^2(N) \propto <N>^g$ (Taylor, 1961; Taylor & Woiwod, 1980; Anderson *et al.*, 1982; Hanski & Tiainen, 1989; Boag, Hackett & Topham, 1992; Keitt & Stanley, 1998). For the vast majority of species, the power-law scaling parameter, g, is found to lie between 1 and 2, with many species lying close to the extremes (Anderson *et al.*, 1982). This scaling relationship has been described for a wide range of taxa, in both space and time.

It is interesting to note that, should Taylor's power law hold for temporal variation in abundance, and if the temporal mean abundance follows a negative relationship with body size, the scale invariance in both power-law relationships make it possible to derive the scaling in population variability as a function of body size, and it can be expected that $s^2(N) \propto (<M>^n)^g \propto <M>^{ng}$. Thus, as n

is expected to be $-3/4$ and g is usually between 1 and 2, hence population variability should show a negative scaling relationship with body mass, taking values between $-3/4$ and $-3/2$. Although this relationship has not been tested explicitly in the literature, the work by Keitt *et al.* (2002) provides evidence that such a negative scaling may hold for North American birds when studied at the population level. These authors show that the standard deviation $s(r_s)$ of population growth rates in North American birds is strongly related to the average total population size. The relationship follows a power law $s(r_s) \propto <N>^b$, for over four orders of magnitude in $<N>$, the total population abundance averaged across all 31 years studied. Using major axis regression with bootstrap precision estimates, Keitt *et al.* (2002) find $b = 0.36 \pm 0.02$, so that Taylor's exponent (here replicated across species) is found to be $g = 1.28 \pm 0.04$. Again, under the assumption that there exists a negative relationship between average abundance in time and body size: $<N> \propto <M>^n$, with $n = -3/4$, it can be seen that the temporal variance in population abundance should scale approximately as $M^{-1.0}$ (-0.96 ± 0.03). By contrast, the standard deviation in population growth rate should scale as $s(r_s) \propto <M>^{bn}$, which predicts then that fluctuations in growth rates should show a $M^{-1/4}$ scaling (the predicted value is -0.27 ± 0.05), as do other temporal phenomena in ecology and biology (Calder, 1983; West, 1999). It certainly would be interesting to test whether these predictions hold to empirical scrutiny for the species studied by Keitt and collaborators (Keitt & Stanley, 1998; Keitt *et al.*, 2002) as well as for other taxa and at other spatial scales of study.

Concluding remarks

We have shown that power laws may characterize the statistical behavior of several ecological quantities associated with population abundance, growth and fluctuation. Further, the scale invariance that power-law distributions entail suggests that, despite the idiosyncrasy that might dominate the interaction among system components, there are some general principles underlying the dynamics of the system at different scales. The empirical verification of power-law behavior, however, should not be taken as an end in itself but as the starting point for analyzing the complexity of ecological systems. Power laws are in essence empirical laws that allow for a statistical description of complex systems where the nature of the interaction among system components is unknown. The challenge ahead is to develop theoretical models that on the one hand explain observed patterns and, on the other, make quantitative predictions of new ones. Unless this agenda is carried out, we risk the possibility of being adrift in a sea of empirical relationships and idiosyncratic explanations. This assumes, however, that well-resolved and comprehensive data sets on ecological quantities, which will allow for a good documentation of extreme events that occur in the tail of frequency distributions, are available. Otherwise is the risk of working with truncated distributions that may give rise to false power laws. As recently shown by Perline (2005) truncated lognormal-like distributions can mimic power-law behavior. Unfortunately, the reverse can also be true; that is, a distribution can be a power law but the existence of an exponential cutoff (a fast exponential decay in the tail probabilities) can blur the pattern. Such behavior could emerge as a consequence of the finite nature of the system (but see Laherrère & Sornette, 1998; Fenner, Levene & Loizou, 2005) as is known, for example, in the study of critical phenomena that take place in the thermodynamic limit (infinite system size). Fortunately, information obtained for finite systems can be extrapolated to infinite size by using a phenomenological approximation known as finite size scaling (FSS; Cardy, 1988). In principle, any finite variable showing power-law distribution ought to exhibit finite size scaling and thus the effect of system size dependence can be explicitly modeled, allowing for an assessment of their power-law behavior and the value of its associated scaling exponents. This technique can be of great relevance for the analysis of ecological systems, as demonstrated by recent applications (Banavar *et al.*, 1999; Keitt *et al.*, 2002; Rinaldo *et al.*, 2002; Niwa, 2005). Power laws might provide a new venue for research into biodiversity. It remains to be seen, however, to what extent the challenge of embracing a non-Gaussian world can be met both in theoretical and empirical terms.

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