Scuola Internazionale Superiore di Studi Avanzati
- ma per seguir virtute e conoscenza -

Neutral models in ecology: species abundance and extinction dynamics

Thesis submitted for the degree of
Doctor Philosophiæ

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October, 18th 2004

Contents

Introduction

> *In the survival of favoured individuals and races, during the constantly-rucurrent Struggle for Existence, we see a powerful and ever-acting form of Selection. The struggle for existence inevitably follows from the high geometrical ratio of increase which is common to all organic beings. This high rate of increase is proved by calculation, by the rapid increase of many animals and plants during a succession of peculiar seasons, and when naturalized in new countries. More individuals are born that can possibly survive. A grain in the balance may determine which individuals shall live and which individuals shall due, which variety or species shall increase in number, and which shall decrease, or finally become extinct.*
>
> Charles Darwin, *The origin of Species* [1]

In the last years, tools borrowed from statistical physics have shown to be very helpful to understand problems arising in various fields of biology. This kind of approach is well estabilished in some field, for example in the study of biopolimers and proteins, and is getting more and more interesting also in other fields; ecology is among these fields.

The fundamental problem in ecology is the understanding of the *stability* properties of ecosystems, i.e. collections of species in a given environment; the classic ecological theory states that ecosystems are stable because every species has a well defined role.

According to this view, an ecosystem reaches stability because each species evolves to be the best competitor in its own ecological niche [2]; this is the *niche assembly* point of view. The concept of niche is purposely vague: it comprehends several aspects of species behavior like diet, diurnal/nocturnal activity, foraging strategy, habitat and so on. The whole system reaches an equilibrium when all the possible niches are occupied. In this situation, it is very hard for an invader species to modify the equilibrium, because it will necessarily enter in competition with other species which are very well specialized in their own ecological niche. Summarizing, the “classical” perspective states that ecosystems are far from being a random collection of species: species evolve togheter, and the whole system shows well organized patterns [3]. Ecology aims to undercover how these organization structures work.

Recently, it has been pointed out that this ’stable’ picture is not fully correct [4]. Extinctions of species and speciations (i.e. birth of new species) are very common event in the history of life. More precisely, the stable picture may or may be not correct depending on the timescale on which we are looking at the system - evidences from the fossil record show that there have been long periods of relative stasis, characterized by sporadic extinction and speciation events, separated by periods of very abrupt changes. This peculiar aspect of life history has been named “punctuated equilibrium” by Gould and Eldredge [5]. Several authors pointed out [6, 7] that there is a strong analogy with the stock market: if one looks at the assets value on the day timescale, the oserved variations are typically small, and a stable, organized picture may emerge; however, we know that there are famous examples of market crisis, characterized by crashes of even well established assets. Ecosystems are thus characterized by phenomena acting on very different timescales [7], and there is interactions among these levels of descriptions, meaning that it can be misleading to study the system on a given timescale and neglet phenomena occurring on different scales (for example, studying a living ecosystem neglecting evolution). All these features make ecosystems a paradigmatic example of complex systems, and the challenge for statistical physics is to “scale up” the results, infering what happens on large scale from a model of the local dynamics.

For these reasons, it is crucial to have the possibility to build up statistical models grounded on very simple hypothesis. One of them is the neutral hypothesis. Even Darwin admitted that a fitness advantage can be, using his words, just “a grain in the balance”. Kimura [8] was the first to realize that it is very unlikely that a single mutation in a molecule can bring a concrete gain of fitness for the organism. Thus, many of the non-harmful mutations are neutral, meaning that the mutant has essentially the same survival and reproduction probability as the wild type. Evolution, thought as selection of a mutant species with higher fitness, is related to rare events, and many observed pattern are essentially generated by random mutation processes. The concept of neutrality was later imported by Hubbell [4] in the field of ecology. Looking at single-trophic level species, one can assume that every individual in the ecosystem obeys the same dynamical rule, regardless of the species it belongs to. This assumption can be justified in some way invoking the Red Queen effect [9]: due to the changing environment, it is very hard for a species to gain an advantage on the other species. Thus, every species evolves, but older species are not better adapted than new species [10]. In some sense, a neutral theory is the opposite perspective with respect to a niche-assembly theory: it is assumed that randomness and not niche differentiation is responsible for the emergence of the observed patterns. Even if the validity of the neutral approximation is still under debate [11, 12], the advantage of neutral models is that they are enough simple to be analytically tractable; furthermore, the predictions based on neutral models fit often very well the experimental data on single-trophic level ecosystems [4].

As we anticipated above, all these theories and approximation can be valid or not depending on the time (and spatial) scale on which we look at the ecosystem [7]. This is a typical feature of complex systems and statistical mechanics has also shown to be very useful to relate phenomena occurring on different scales.

This research work is organized as follows:

- In Chap. 1, we discuss some of the statistical patterns that seem to be ubiquitous in ecosystems. Evidences for these patterns are collected both in study of living ecosystem and in quantitative study of the Fossil Record.
- In Chap. 2, we introduce the most important models that tried to give an explanation for the observed patterns. The important concept of neutrality will be also discussed.
- In Chap. 3, we present a stochastic neutral model of the populations in a single-trophic level ecosystems. A continuous version of this model is analytically solvable; we compare the analytical solution with numerical simulations and with experimental data coming from studies of tropical forests.
- In Chap. 4, we address the problem of calculating the species lifetime distribution function for the “standard” formulation of the ecological neutral theory [4, 13]. Depending on the parameters range and on the initial condition, the solution has several different asymptotic behaviors We study them and make a comparison with evidences of the fossil record. In a realistic parameter range, we obtain the correct scaling.
- In Chap. 5, we discuss the possible ecological implications of the result of Chap. 4. In particular, we try to “scale up” the predictions of the neutral theory on a long timescale. We predict in the same framework the lifetimes of species and genera and the distribution of species among genera.

Finally, we outline final conclusions and perspectives.

Chapter 1

Statistical patterns in ecological systems

This chapter is devoted to outline some statistical patterns that seem to be ubiquitous in ecosystems. There are basically two ways to discover these patterns:

- observation of living ecosystems
- study of collections of fossils

The studies of living systems give usually better data than fossils: quantitative studies of the fossil record suffer from several statistical biases that will be briefly described in the following. What is really important for our discussion is that these two kind of observations let us know something about very different timescales. Living systems are studied year by year, and it is very hard to find detailed data spanning more than a decade. On the other hand, fossils give us informations about phenomena occurring on a timescale on the order of a million years. As we anticipated in the introduction, several phenomena may be very important on one timescale, and almost negligible on the other. Among these phenomena, the most important is evolution: for sure it is very important on the fossil timescale, while the role it plays on the year timescale may be not so crucial. We will begin our discussion with the studies of living systems, and talk about the fossil record in the second part of this Chapter.

1.1 Statistical description of ecosystem: definition of community and metacommunity

It is very hard to make a reasonable study of a complete ecosystem. The reason is that ecosystems are composed by very different species, having different size, behavior, and survival strategy. Also the interaction among species can be of different types: there can be competition, symbiosis, predator-prey relationships and so on. Furthermore, ecosystems are not isolated systems and are subject to immigration, environmental and climate change, etc. Even from an experimental point of view, it is sometimes convenient to restrict the observations on something simpler than the full system.

Many choices are possible: one possibility is to study only the behavior of a small number of species (typically 2 or 3), and considering all the remaining system as an external perturbation. The hope is to reconstruct the behavior of all the system starting from these simpler interactions [14]. This kind of approach can be very successful, and helped a lot in underlining some general features of ecosystems, like Lotka-Volterra oscillation [15, 16] and the exclusion principle [17].

Another useful approach is to restrict to a set of species *belonging to the same trophic level*. This assumption means that:

- The species compete, actually or potentially, for the same pool of resources.
- The species are similar, meaning roughly of the same size, with the same lifespan, etc.

A group of species satisfying these assumptions and living in a local and confined area (for example, an island) is defined as an *ecological community*. Of course, the same kind of species may exist also on larger spatial scale, like continental scale. The group of trophically similar species on this scale is defined as a *metacommunity*. The main difference is that species belonging to the metacommunity may not compete because of spatial separation.

There are several reasons for studying single-trophic level ecosystems. First of all, due to the fact that species interact only in a competitive way, these systems are simple and amenable to be studied in more depth than complete ecosystems, still being composed by a large number of species. Moreover, due to the similarity of the species (and of their role in the ecosystem), it is a crucial issue to understand why some of them are very abundant, while others are less common. This issue can have a profound importance, for example in determining the policies for the preservation of endangered species.

The first quantitative observations of single-trophic level ecosystems were done on insects [18]; today, better datasets are available from extensive studies of tropical forests [19]. We will show in the following sections several features that seem to be independent on the particular group of species under study.

1.2 Density of individuals

One of the simplest law of an ecosystem is the one relating the number of the individuals present in a given region and the area of that region. The observational result is that a very good linear relationship holds between the number of individuals and the area:

$$N = \rho A \tag{1.1}$$

where ρ is the total density of individuals, regardless of the species they belong to. This linearity is independent on the sampling method (one can choose between sampling non-overlapping areas or nested areas). The common explanation for this law is simply that ecological communities are always saturated: that the resources available are just enough to support the individuals present at the moment. This implies that

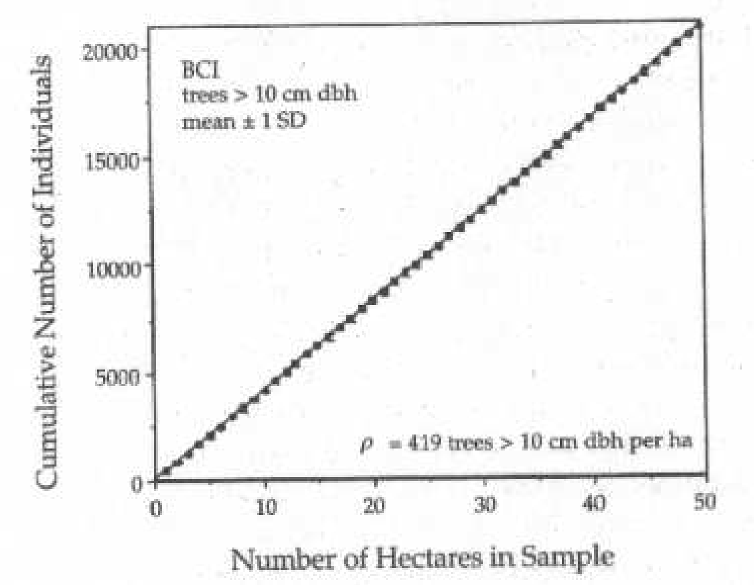

Figure 1.1: Experimental number of trees as a function of the area sampled in Barro Colorado Island, Panama [4].

the number of individuals is linear in the area simply because the amount of common resources (light, water and so on) is linear in the area. This apparently trivial law has important theoretical consequences. For example, many aspect of ecosystem dynamics can be explained by means of evolutionary game theory [20]. In this framework, species traits and behaviors are considered as strategy of a game, and the fitness of the species is proportional to the payoff of that strategy in that situation: a species with positive (negative) payoff will increase (decrease) its population. Coevolution is the key idea behind these models: the success (or failure) of a given strategy depends on the strategy adopted by the competing species. Eq. 1.1 tell us that a realistic game should be zero-sum, meaning that if the total population is constant, no species can have success and increase its population without subtracting resources to the other species. We will see in Chap. 3 the effect of introducing this law into a stochastic model for species populations.

1.3 The species abundance

The species abundance $\langle\phi_N\rangle$ is defined as the average number of species in an ecosystem having a given number of individuals N. This quantity is used to determine how many rare species there are, with respect to abundant species, in various kind of ecosystems. The first data were obtained by S.Corbet in 1941, an entomologist studying the butterflies in Malaya; two years later, was published the work of Fisher, Corbet and Williams [18], that obtained similar results with a light-trap study on the moths at Rothamsted Experimental Station in England. The result was that the distribution was monotonic and long-tailed, with many rare and few common species. Fisher found that the data were fitted very well by a distribution of the form:

$$\langle\phi_N\rangle \propto \frac{\alpha^N}{N} \tag{1.2}$$

with $\alpha < 1$ being a parameter characterizing the size of the system; typically α turns out to be very close to 1. Distribution 1.2 is known in the literature as the Fisher log series.

Some years later, Preston, looking at data from bird species abundance, found that the Fisher log series didn't fit in a satisfactory way [21]. In particular, his data were not monotonic, but shown a maximum for species with an intermediate abundance. In order to obtain a clearer plot, he made a $\log 2$ binning of his data, with the prescription that species at the edge of a bin are equally divided between the two adjacent bins

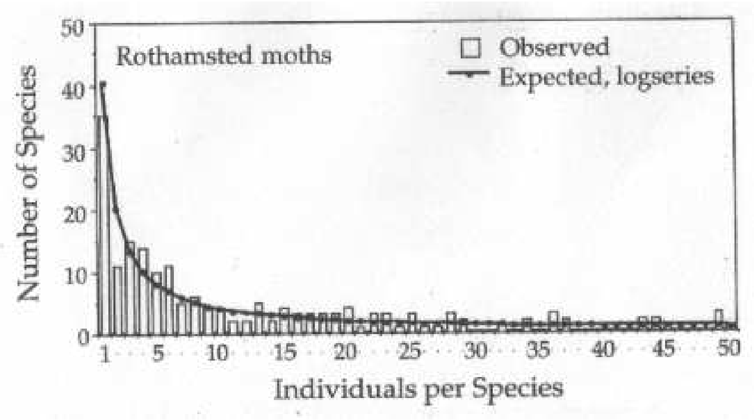

Figure 1.2: Corbet data set and log series fit. Picture taken from [4]

(Preston plot). The obtained histogram was well fitted by a lognormal distribution (see fig. 1.3).

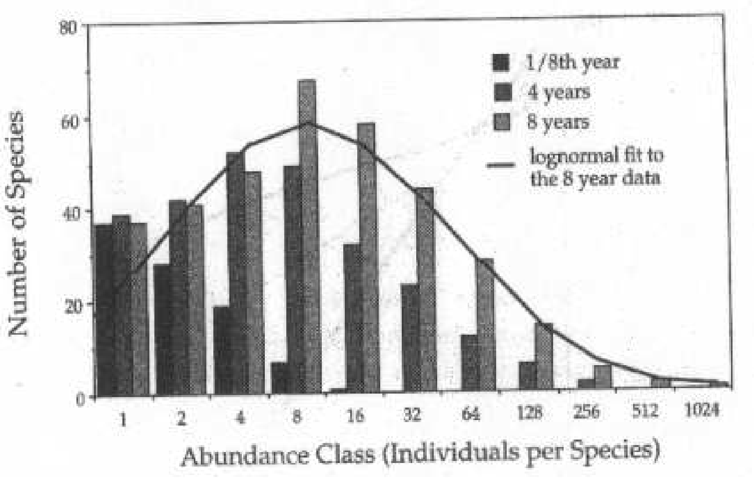

Figure 1.3: Lognormal fit to species abundance data. Picture taken from [4]

These observations raised two important questions:

- Is there any reason to assume that different ecosystems should have similar species abundance distribution? Is there some kind of 'universal' explanation for the distributions obtained, without taking into account the details of the specific system? Are the Fisher log series and the lognormal two members of the same family of curves, meaning that it is possible to switch from one to the other by varying some parameter?

- Are the observed distributions the necessary consequence of some *dynamical model*, meaning that they emerge as stationary distributions if one imposes some simple dynamical rule?

We will try to answer these questions in Chap. 3.

1.4 Species Area laws

Another interesting law that is widely studied in ecosystems is the relationship between the number of different species present in a given region and the area of that region. The most accepted relationship among these quantities [22] is a power law:

$$S = C\, A^{z} \tag{1.3}$$

The exponent z is in some sense a measure of the biodiversity: for example a value $z = 1$ denotes an ideal infinitely diverse ecosystem, where there are always new species as the area increases. In real ecosystems, the exponent z is always less than one; hence, the growth of the number of species with the area is always sublinear. Typical values for z are in the range $0.2 - 0.4$, depending on the specific ecosystem. It was pointed out [23] that this relation is caused by a self-similar distribution of the abundance of species, meaning that the value of the exponent can be easily derived assuming that the probability that a species living in a given area A is also present in a similar region of area $A/2$, is a constant independent of A. However, the scale invariance don't explain the *dynamical* origin of species area relations. The problem of finding a dynamical model explaining this power law behavior has been addressed only recently: scaling behaviors similar to that of real ecosystem have been numerically observed in simple, spatially-explicit birth and death models (for example, the voter model with speciation [24]). Despite the simplicity of these models, it is still very hard to obtain from them an analytic expression, or estimate, for the exponent z.

1.5 The fossil record: quality of the datasets

Large collections of fossils, with their dating and the place of their retrieval, can be sources of useful informations about the behavior on long timescales of living systems.

It has been estimated [25] that about 5 billions species did live in the geological past since the appearance of life on Earth, dated about 3.5 billions years ago. One of the most relevant events in these 3.5 billions years was the Cambrian explosion, a period of about 25 millions years starting from 545 millions years ago, during which multicellular life underwent an extraordinary diversification producing a multitude of new evolutionary lineage in a relatively short time. The period of time spanning from the Cambrian explosion until our days is called the Phanerozoic: we have little knowledge of events preceding the Cambrian explosion, due to the rareness and poorness of conservation of fossils.

The database for extinction analysis [26] is the distribution in space and time of about 250000 Phanerozoic fossil species (that can be subdivided in about 18.000 genera). Most of them are marine species, because of the better condition for deposition and conservation with respect to land-dwelling organisms. This is not an huge sample, and suffer from several biases:

- quality of deposition can vary greatly with time. A period of poor preservation can give the appearance of a large extinction event
- recent fossils are more available and often better conserved than older ones. This may give the impression of greater biodiversity in the present, where this may be not true. This is called the “pull of the recent”
- not every species and genera have been equally studied. There can be “monographic effects”, meaning that some group of species in the fossil record can give the false impression of being very abundant, just because it was intensively studied by some research group, or because several well-conserved fossils were found that allowed a good and detailed classification.
- there can be several other possible sources of errors and biases: species may seem to disappear for a period of time and then reappear again (the so called “Lazarus effect”), the same species may have called in different ways, etc.

A lot of care were dedicated in the last years [26, 6, 27] to analyze the database with sophisticated statistical methods, in order to eliminate every possible source of errors and outline a list of reliable evidences. We will sketch in the following some of these evidences.

1.6 Biodiversity, speciation and extinctions

The fossil record allow to estimate how the overall number of species, genera and families did vary through the Phanerozoic [27]. Looking at various classes of organism, the general trend of these graphs is a sudden growth (exponential, according to [26]) from the beginning of the Cambrian, followed by a slower, linear growth rate.

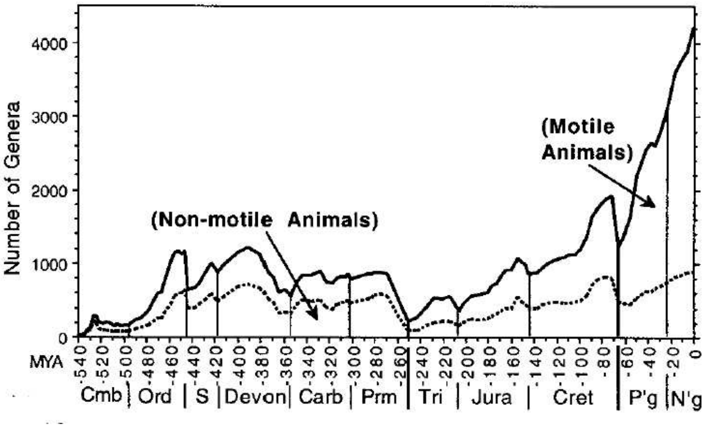

Figure 1.4: Variation of marine biodiversity through the Phanerozoic.

The Cambrian Explosion was related to the first appearance of multicellular life. Multicellular organisms had many possibilities to differentiate and occupy new niches. According to the classical ecological perspective, this period of sudden life growth ended when all the resources were saturated. After that, the growth was slower, corresponding to the search of more complex equilibriums compatible with the available resources. We anticipated in the introduction how this “static” view may be in contrast with the enormous amount of extinctions during the Phanerozoic: if one look at the actual estimated biodiversity on Earth (about 10 million species) the conclusion is that about 99.9 % of the species ever lived are now extinct.

Understanding the causes of extinctions in the framework of evolutionary theory is not a trivial task [6]. The main reason is that evolution acts at the level of individuals [28]. The “survival of the fittest” rule explains how a species evolve, but it is not obvious how to deduce from this rule a mechanism for species extinctions. Darwin [1], talking about fossils, wrote that due to the incompleteness of the fossil record, it is impossible to find in it good arguments pro or against the evolutionary theory. Today, evolutionary theory is widely accepted and we have more detailed data about fossils; a careful study of these data may provide useful information to shed some light on the problem of species extinctions.

1.7 Mass extinctions vs. background extinctions

The fossil record shows a striking “clustering” of extinction events. During the Phanerozoic several catastrophic events did occur. Each of the most important five among these mass extinctions (“the Big Five”, as they are called by paleontologists) killed more than the 70% of the species present at that age. It is a challenging task to estimate the duration of these events, and understand what provoked them. Several possible causes have been proposed for each of them, like the impact of a meteorite [29], sudden variations in the environment like climate changes [30], different salt concentration in the ocean water, abrupt changes in the seas level [31] and so on. Despite the dramatic size of these events, they are not the only contribution to the extinction of species, and very likely they are not even the most important one. The great majority of species (from 90% to 95%, according to some estimates) go extinct in events that do not show a particular clustering in time with other species extinctions. These events form the so-called background extinctions. An important question is, whether there is or not a *qualitative* difference between background and mass extinctions [32, 33]. It may be also that there could be extinction events of all sizes, and that only events greater than a certain size (related to the size of the sample) are recognized as collective events. Raup [32] tried to answer these question measuring the typical waiting time between extinctions events greater than a given size vs. the size of the event. Analyzing the results [33] it is hard to give an ultimate answer to this question, due to the poor statistics. Anyway, the distribution of sizes of extinction events seem to show a power law tail $s^{-\tau}$, with τ being close to -2. [34, 35] (see fig. 1.5).

1.7.1 Selectivity of extinctions

It seems quite natural from a statistical point of view to take the fossil record as a sample of extinction events in the history of life; we already talked about the possible errors and bias in this sample. Now, we want to consider another possible problem: is the sample *equidistributed*, meaning, is it possible to consider species lifetimes and size of extinctions, without caring about the type or the characteristic traits of species involved? There are for example species that have survived unchanged for hundreds of millions of years (for example, some deep-sea fishes like sharks): their habitat didn’t change much through time and they do not seem to risk extinction. On

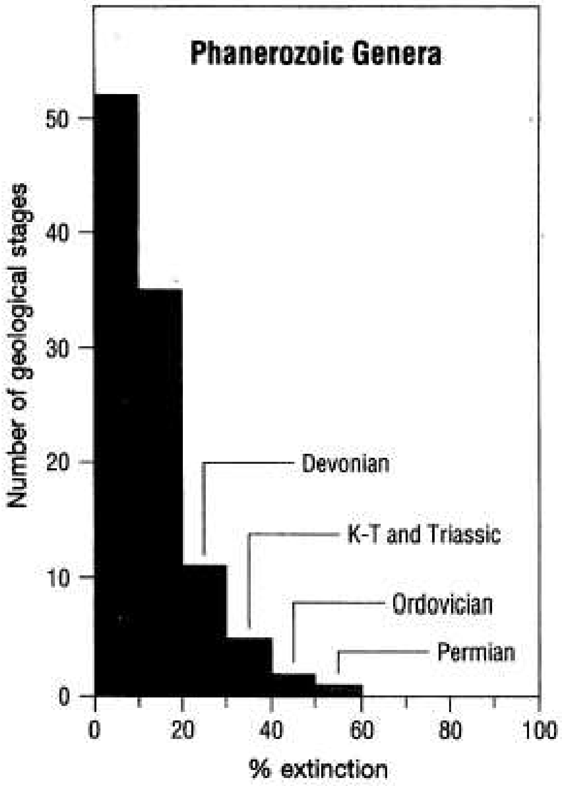

Figure 1.5: Distribution of size of extinction events. The data are well fitted by a s^{-2} power law. Picture taken from [35].

the other hand, there have been several claim of selectivity in mass extinction, for example correlation of the extinction risk with body size [36].

Despite all these considerations, it has been pointed out [6] that there are not sufficient elements to conclude that some physical trait is strongly correlated with the extinction risk of a species. The reason is that one can consider a lot of possible traits: size, diet, habitat, behavior, diurnal-nocturnal activity and so on. We must consider that we do not have an infinite sample of extinction events: just a few mass extinctions have been extensively studied; we also know that also our knowledge of the fossils do not allow to access an infinite database. These observations imply that it is very likely to find traits that correlate rather well with the extinction probability, just because there are a lot of traits, but it is hopeless to understand if it was a chance or of really, for example, a great body size or a very localized geographical range may expose a species at risk of extinctions.

Models of extinctions dynamics often refer to a notion of “fitness”, as a real number quantifying the ability to resist to environmental stresses [37]. One can extend this picture with multi-traits species, having a fitness represented by a vector; each component of the vector is the resistance to a specific kind of stress. The conclusion is that, as far as we are talking about simple statistical models, it is reasonable to consider these numbers as random number extracted from an unique probability distribution.

1.8 The species and genera lifetimes distribution

Species lifetimes are well fitted by an exponential distribution. The common explanation for this lifetime distribution is the Red Queen effect [9]: extinctions are thought to be caused mainly by change in the environment, and change (or extinction) of other interacting species. From this follows that a long living species gains no advantage over a younger one, since it has to face a new environmental situation. In conclusion, the probability of extinction per unit time must be independent on the age of the species, and this implies an exponential lifetime (see fig 1.6).

When looking at genera lifetime, rather than species, there is some evidence of a power law behavior [34]. In fig. 1.7 it is shown a typical plot of genera lifetimes. The fitted exponent seems to be close to -2. There is not a full agreement on whether this power law holds or not [38]. An exponential fit for the same curve is also reasonable, but one has to include the effect of living species, which are of course not taken into account in this case [38]. The common hypothesis [38] is that this power law is a

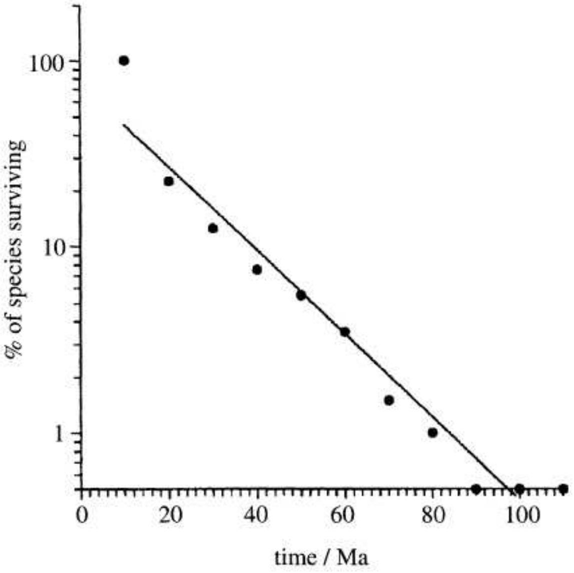

Figure 1.6: Lifetimes of species belonging to the Foraminifera genera. Data taken from [10]. The straight line is the exponential fit.

consequence of the power law of the extinction size, and that an explanation for the distribution of extinction events size can be an explanation also for the lifetime distribution. According to this explanation, species do not display a power law lifetime just because they have typically a shorter lifetime, and are less likely to be affected by these mass extinction events.

We will propose in Chap. 4 and 5 a possible, simpler explanation for the emergence of this power law behavior in the genera lifetime distribution.

1.9 Conclusions

In this Chapter, we sketched some empirical evidences about ecosystems, collected by means of observations of both living and extinct (fossil) species. We purposely stressed two important aspects:

- It is pratically impossible to have very good statistics for this kind of systems. Dataset are on the order of $10^2 - 10^3$ experimental points for observational data of living systems, and on the order of $10^4 - 10^5$ data points for the best collection of fossils species. We mentioned also a lot of possible source of problems

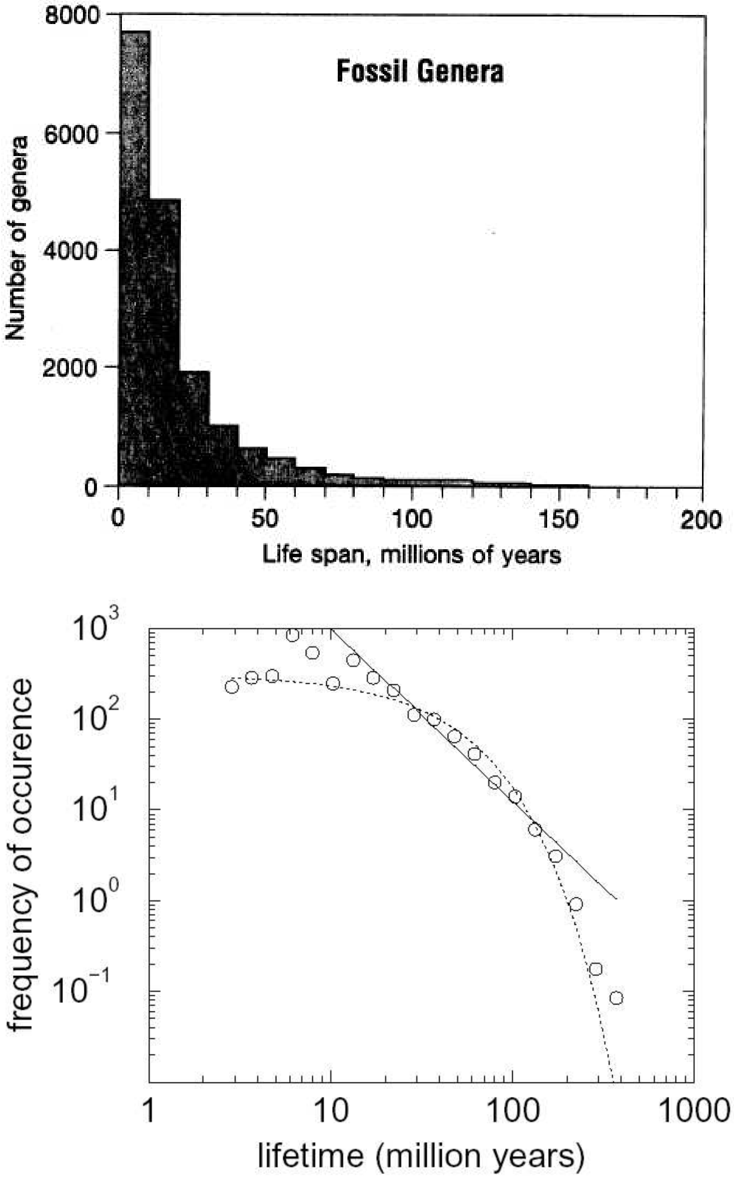

Figure 1.7: lifetimes of genera, according to [6]. Data are well fitted with a power law $P(t) \sim t^{-\alpha}$, with α close to -2.

and biases. Furthermore, it is almost always impossible to vary the parameters, or the external condition of the system. This implies that the comparison of models with the data can only give qualitative information, and rarely an ultimate proof.

- We also underline the importance of the timescale. Quantitative studies of ecosystems do not have a lot of history, it is very hard to find an ecosystem studied for a period longer than 10 years. It was argued [4] that the commonly accepted equilibrium view of ecosystem [2] is related to this short-term view: it is very hard to look at large changes on this timescale, which is much shorter than the typical lifetime of a tree! On the other hand, fossil studies allow us to look on the opposite limit of very large timescales. It is very important to try to build up theories which are capable of predictions on very different scales.

In the next Chapter, we will review some of the more influent models which tried to capture the origin of these observational patterns.

Chapter 2

Models for ecological system, neutral theory and species extinctions

In this Chapter, we would like to outline some of the more relevant theories and models for ecosystem dynamics. It is clearly beyond the purpose of this work to give an exhaustive survey of all the important concepts in this field; we will sketch the most relevant of them, focusing more on the aspects related to this research work.

2.1 Deterministic models: the Lotka-Volterra equation

One of the first mathematical models that addressed the issue of the existence of a stable equilibrium situation of a set of interacting species is the work of Lotka [15] and Volterra [16] on predator-prey dynamics. They studied a system of differential equation of the form:

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned} \tag{2.1}$$

where a, b, c and d are positive real parameters. The variable x represent the number of preys, while y is the number of predators. This system have been widely studied, and displays some interesting features, like periodic oscillations around the fixed point $x = c/d$, $y = a/b$. These oscillation have been also observed experimentally [39].

The Lotka-Volterra equations can be generalized to a system with more than two species, and more complicated interactions:

$$\dot{x}_i = x_i(b_i + \sum_j a_{ij} x_j) \tag{2.2}$$

In this case, a species i with $b_i > 0$ is a renewable resource, while a species with $b_i > 0$ needs to feed on other species to support its growth. The matrix a_{ij} determines the kind of interaction:

- $a_{ij} > 0$ and $a_{ij} < 0$: species i feeds on species j (predator-prey or parasite interaction)
- $a_{ij} > 0$ and $a_{ij} > 0$: symbiotic kind of interaction
- $a_{ij} < 0$ and $a_{ij} < 0$: competitive interaction.

Many interesting mathematical results are known for this kind of systems [16, 40, 41, 42]. In Chapter 3 we will review some result on Lotka-Volterra systems when the matrix a_{ij} is antisymmetric and the number of species is very large.

2.2 Biogeography: basic concepts

A milestone in the modern study of ecology is the work done by MacArthur and Wilson on the island biogeography [22]. Their work aimed to explain in a simple way the fact that the number of different species coexisting in a given island has a functional dependence from various parameters like the distance from the mainland, the area of the island and so on. In particular, a larger island - and nearer to the coast - commonly hosts more species than one smaller or less close to the mainland. The theory of island biogeography states that the number of species in a given island varies as an effect of immigration and local extinction. The basic assumption is that the rate of arrival of new species and of local extinction (local disappearing of species) are only functions of the number of species present at the moment in the island. In particular, one can assume that the rate of immigration is a decreasing function of the number of species, because of the difficulty to settle in an overcrowded environment. On the other hand, extinction will be an increasing function of the number of species, because if the island is very crowded, it is more likely that one of the inhabitant species will go extinct. The conclusion is that an equilibrium holds for a number of species that balances the two rates. Of course the shape of the two functions may be modified, moving the equilibrium point s^*, by several factors: for instance, there will be a larger immigration rate in an island nearer to the mainland.

When the theory was presented in the ’60, there was a lot of debate about its validity. Surprisingly, the authors didn’t stress so much the most revolutionary aspect of the theory: in the theory of island biogeography, the equilibrium among

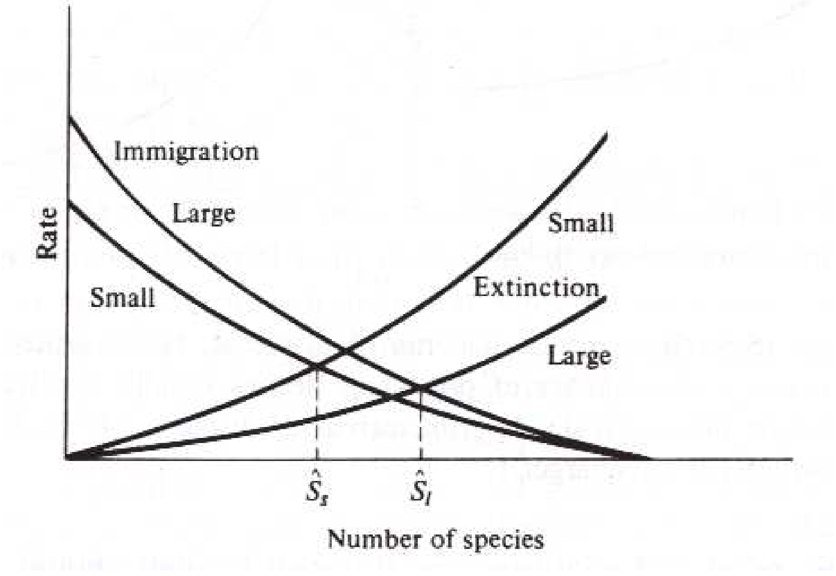

Figure 2.1: Immigration and extinction rate as a function of the number of species s present in the island, according to [22].

species is a *dynamical* equilibrium. Moreover, in fig. 2.2, the immigration and extinction/emigration rates are only function of the *number* of species, without taking into account what kind of species they are, how much abundant are them, or any other detail; in this framework, a species may be ’replaced’ by another with very different habits without altering the behavior of the whole system. The view of the ecosystem as a stable organization seems very far from this description, even if MacArthur was a firm sustainer of the niche assembly perspective.

2.3 The concept of neutrality

The concept of neutrality was introduced in the field of molecular evolution by Kimura [8]. According to Kimura’s theory, several pattern of molecular evolution can be explained postulating that the great majority of possible molecular mutations are neutral, meaning that they don’t bring a relevant change in the fitness of the molecule. In other words, the mutants perform the same function of the wild type, without any improvement or loss of performance. This assumption explains, for example, the constant rate of mutation of many phylogenetic branches. It explains also why the great majority of molecular mutations occur far from the active site of the molecule.

This assumption is not antievolutionistic: the key idea is that mutations that bring an advantage are rare, and most of the time the genes perform a sort of random walk in sequence space. It may be also that neutral mutations become advantageous due to the changing environment.

The neutral assumption was extended, in some sense, to the field of ecology by Hubbell [4]. The approximation consists in assuming that *every individual in the ecosystems undergoes the same dynamical rules, regardless of the species it belongs to*. The neutral hypothesis is applied at the individuals level, not necessarily at the species level: in a neutral model, an abundant species may undergo a different dynamics from a rare one. The relationship with Kimura's neutral theory is the following: here individuals play the role of mutants of the molecule. Assuming the same dynamics for every individuals means that we are neglecting fitness differences with respect to "demographic stochasticity" , as far as we are considering members of the same community. The "demographic stochasticity" is, in ecological terms, the randomness associated to the birth and death process of a species. We stress the fact that the concept of neutrality in ecology should be considered as an approximation, rather than a proper theory. The reason is that microevolution shows direct evidences of neutrality: for example, the rate of mutation per amminoacid seem to be almost constant for many phylogenetic branches. In addition, mutations happen more commonly far from the active site of the proteins, in places where changes are not relevant. On the other hand, macroevolution seems to be less gradual and random, meaning that different species can have very different behavior with respect to lifetime, speciation rate and so on. Many authors claimed [11, 12] that there are no direct evidences of neutrality in ecosystems. However, this assumptions may be consider a zero-order hypothesis, and has the relevant advantage of producing ecological models tractable from an analytical point of view. Furthermore, many predictions based on this neutral assumption compare surprisingly well with experimental data.

It is crucial to assess completely the predictions that can be made in this framework, in order to understand if this approximation is enough to understand the general statistical behavior of an ecosystem, or if there are effects that cannot be explained in this simple context, without taking into account explicitly the differences among individuals, as well as the interaction among them.

2.4 The unified neutral theory of biodiversity

In this section, we want to outline the basic ingredients and results of an implementation of the concept of ecological neutrality proposed by Hubbell [4], and studied later from an analytical point of view [13, 43] known as unified neutral theory of biodiversity. The ingredients are the following: let us consider a community with a fixed number J of individuals. At each discrete time-step one individuals, chosen at random, dies. With a given probability $1-m$, m being a parameter of the model, it is replaced by an individuals belonging to a random species in the community, with a probability proportional to the abundance of that species at the moment. With a probability m, there is an immigration event: the individual is replaced by another one belonging to a species present in the metacommunity, with probability proportional to the abundance of that species in the metacommunity. The model is based on the assumption that species abundances in the metacommunity are distributed according to a Fisher log series 1.2. It can be easily shown that the number of individuals of the k-th species belonging to the community, $P_{n,k}$, evolves with time according to an effective birth and death master equation:

$$\dot{P}_{n,k}(t) = d_{n+1,k}P_{n+1,k}(t) + d_{n-1,k}P_{n-1,k}(t) - (d_{n,k} + b_{n,k})P_{n,k}(t) \tag{2.3}$$

with the following expression for the birth and death rates:

$$\begin{aligned} b_{n,k} &= (1-m)\frac{n}{J}\frac{J-n}{J-1} + m\frac{\mu_k}{J_M}(1-\frac{n}{J}) \\ d_{n,k} &= (1-m)\frac{n}{J}\frac{J-n}{J-1} + m(1-\frac{\mu_k}{J_M})\frac{n}{J} \end{aligned} \tag{2.4}$$

where μ_k is the abundance of the k-th species in the metacommunity and J_M is the total number of individuals in the metacommunity. Notice that, for $n \ll J$, both the birth and the death rates contain a term proportional to n, plus a constant (independent on n). It is possible to find a stationary solution for this equation satisfying detailed balance [13]; after averaging over μ, one obtains a prediction that can be compared with the experimental species abundance distribution:

$$\sum_k P_{n,k}^{(stat)} = \langle\phi_n\rangle = \theta\frac{J!}{n!(J-n)!}\frac{\Gamma(\gamma)}{\Gamma(J+\gamma)}\int_0^\gamma \frac{\Gamma(n+\gamma)}{\Gamma(1+\gamma)}\frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)}e^{(-y\theta/\gamma)}dy \tag{2.5}$$

Here, $\langle\phi_n\rangle$ are the average number of species having n individuals. The comparison with the data is rather good; looking at the fit, it is hard to discard either the

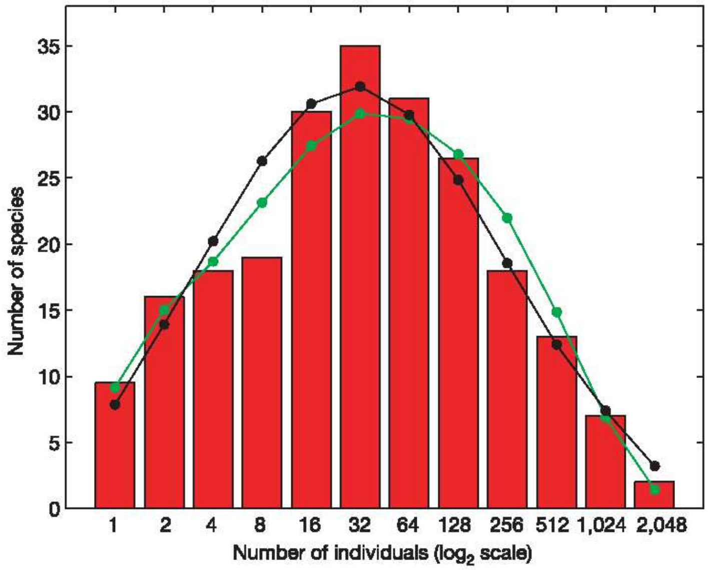

Figure 2.2: Preston plot of BCI dataset. The black curve is the lognormal fit, the green curve is the fit according to 2.5. Picture taken from [13].

lognormal distribution or the neutral solution due to the experimental errors. The important difference between the two is that the neutral solution is based on a dynamical model. It is very hard to justify a lognormal distribution in terms of dynamical processes: often, the lognormal distribution is proposed just because it is the stationary distribution of multiplicative random processes, which can be used to model the number of offspring's as a function of the number of individuals in the previous generation. The problem with this kind of models is that they admit a lognormal solution, but with a variance growing linear with time, which is unphysical.

We will introduce in Chap. 3 a multiplicative-like process which is bounded for every choice of the parameters and bring to a realistic stationary distribution for the species abundance.

2.5 Modeling the extinction dynamics

In these section, we would like to present a couple of models that have been proposed to explain the observed patterns of extinctions. There is a lot of literature about this subject (see [44, 35, 45] and [38] for a review) and enumerating all these proposals is beyond the scope of this work. We just want to sketch the main results and stress that similar distributions can be the result of very different dynamics and assumptions. This implies that the result of these statistical models should be analyzed with care and compared with other evidences, in order to have results truly relevant from a biological point of view.

2.5.1 Self-organized criticality: the Bak & Sneppen model

In the 1990s there has been a lot of interest around the idea that evolution could drive the ecosystem into a self-organized critical state [46], meaning that a small modification in an ecosystem at equilibrium may provoke an avalanches of extinction events without a characteristic scale (power-law distributed). This was a simple and appealing explanation for the phenomena named ’punctuated equilibrium’ by Eldredge and Gould [5]: looking at the fossil record, it seems that evolution (and extinctions distribution) shows an intermittent behavior, with long periods of stasis followed by sudden bursts of activity.

The toy model proposed by Bak and Sneppen [44, 35] is a simple demonstration of these ideas. The model is defined as follow: suppose to have a set of real variables $0 < x_i < 1, i = 1 \ldots s$ defined on a lattice (one-dimensional, in the simplest case). The variables represent species fitness: a species i with lower x_i is supposed to be more at risk of extinction under the effect of environmental stress. Nearest neighbor of species i are supposed to be species interacting with species i. The x_i are initialized as random variable with constant distribution between 0 and 1. At each time-step the species i with lowest x_i is replaced, and the variable x_i is extracted again from the same distribution. This can be thought as an extinction of species i, and replacement by another species, or as a mutation activity: the hypothesis is that the change strikes the less fit species Due to the change of environmental condition, also the nearest neighbor variable of x_i are reassigned. In the large s limit, after a transient, the system reaches a stationary state, meaning that the probability distribution of the x’s does not change with time. This state is characterized by power law distribution of size of extinction events and species lifetimes. In particular, the probability of having an extinction event of size S scales as $S^{-\tau}$, with $\tau \sim 1.1$ in one dimension (see fig. 2.3). This exponent depends on the dimensionality, and it is always less than the mean-field value $\tau_{MF} = 1.5$. It can be also shown that the lifetime have also a power law behavior t^{-k}, with $k = 1$ in all dimensions [47].

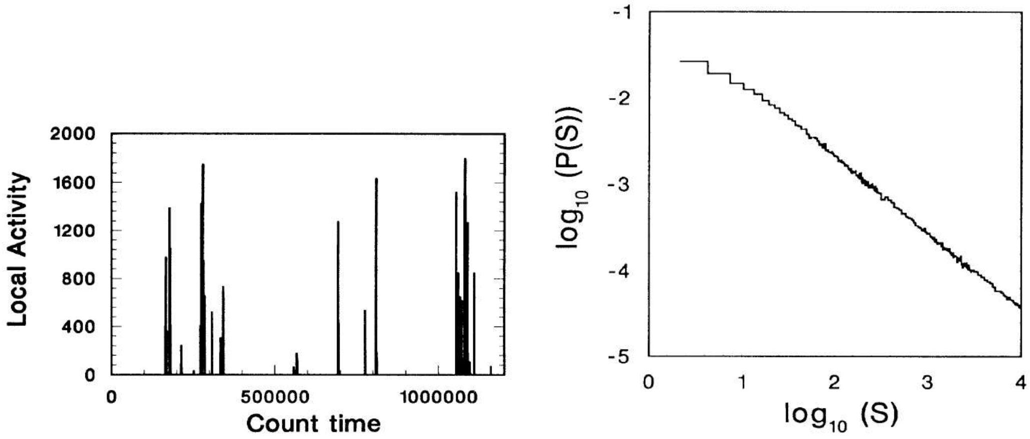

Figure 2.3: Activity vs. time, avalanches size distribution in the Bak & Sneppen model.

2.5.2 The Newman model

As we said, the idea of a self-organized critical ecosystem is very appealing from a physical point of view, because it implies that the power law behaviors are *endogenous*. In this class of models, there is no need to know the entity or the origin of the perturbation which causes the extinctions: the avalanche size is uniquely determined by the internal, critical dynamics of the ecosystem. Anyway, one could obtain a critical behavior in a simpler way by assuming that major external stresses are the cause for large extinction events. Among the models that outline this point of view, we present in this subsection the Newman model [37]. Also in the Newman model we have a given number of species $i = 1 \ldots s$ represented by a single real number $0 < x_i < 1$ characterizing their fitness. However, in this model one can suppose that the species are independent, thus there is no lattice structure. The fitness variable have the same meaning as in the Bak-Sneppen model and are again initialized with an uniform distribution between 0 and 1. At each time-step, a small fraction ν of the species mutate, and their fitness is extracted again from the same distribution. Then, a stress η is chosen randomly from a given stress probability distribution $p(\eta)$. All the species having a fitness lower than η become extinct, and are replaced by new species having fitness again chosen uniformly at random between 0 and 1. Also this noninteracting model displays power-law distribution of extinction events and species lifetimes, for quite different choices of the stress probability distribution function (Gaussian, exponential, Lorentzian). The predicted exponent values are very realistic for the avalanches ($\tau = 2$ for a Gaussian stress and it is close to 2 with other choices of the distribution), but are further for the observed value for the lifetimes ($k = -1$ for a Gaussian stress).

2.5.3 Discussion

We presented in this section two apparently similar coarse grained models for evolution and extinctions. These models have indeed a very different biological meaning, but both show scale free lifetimes and extinction size distribution. We saw that the two models predict quite different numerical value of the critical exponents. Statistical physics, and in particular the theory of critical phenomena, suggest that the critical behaviors should be independent on the details of the models. If this is true also in our case, a direct comparison with the observed exponent should be an argument against the Bak and Sneppen mechanism [35].

Of course, common wisdom suggests not to take too seriously the concept of universality when one deals with complex systems. The reason is that often models for complex systems are really abstract with respect to reality: while it is reasonable to assume that the Ising model is a simplified version of the Hamiltonian for a ferromagnet, and should belong to the same universality class, it is very hard to make a similar claim for a model of evolution. In this context, the numerical value of an exponent can be just considered as an useful hint to understand the underlying dynamical mechanism, and not as an ultimate benchmark. For example, models based on self-organized critical dynamics, but with a more realistic topology of the interactions seem to predict a value of the exponent more close to the reality [48]. On the other hand, "exogenous" models can often predict realistic exponents with simpler assumptions (in the case of the Newman model, it it sufficient to assume that the stress distribution in Gaussian).

The real behavior is clearly a result of the interplay between both exogenous (environmental shocks) and endogenous (avalanches of extinctions) factors. Furthermore, it is very hard to determine a stress p.d.f., and even the definition of "fitness" as the ability to resist to stresses is questionable. A reasonable conclusion may be that the distribution of large events is determined mostly by the presence of exogenous factors, rather than by large-scale avalanches. This is coherent with several studies of environmental phenomena [29, 31], which are surely capable to cause large scale extinction events. Extinction avalanches are still an important phenomenon, but it is not clear how much they have been crucial in the history of life.

A more subtle problem is that all of these models neglect completely the population size. Species are treated as a whole: shocks, both endogenous and exogenous, are supposed to affect the entire population. On the other hand, we know experimentally [6] that an abundant species has, in general, more chance to survive an environmental stress than a rare one, especially if the species has a great geographical range. Extinctions are more likely to affect species which are already small in number, and confined in a small geographical range. MacArthur and Wilson [22] were fully aware of this fact: they introduced the concept of Minimum Viable Population (MVP), which is a threshold value of the population size depending on the species. It is widely believed [49] that a species with population above its MVP is virtually immune from the risk of going extinct.

We will show in Chap. 4 and 5 how demographic stochasticity alone can explain some of the observed patterns.

2.6 Conclusions

In this Chapter, we introduced and discussed some basic ideas and theory that influenced the modern ecology and palaeontology. We stressed the fact that it is preferable to have an individual-based model, instead of considering the species as a whole. We also underline how the organization in ecosystem can be somehow neglected when one look on long timescales, and how the observed patterns can emerge from simple stochastic models. All these ideas are the basic ingredients for our work, that will be the subject of the following Chapters.

Chapter 3

A stochastic process for the neutral theory

In this Chapter, we propose a stochastic model for the dynamics of competing species in an ecological community [50]. The neutral assumption allows us to obtain a simple model and calculate analytically a stationary solution. This solution is compared with simulations and from observational data from tropical forests.

3.1 Introduction of the model

A milestone in the study of multiplicative stochastic process is the work done by Kesten [51]. Kesten studied equations of the form:

$$X_{t+1} = \lambda_t X_t + b_t \tag{3.1}$$

where $X(t)$ is the variable belonging to a proper vector space and both λ and b are random independent variables. He found that, depending on the mean value of λ and on the boundary conditions, one retrieves a lognormal or a power-law regime. Multiplicative random processes have been widely studied [52, 53] and several models for distributions commonly found in economic and natural systems based on this kind of processes have been proposed [54, 55]. In the economic models, essentially, the random variable λ_t represents the income of a given asset at time t, while b_t is a sort of "welfare term", a random contribution given by the society and independent on the value of the asset.

When $\langle \lambda \rangle < 1$; Kesten show that the stationary solution has an asymptotic power law tail $x^-1 + \alpha$. The parameter α can be obtained as a solution of the transcendental equation:

$$\langle \lambda^{\alpha} \rangle = 1 \tag{3.2}$$

It can be show that (apart from the trivial solution $\alpha = 0$), the solution is always $\alpha \geq 1$. On the other hand, while size distributions of firms and assets often seem to display x^{-2} power law tail, ecological system are characterized by longer tails (for example, Fisher's $1/x$ with a cutoff [18]). Our goal is to propose a multiplicative stochastic model, based on simple hypothesis, which can lead to a stationary solution comparable to the species abundance of real ecosystems.

According to MacArthur and Wilson theory of island biogeography [22], the number of species in a community approaches a dynamical equilibrium between immigration, speciation and extinction. We assume that we can neglect the fluctuations around this equilibrium value: in our model, when a species go extinct, it is immediately replaced by another one, thus the total number of species, s, is kept fixed.

We also assume that the net effect of the competitive interaction between species in the community is just to keep also the total number of individuals in the community fixed: the resources available are enough to support just N individuals across all the species; we saw in the first chapter that also this hypothesis is well confirmed by experimental data [21, 22]. At the end of section III, we will show that relaxing these constraints does lead to similar conclusions in the large N limit.

We introduce the s variables x_i^t, representing the population of the i-th specie at (discrete) time t, with the condition:

$$\sum_{i=1}^{s} x_i^t = N \qquad \forall t$$

Let $P(\lambda)$ be the probability that an individual in the community has λ offspring during one time step. Here, we make use of a neutral approximation: we assume that we can consider the same distribution $P(\lambda)$ for all individuals, regardless of the species. The population of the i-th species evolves according to the following equation:

$$x_i^{t+1} = N \frac{\sum_{k=1}^{[x_i^t]} \lambda_{k,i}^t + b}{\sum_{j=1}^{s} \left(\sum_{k=1}^{[x_i^t]} \lambda_{k,i}^t + b \right)} \tag{3.3}$$

where [ ] means the integer part. We are assuming that the existence of species with a non integer number of individuals is not too drastic. This might lead to round-off problems only for rare species. At each time step (generation) we just sum the number of offspring of every individual belonging to that species, and then add a small quantity b. This quantity becomes relevant only for small x_i, and this describes the behavior of species near their extinction threshold. We are assuming that the net effect of extinctions, immigration pressure and speciation can be modeled in a simple way with the introduction of this term, whose effect is to force the x_i's to be greater than zero. Indeed, for $b = 0$, our system admits an absorbing state with only one x_i equal to N and the others equal to 0, the so-called monodominance [4]. Notice that species are only coupled through the denominator, that simply preserves the normalization condition.

The number of individual of each species will be typically large, so we apply the central limit theorem to the sum of random variables in this equation, obtaining the following model:

$$x_i^{t+1} = N \frac{\bar{\lambda} x_i^t + \sigma \sqrt{x_i^t} \xi_i^t + b}{\sum_{j=1}^{s} \left(\bar{\lambda} x_j^t + \sigma \sqrt{x_j^t} \xi_j^t + b \right)} \tag{3.4}$$

where $\bar{\lambda}$ and σ are the mean value and the r.m.s.d. of the distribution $P(\lambda)$, and the ξ's are uncorrelated Gaussian variables with zero mean and unit variance.

In our model the number of individuals of different species can be thought as following a multiplicative process rather similar to a Kesten process (except that for the square root). The coupling is a consequence of the constrain that keeps fixed the number of individuals in the community and that is enforced in equation (1) by the factor N and by the denominator.

3.2 The continuum limit

In order to obtain an analytically tractable equation, we achieve the continuous time limit of this model, by introducing the time interval dt in the following way:

$$\begin{aligned} \lambda &\rightarrow 1 + \lambda dt \\ b &\rightarrow b\, dt \\ \sigma &\rightarrow \sigma\, dt \end{aligned} \tag{3.5}$$

By means of this substitution, our model becomes:

$$x_i^{t+dt} = \frac{x_i^t + dt(\bar{\lambda} x_i^t + \sigma \sqrt{x_i^t} \xi_i^t + b)}{1 + \frac{dt}{N} \sum_{j=1}^{s} (\bar{\lambda} x_j^t + \sigma \sqrt{x_j^t} \xi_j^t + b)} \tag{3.6}$$

Expanding the denominator and using the fact that $\sum_j x_j = N$, we get the Langevin equation:

$$\dot{x}_i = f_i(x) + \sigma \sum_{j=1}^{s} B_{ij}(x)\xi_j \tag{3.7}$$

where:

$$\begin{aligned} f_i(x_i) &= b(1 - \frac{s}{N}x_i) \\ B_{ij}(\underline{x}) &= (\delta_{ij} - \frac{x_i}{N})\sqrt{x_j} \end{aligned} \tag{3.8}$$

The Fokker-Planck equation [56] associated to this Langevin equation is :

$$\dot{P}(\underline{x}, t) = \sum_{i=1}^{s} \partial_i \left[-f_i P(\underline{x}, t) + D \sum_j \partial_j (g_{ji}(\underline{x}) P(\underline{x}, t)) \right] \tag{3.9}$$

with $D = \frac{\sigma^2}{2}$ and:

$$g_{ij}(\underline{x}) = g_{ji}(\underline{x}) = \sum_k B_{ik} B_{jk} = (\delta_{ij} - \frac{x_j}{N})x_i \tag{3.10}$$

We search for a solution of this equation satisfying detailed balance (i.e. $P^{st} f_i = D \sum_j \partial_j (g_{ij} P^{st})$). Defining the marginalized probability distribution function:

$$p(x) = \int_0^\infty \prod_{j \neq i} dx_j P^{st}(\underline{x}) \tag{3.11}$$

we can easily obtain an equation for $p(x)$.

$$b\left(1 - \frac{sx}{N}\right) p(x) = D\frac{d}{dx}\left[\left(x - \frac{x^2}{N}\right) p(x)\right] \tag{3.12}$$

This equation can be easily solved, giving:

$$p(x) \propto x^{\beta-1} \left(1 - \frac{x}{N}\right)^{\beta(s - \frac{1}{N}) - 1} \qquad \beta = \frac{b}{D} \tag{3.13}$$

Notice that this distribution correctly shows the monodominance behavior $\delta(0)$ or $\delta(N)$ in the limit $\beta \to 0$. Finally, if we fix $\mu = \frac{\beta s}{N}$, in the limit for $N \to \infty$ we obtain:

$$p(x) = \frac{\mu^\beta}{\Gamma(\beta) x^{1-\beta}} e^{-\mu x} \tag{3.14}$$

In fig. 3.1 we plot simulation of the stationary p.d.f. for various value of the parameter β, and check the validity of (3.14).

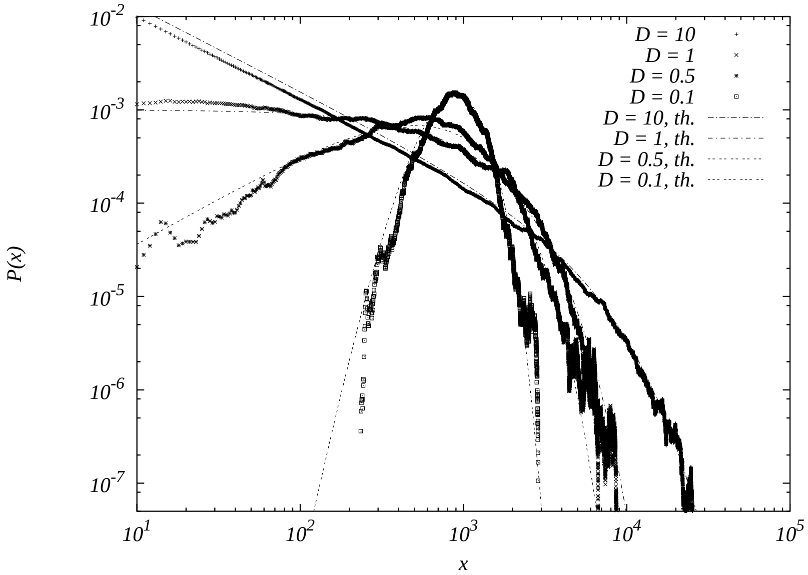

Figure 3.1: simulation of marginalized stationary p.d.f. for various values of the diffusion coefficient D, compared with theoretical curves. For all curves $b = 1$, $\bar{\lambda} = 1$ $s = 100$,$N = 10^9$ Curves are binned linearly with binning size $\delta x = 10^4$. Notice that as D increases the curve approaches the Fisher log series.

3.2.1 Grancanonical approach

Instead of having a system of stochastic differential equation, it is possible to take into account the interaction of a species with the ecosystem in an averaged way. Let us consider the Langevin equation:

$$\dot{x}(t) = b + \bar{\lambda}x - \gamma x + D\sqrt{x}\xi \tag{3.15}$$

where the parameter γ takes into account the effect of competition. In order to have normalizable solutions, we have to require that $\gamma > \bar{\lambda}$. When this condition holds, it is straightforward to show that the stationary p.d.f. satisfying detailed balance is the same as (3.14), with $\mu = -(\bar{\lambda} - \gamma)/D$. Notice that in this case, the detailed balance solution is exact; Eq. 3.15 can be considered as a grancanonical version of our model: in this case, we do not fix the number of individuals, and take into account the finite resource via the parameter γ, which may be thought as a Lagrange multiplier corresponding to the constraint of finite total population N. It is remarkable that, in the large N limit, the solution of model 3.14 and the solution of eq. 3.15 are the same: the same stationary distribution can be achieved without fixing neither the number of species, nor of individuals.

3.3 Connection with the neutral theory of biodiversity

An interesting question is if there is some relationship between our model and the neutral theory of biodiversity [4], as formulated by Volkov et al.[13] (see also [43]). More precisely, one could ask if our model arises from the continuum limit of a master equation similar to the one proposed for the neutral theory. Let us write the master equation for the generic birth and death process:

$$\begin{aligned}\dot{P}(x) = \; & d(x+1)P(x+1) + b(x-1)P(x-1) - \\ & -(d(x)+b(x))P(x)\end{aligned} \tag{3.16}$$

for $x > 1$ (we set $d(1) = 0$ to avoid that a species disappears without being replaced by another one [13]). Equation (3.16) can be converted in a Fokker-Planck equation assuming that x is a continuous variable and that $b(x)$, $d(x)$ and $P(x)$ are smooth enough that we can expand them in Taylor series. Thus, for example:

$$\begin{aligned} d(x+1)P(x+1) - d(x)P(x) = \\ = \frac{\partial}{\partial x}[d(x)P(x)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[d(x)P(x)] + \ldots \end{aligned}$$

It can be shown [56] that only the first two terms in this Taylor series do not vanish. Thus, we can derive from Eq.(3.16) the following F-P equation:

$$\dot{P}(x) = -\frac{\partial}{\partial x}J(x) \tag{3.17}$$

with:

$$\begin{aligned} -J(x) = [d(x) - b(x)]P(x) + \\ +\frac{1}{2}\frac{\partial}{\partial x}[(d(x)+b(x))P(x)] + ... \end{aligned}$$

$J(x)$ has the meaning of a probability current and we can write the general form of the stationary solution satisfying detailed balance as a function of $d(x)$ and $b(x)$ setting $J(x) = 0$:

$$p(x) = \frac{p(1)}{d(x) + p(x)} \exp\left[- \int_1^x \frac{d(x') - b(x')}{d(x') + b(x')} dx' \right] \tag{3.18}$$

One can easily check that our stationary p.d.f. (3.14) is recovered, provided the following particular choice of the birth and death coefficients:

$$\begin{aligned} d(x) &= \frac{1+\mu}{2} x + b \\ b(x) &= \frac{1-\mu}{2} x + b \end{aligned} \tag{3.19}$$

This choice [13] implies that there is balance between immigration and emigration in each species. The more general case, in which this equilibrium does not holds, is treated in [57].

3.4 Comparison with experimental data

Among the most reliable data on single-trophic species distribution of species abundance are tropical forest census [19]. In order to make a coarse graining, a Preston plot is used: data are collected via a logarithmic binning in base 2, and species at the edge between two consecutive binning are equally divided between them. Since we have a continuous probability density, we compared the histogram with the integral over the bins of the distribution with the experimental data, and made a least-square fit of the parameters β and μ, plus the normalization. We found a good agreement of our predicted curve with the histogram; in fig. 3.2 it is shown the comparison between our solution and the lognormal. Notice that the two distributions have the same number of fitted parameter. It would be interesting to compare our distribution with data collected form other kind of ecosystems, and to try to clarify the dependence of our free parameter β from ecological quantities like the immigration pressure, the speciation rate and the extinction threshold.

3.5 The Kernen's biological ensemble

It is remarkable that our distribution is the same found in studies made by Kerner in the '50 [40, 41] (see also [14] for a review) on the invariant measure in a system of Lotka-Volterra equations [15, 16] with purely asymmetric couplings.

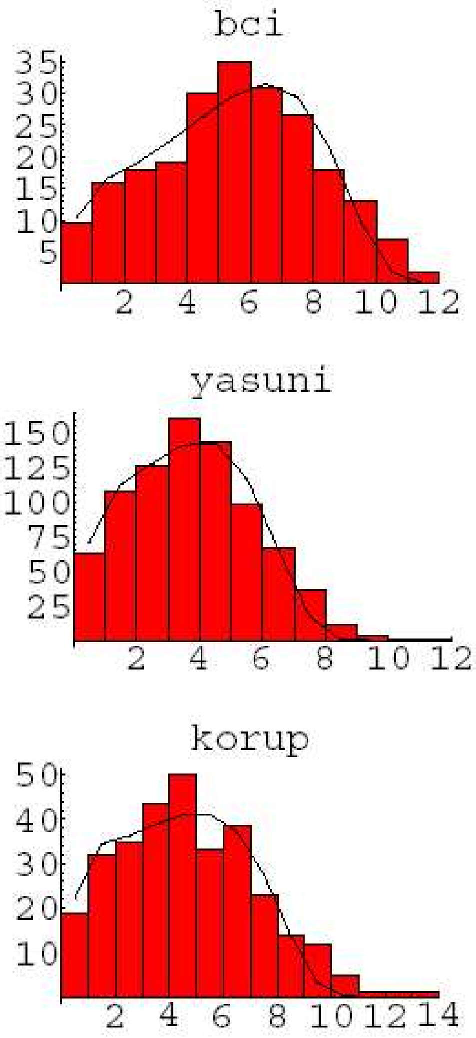

Figure 3.2: Fit of tree species abundance data taken from different tropical forests, plotted via a Preston binning, with our model. On the x-axis, it is shown the $\log 2$ of the number of individuals. Picture courtesy of I.Volkov.

Let us briefly describe his results: we consider a system of $s \gg 1$ species, whose populations are denoted by real variables $x_i, i = 1 \dots s$. These variables depend on time and evolve according to a system of Lotka Volterra equations:

$$\dot{x}_i = x_i \left(\epsilon_i + \frac{1}{\beta_i} \sum_j a_{ij} x_j \right) \tag{3.20}$$

where ϵ_i is the growth (or decay, if negative) rate of species i in absence of interaction, and $\frac{1}{\beta_i}$ are Volterra's "equivalent numbers"[16], and are defined such as the ratio of increase of species i and j should be β_i/β_j. We impose also that the matrix a_{ij} is antisymmetric: $a_{ij} = -a_{ji}$. This implies that the interaction are purely of the predator-prey type, and there is no competition or symbiosis among the species. Lotka-Volterra dynamical system are widely studied from a mathematical point of view [42]; among the results, it can be shown that stable coexistence of s species implies the presence of an interior fixed point in $\Re^{+n}$. Since we are interested in finding a stationary solution, we suppose that this fixed point $\bar{\mathbf{x}}$ exists:

$$\epsilon_i + \sum_j a_{ij} \bar{x}_j = 0 \qquad \forall i \tag{3.21}$$

and make the change of variable $y_i = \log(x_i/\bar{x}_i)$. The dynamical equation for the y_i writes:

$$\beta_i \dot{y}_i = \sum_j a_{ji} \bar{x}_j (e^{y_j} - 1) \tag{3.22}$$

It follows that the quantity:

$$G(\{y_i\}) = \sum_i \beta_i \bar{x}_i (e^{y_i} - y_i) \tag{3.23}$$

is a constant of the motion (indeed, Volterra firstly recognized the presence of this conserved quantity [16]). Notice also that the function G is a sum of terms G_i, depending only on the i-th variable. The system of equation can be now written in the form:

$$\dot{y}_i = \left(\sum_j \gamma_{ij} \partial_{v_j} \right) G(\{y_i\}) \qquad \gamma_{ij} = \frac{a_{ij}}{\beta_i \beta_j} \tag{3.24}$$

These equations are reminiscent of the Hamilton equation, with the function G playing the role of the Hamiltonian. Since this is the only evident constant of the motion, one can proceed like in statistical mechanics assuming the microcanonical hypothesis, considering all possible copies of the system compatible with the informations we have about it, and giving to all of them equal probabilities, assuming total ignorance about the system, beyond this constant of the motion. This hypothesis implies the following form for the stationary measure:

$$\rho = \rho_0 \delta(G - G_0) \tag{3.25}$$

where δ is the Dirac delta, ρ_0 is a normalization factor and G_0 is the initial value of the function G. Even if the system is not Hamiltonian, the microcanonical hypothesis allows to obtain results very similar to that of statistical mechanics. For example, it can be demonstrated an analogous of the equipartition theorem: let us show that the ensemble-average of the functions:

$$\langle T_r \rangle = \langle y_r \frac{\partial G}{\partial y_r} \rangle = \int d\rho \; \beta_i \bar{x}_i \left(\frac{x_i}{\bar{x}_i} - 1 \right) \log \frac{x_i}{\bar{x}_i} \tag{3.26}$$

are independent on the index r. We use the fact that the measure $d\rho$ can be expressed as the differential of the surface of constant G, divided by the gradient of G:

$$d\rho = \frac{dS}{|\nabla G|} \tag{3.27}$$

Since the gradient of G is orthogonal to the surface of constant G, it follows that:

$$y_r \frac{\partial G}{\partial y_r} \frac{dS}{|\nabla G|} = \hat{n} \cdot \mathbf{y_r} \; dS \tag{3.28}$$

$\hat{n}$ being the unit vector normal to the surface and $\mathbf{y_r}$ the vector with components $(0, 0, \ldots v_r, 0, 0, \ldots)$. Finally we can compute the average:

$$\langle T_r \rangle = \mathcal{N} \int_S \hat{n} \cdot \mathbf{y_r} \; dS = \mathcal{N} \int_V \nabla \cdot \mathbf{y_r} d\tau = \mathcal{N} \tau_0 \tag{3.29}$$

Here we used Gauss divergence theorem; τ_0 is the volume enclosed by the surface G_0. The final expression is independent of r; this complete our proof.

This result is somewhat an analogous of the equipartition theorem in classical statistical mechanics; further, it allows us to introduce a canonical ensemble, by considering a small subset of all the species in contact with a larger environment that acts as a thermal bath. It is straightforward to show that this construction correspond essentially to fix the value of the function T, instead of fixing the value of G. In this ensemble, every x_i, rescaled at his fixed point, is distributed in the same way. Of course, the distribution turns out to be similar to the Maxwell-Boltzmann:

$$p(y_i) \propto \exp\left(-G_i(y_i)/T\right) \tag{3.30}$$

with the parameter T playing the role of a temperature. Surprisingly, if we write explictily the form of the distribution $p(y)$ and make again the change of variable $y \to x$, we recover the same class of distributions found in 3.14:

$$p(x) \propto \frac{1}{x} \exp\left\{\frac{\beta\bar{x}}{T}\left[\frac{x}{\bar{x}} - \log\left(\frac{x}{\bar{x}}\right)\right]\right\} \propto \frac{1}{x^{1-\frac{\beta\bar{x}}{T}}} \exp\left(-\frac{\beta\bar{x}}{T}\frac{x}{\bar{x}}\right) \tag{3.31}$$

3.6 Conclusions

The model we introduce admits a family of stationary p.d.f. depending on the parameter β. This parameter fully determines the shape of the distribution: for $\beta << 1$ one recovers the Fisher log series, while for β large, one obtains a bell-shaped distribution, similar to a log-normal. As we already pointed out, both these distributions are well known in the population biology literature as possible candidate to be the ‘right’ distributions found in nature. Within this model, there is no need to make any distinction between ecological communities and metacommunities: both species abundance distribution can be fitted by the resulting stationary distribution, just by varying the range of the parameter β.

Let us also comment about similar aspects and differences between this process and the one proposed by Kesten [51] Indeed, also the Kesten process admits two different regimes, one lognormal and one with a power law tail. The main differences is that in our case the multiplicative random process is applied to the square root of the variables, rather than to the variable itself. As a consequence, in the Kesten case, the exponent of the power law tail of the stationary distribution is always greater than two, while the small β regime of our system is characterized by a power law tail over many decades, with an exponent that is always less than 1: the cutoff due to the conserved number of individuals ensures the normalization of these long-tailed distributions. In some sense, ecological systems are less “coherent” than economic systems: the longer tail is due to the fact that randomness act differently on each individuals. In the original model, as proposed in eq. 3.3, one retrieve the Kesten process if the same λ is extracted at each time step for every individuals belonging to the same species.

We also mentioned the fact that our distribution (eq. 3.14) has been already discovered in a completely different framework: the study of antisymmetric Lotka-Volterra systems with a large number of degrees of freedom. While we started from a stochastic model, and considered only competition, in that studies, the system is completely deterministic and the interactions are only of prey-predator type. It would be very interesting to discovery if the solution is the same by chance, or if this distribution can be thought as a solution of a more general model, with even more general assumptions on the dynamics and on the kind of interaction among species.

Chapter 4

A neutral model for extinctions dynamics

In this Chapter, we address the problem of calculating the lifetime probability distribution function according to the neutral theory of biodiversity [58]. We will show that the equation for the lifetimes has various critical regimes, depending on the parameters, and on the choice of the initial condition; we will provide an analytical solution and study all of these regimes. The central result of this Chapter is that, in a realistic parameter range, the solution shows (at criticality) a t^{-2} power law tail, as it was observed in the fossil record analysis. We will devote the next Chapter to the consequences of this result.

4.1 Formulation of the problem

We already underline in Chap. 2 that, according to the neutral theory of biodiversity [4, 13], the probability of having a species with a given number n of individuals evolves with time according to a birth and death master equation:

$$\dot{P}_n(t) = b^{(n-1)}P_{n-1}(t) + d^{(n+1)}P_{n+1}(t) - (d^{(n)} + b^{(n)})P_n(t) \tag{4.1}$$

where $b^{(n)}$ and $d^{(n)}$ are birth and death coefficients of the form:

$$\begin{aligned} b^{(n)} &= b_0 + b_1 n \\ d^{(n)} &= d_0 + d_1 n \end{aligned} \tag{4.2}$$

The parameters b_1 and d_1 represent the reproduction and death rate per individuals, while b_0 and d_0 are introduced to take into account several frequency dependent effects in an averaged way; among these effects are immigration, emigration and niches assembly. In the classical formulation [13], $b_0 = d_0$, but one can also consider the more general case $b_0 \neq d_0$ [57]. In order to study the lifetimes distribution, we erect an absorbing barrier for $n = 0$, imposing $b^{(0)} = d^{(0)} = 0$. The initial condition is that the new species at time $t = 0$ has just one individuals:

$$P_n(0) = \delta_{n,1} \tag{4.3}$$

Making these assumptions, $P_0(t)$ represents the probability of being already extinct at time t. From this follows that the lifetime probability distribution function is the time derivative of $P_0(t)$:

$$p(t) = \frac{d}{dt}P_0(t) \tag{4.4}$$

Our goal is to find a general solution for $p(t)$.

From a physical point of view, the problem translates in the study of an exit time problem for a stochastic process involving two different kind of dynamics: a random walk dynamics (the b_0 and d_0 terms) and a dynamics typical of simple branching process (the b_1 and d_1 terms).

We will show the behavior in the two simple limiting cases, then we will provide an analytic solution for the general case.

4.2 Exit time distribution for random walk and for branching processes

In this section we will analyze two limit cases of the problem. The first limit case is $d_1 = b_1 = 0$. In this case, the number of individuals belonging to a species evolves according to a random walk. Then we will consider the other case $b_0 = d_0 = 0$, that can be mapped in a Galton-Watson process in continuous time.

4.2.1 Case $b_1 = d_1 = 0$: the random walk

In the case $b_1 = d_1 = 0$, the number of individuals belonging to a given species performs a simple random walk. Random walks processes have a lot of application in physics and, more recently, have been proposed as a possible model for some time series extracted from the fossil record [6, 59]. The problem of exit-times distribution for a random walk process has been widely studied in the literature (see, for example, [60]). The easiest way to obtain the lifetime distribution is to take the continuum limit of eq. 4.1 and then work with the resulting diffusion equation. We show in Appendix

A an alternative way to obtain the lifetime distribution for the one-dimensional random walk problem, without achieving the continuum limit; the strategy utilized there can be used also to study more complicated models.

4.2.2 Case $b_0 = d_0 = 0$: the Galton-Watson Process

The problem with $b_0 = d_0 = 0$ has a very long history: the first formulation was presented by Galton and Watson in 1874 [61]:

> Let $p_0, p_1, p_2, \ldots$ be the respective probabilities that a man has $0, 1, 2, \ldots$ sons, let each son have the same probability for sons of his own, and so on. What is the probability that the male line is extinct after r generation, and more generally what is the probability for any given number of descendants in the male line in any given generation?

The Galton-Watson process was the first simple example of branching process[62], and was generalized in a lot of ways. It is easy to recognize that the case $b_0 = d_0 = 0$ of our equation is simply a continuous time version of the Galton-Watson process, where d_1 is the probability of dying per unit time per individuals, and b_1 is the probability of having a son per unit time per individuals.

This limiting case is interesting from an ecological point of view because the d_0 and b_0 terms happen to be small when one looks on a very large scale (like on continental scale). If one allows transitions $0 \to 1$, for example including speciation in an explicit way, the resulting stationary distribution is the celebrated Fisher log series [18]:

$$P(n) = \mathcal{N}\frac{\alpha^n}{n} \tag{4.5}$$

where $\mathcal{N}$ is a normalization constant and $\alpha = \frac{b_1}{d_1}$. In this case, the birth and death equation can be analytically solved in time: by introducing the characteristic function

$$G(x,t) = \sum_{n=0}^{\infty} P_n(t) x^n \tag{4.6}$$

the birth and death equation can be transformed in a first-order p.d.e. for the function $G(x,t)$:

$$\partial_t G(x,t) = (bx^2 - 1 + (b+1)x)\partial_x G(x,t) \tag{4.7}$$

This equation can be integrated using, for example, the characteristic method; notice that, by rescaling the time, we can set $d_1 = 1$ without loss of generality. Calling

$b_1 = b$ and taking as initial condition $G(x,0) = x$, the complete solution is:

$$G(x,t) = \frac{(1-x) - (1-bx)e^{(1-b)t}}{b(1-x) - (1-bx)e^{(1-b)t}} \tag{4.8}$$

from which we can obtain:

$$P_0(t) = G(0,t) = \frac{1 - e^{(1-b)t}}{b - e^{(1-b)t}} \tag{4.9}$$

The lifetime p.d.f. is proportional to the time derivative of $G(0,t)$:

$$p(t) = \partial_t G(0,t) = \left(\frac{1-b}{e^{(1-b)t} - b}\right)^2 e^{(1-b)t} \tag{4.10}$$

This distribution has an exponential-like shape when $d_1 - b_1$ is not too small. On the other hand, when b_1 approaches d_1, the distribution has a power law behavior with exponent -2, with a cutoff of the order $t^* = \frac{1}{1-b}$. Using the language of critical phenomena, it can be show that p(t) obeys a scaling law of the form:

$$p(t) = \frac{1}{t^2} f(\frac{t}{t^*}) \tag{4.11}$$

with $f(x) = [x/(1-e^{-x})]^2 e^{-x}$

From this distribution one can also calculate the expected lifetime for a species that is chosen at random in the ecosystem, instead of a species just born. We imagine that, via some speciation mechanism, an extinct species is immediately replaced by another one; in this case one can set as initial conditions the characteristic function associated to the Fisher log series (again, we set $d_1 = 1$):

$$G(x,0) = \frac{\log(1-xb)}{\log(1-b)} \tag{4.12}$$

is it possible to solve again the problem and compute the lifetime probability distribution function. The result is:

$$G(0,t) = \frac{1}{\log(1-b)} \log\left[\frac{be^{(1-b)t} - e^{(1-b)t}}{b - e^{(1-b)t}}\right] \tag{4.13}$$

In this case, one can easily show that the critical exponent for the lifetimes p.d.f is -1.

4.3 The general case: crossover and solution

Now, we would like to answer the question, what kind of critical behavior there is when all the coefficients are different from zero and $b_0 \to d_0$, $b_1 \to d_1$. One may argue that, typically, species living for longer time should have larger population. In the large population limit, the b_0 and d_0 term can be neglected with respect to b_1 and d_1. So, we expect the t^{-2} regime to occur *later*, i.e. for larger times, that the $t^{-\frac{3}{2}}$ regime. Numerical simulations suggests that in the critical case $b_0 \to d_0$ and $b_1 \to d_1$, the crossover time is proportional to the ratio b_0/b_1.

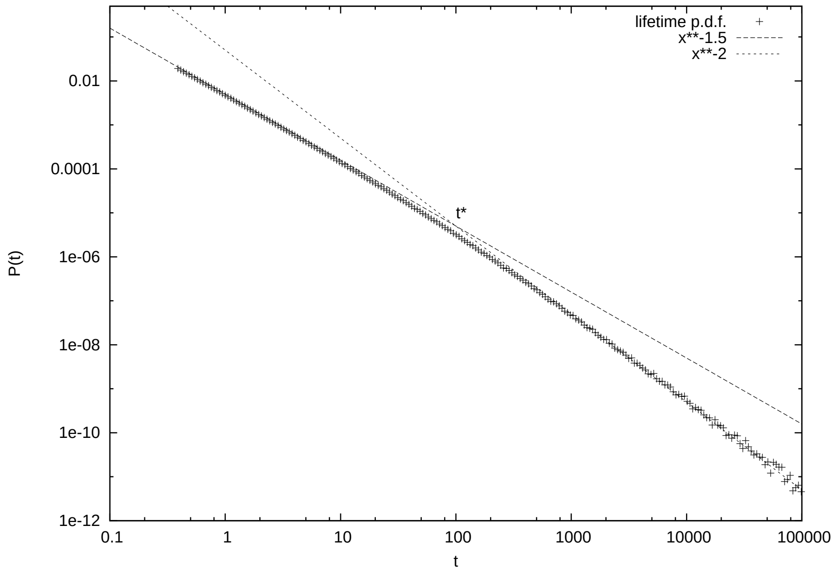

Figure 4.1: numerical sample of the lifetime probability distribution function with parameters $d_1 = 1$, $b_1 = 1 - 10^{-5}$, $b_0 = d_0 = 10$. Notice the crossover between the two regimes.

In the Appendix B, we show how is it possible to calculate analytically the distribution for any choice of the parameters; now, we consider the solution in the case $b_1 = d_1$ and $b_0 = d_0$. Notice that, by a time rescaling, we can alway fix one of the two parameters; we make the choice $d_1 = b_1 = 1$ and $b_0 = d_0 = r$. In this case, we show in the Appendix that $g_0(s)$, which is the Laplace transform with respect to time of the probability of being extinct $P_0(t)$, has the following expression:

$$sg_0(s) - 1 = \frac{\int_1^\infty \frac{dy}{y}\, e^{-sy}(1-\frac{1}{y})^r}{\int_1^\infty dy\, e^{-sy}(1-\frac{1}{y})^r} = \frac{1}{\partial_s \log N(s,r)} \tag{4.14}$$

where we have defined:

$$N(s,r) = \int_1^\infty \frac{dy}{y} e^{-sy} (1 - \frac{1}{y})^r \tag{4.15}$$

We want to analyze the small s behavior of this quantity, first at fixed r, then taking $r \to \infty$ and then the limit $s \to 0$. In this way, we would like to recover the two regimes and guess the scaling of the crossover time t^*.

4.3.1 Asymptotic scaling at fixed r

For fixed r and $s \to 0$, the leading contribution to the integral comes from values of $y \gg 1$. This implies that we can estimate the integral just by approximating the term in parenthesis with 1. The exponential e^{-sy} essentially fix an upper cutoff on the integral. Essentially, we can approximate in this limit the function $N(s,r)$ with the following expression:

$$N(s,r) = \int_1^{\frac{1}{s}} \frac{dy}{y} \tag{4.16}$$

In this case, it is very easy to deduce the small-s behavior of $N(s,r)$:

$$\lim_{s \to 0} N(s,r) \sim \log s \tag{4.17}$$

This implies the following small-s behavior for $g_0(s)$:

$$g_0(s) \sim \frac{1}{s} - \log s \tag{4.18}$$

Recalling the definition of $g_0(s)$, by means of the Tauberian theorem [52] we can conclude that for large t:

$$P_0(t) \sim 1 - \frac{1}{t} \tag{4.19}$$

The lifetimes are proportional to the time derivative of $P_0(t)$, and thus have a t^{-2} power law tail. This is a rigorous proof that the exponent is the same, regardless of the value of r.

4.3.2 Asymptotic scaling at large r

In order to analyze the power law regime for times smaller than the crossover time t^*, we perform the limit $r \to \infty$, then we let s go to zero. To obtain the asymptotic behavior in this case, we exponentiate the term in parenthesis:

$$\begin{aligned} N(s,r) = &\quad \textstyle\int_1^\infty \frac{dy}{y} \exp\left[-sy + r\log(1-\frac{1}{y})\right] \quad = \\ = &\quad \textstyle\int_1^\infty \frac{dy}{y} \exp\left[-sy - \frac{r}{y} + \frac{r}{y^2} - \dots\right] \end{aligned} \tag{4.20}$$

We make the substitution $x = \sqrt{\frac{s}{r}}y$:

$$N(s,r) = \int_{\sqrt{\frac{s}{r}}}^{\infty} \frac{dx}{x} e^{-\sqrt{rs}\left(x+\frac{1}{x}-\sqrt{\frac{s}{r}}\frac{1}{x^2}+\dots\right)} \tag{4.21}$$

Due to the order of the limits, we can consider the factor $\sqrt{rs}$ being very large. We can consider just the first term of the expansion of the logarithm. The behavior of the integral can be evaluated with the saddle point method: the maximum of the argument of the exponential occurs at $x^* = 1$. We perform a second-order Taylor expansion around this maximum:

$$N(s,r) \approx e^{-\sqrt{rs}} \int_{\sqrt{\frac{s}{r}}}^{\infty} e^{-2\sqrt{rs}(x-1)^2} \approx e^{-\sqrt{rs}} \frac{\sqrt{\frac{\pi}{2}}}{(rs)^{\frac{1}{4}}} \tag{4.22}$$

Performing the Gaussian integral, we can study the asymptotic behavior of $g_0(s)$ in this case:

$$sg_0(s) - 1 = \frac{1}{\partial_s \log N(s,r)} = -\frac{1}{\sqrt{\frac{r}{s}} + \frac{1}{4s}} \tag{4.23}$$

Again, due to the order of the limits, we can neglect the second term in the denominator, obtaining finally:

$$sg_0(s) - 1 \sim -\sqrt{s} \quad \rightarrow \quad P_0(t) \sim 1 - \frac{1}{\sqrt{t}} \tag{4.24}$$

where, also in this case, we made use of the Tauberian theorem. In this limit, we recover as expected the random walk behavior; we can also make an estimate of the scaling of the cutoff with r: the approximations made are all valid when $\sqrt{rs}$ is a large number. From this fact, we can argue that the crossover time should be inversely proportional to r. More precisely, $g_0(s)$ must obey a scaling law of the form:

$$p(t) = \frac{1}{t^2} f\left(\frac{t}{r}\right) \tag{4.25}$$

where the function $f(x)$ should grow like $\sqrt{x}$ for small value of the argument (i.e. when $x \ll 1$) and approach a constant when x becomes large. In the figure we show the validity of this scaling law collapsing lifetime curves for different values of r.

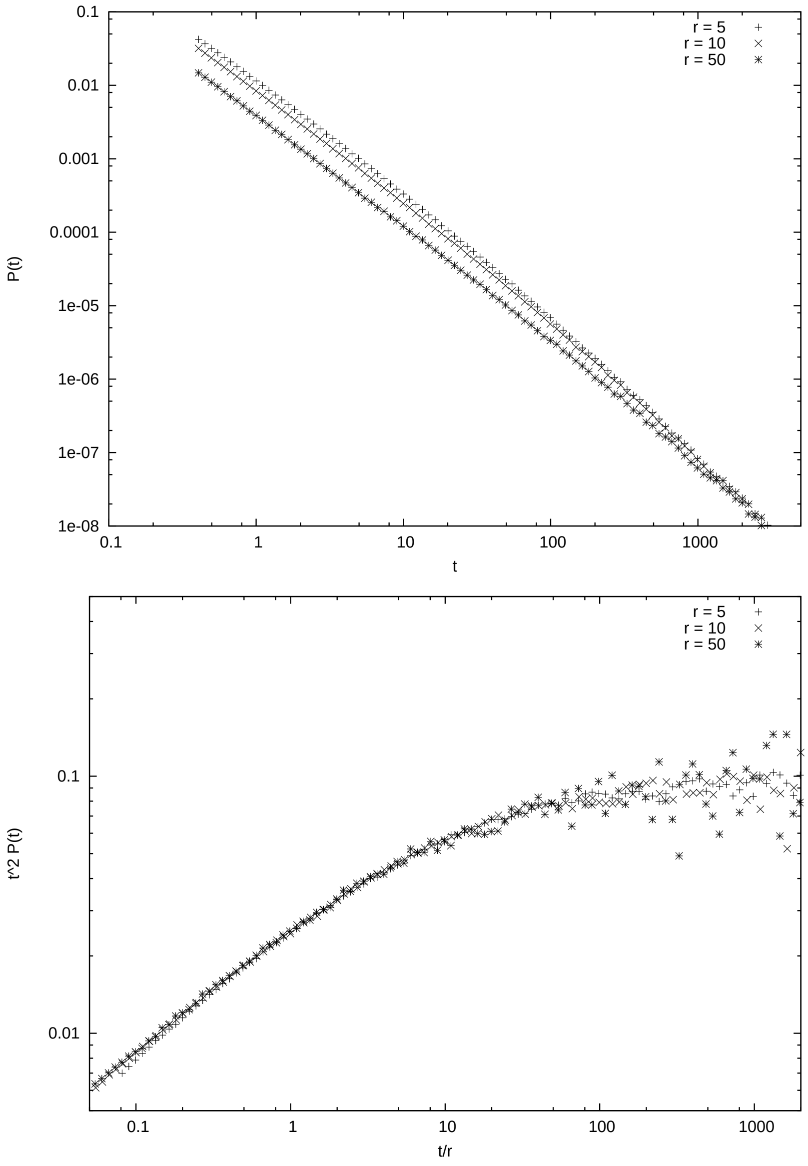

Figure 4.2: Check of the scaling function 4.25. Plot of numerical sample of $t^2P(t)$ vs. t/r for different value of r, shown in the picture.

4.4 Conclusions

In this section we have shown the analytical solution for the species lifetime distribution in a neutral model. Strikingly, this distribution has the correct critical behavior, meaning that in the limit $b_1 \to d_1$ shows a power law tail with exponent -2, as it is observed in some analysis from the fossil record. This exponent, in our model, is a simple consequence of the branching structure of the process, that reduces to a Galton-Watson process in the limit $b_0 = d_0 = 0$. It is interesting that such a simple model shows at least 4 different regimes for the lifetimes, one exponential, and the other characterized by a power law with exponent -2, $-3/2$ and -1, depending essentially on the and on what kind of initial distribution is taken.

From a biological point of view, the main result is that the -2 exponent does not change in the general case $b_0, d_0 \neq 0$: loosely speaking, the reason is that these coefficients are relevant for small population sizes, and small population sizes are related to short timescales. Despite this heuristic argument , the result is not trivial: it is known [63] that there are stochastic models related to this one that exhibit a dynamical phase transition in the lifetime exponent, in the sense that the lifetimes are distributed according to a power law, and the exponent vary in a continuous way by varying any of the parameters.

The robustness of this exponent against small-scale modification of the dynamics is a good hint that we are on the right way to understand the mechanism underlying the power-law behavior of genera lifetimes, , but before making biological claims, we have to consider a number of questions:

- Neutral theory deals with single-trophic level, living system on timescale of the order of years. Is it possible to “scale up” the theory, and deduce properties of the systems on the fossils timescale? Can we still neglect predator-prey interactions and fitness differences, even if we collect data from very different species?

- It seems like the species lifetimes are distributed exponentially, the power law is present when one looks at the genera lifetime distribution. Is it compatible with our scenario? What is the real meaning of the coefficients b_1 and d_1? In other words, what drives the system near to (or away from) criticality?

In the next Chapter we will try to give an answer to all these questions.

Chapter 5

Population dynamics on geological timescale

In Chap.4, we calculated the species lifetime distribution in the framework of the neutral theory of biodiversity. We also pointed out that the predictions of the model are consistent with the observations of the fossil record; more precisely, looking at a species from the time of its first appear to his death, one can have either an exponential or a t^{-2} power law, depending on how much close to criticality the system is.

In the following, we will assess the possible consequences of our result; in particular, we will try to understand what determines the closeness to criticality of species and genera, and, in particular, why genera display a power law behavior in the lifetimes, while species don't. In order to verify the consistency of our approach, we calculate in the same framework another debated statistical quantity: the distribution of species into genera.

5.1 What do the birth and death rates mean?

How meaningful are the prediction of a neutral model on a geological timescale? It is well known that evolution can play an important role also on short timescales: a famous example is the change of color of the peppered moth, *Biston Betularia,* in the industrialized cities of Great Britain around 1850s. Of course, such dramatic changes of the environment (in this case, trees becoming darker due to pollution) on these timescales are not so common, and without them, one may think that it is unlikely that an individuals, or a class of individuals may gain a relevant fitness advantage over the population. This is by no means true on geological timescale: for sure evolution did play a fundamental role in determining the fate of species in the history of life. Is it possible to neglect the fitness difference of individuals belonging to different species, and obtain a simple stochastic model also on these timescale?

To answer these question, we outline an aspect of neutral theory which is often not so considered. A strategy to test the validity of the neutral theory and obtain a reasonable functional form of the birth and death coefficients is to *measure* directly the birth and death rate as a function of the population size of the species in the ecosystem, rather than measuring the species abundance and trying to deduce the birth and death coefficients. Attempt to measure the birth and death coefficients in a tropical forests have been made [19], and the result is that the measured points scatter broadly; it is very hard to observe patterns or relevant correlation on these data.

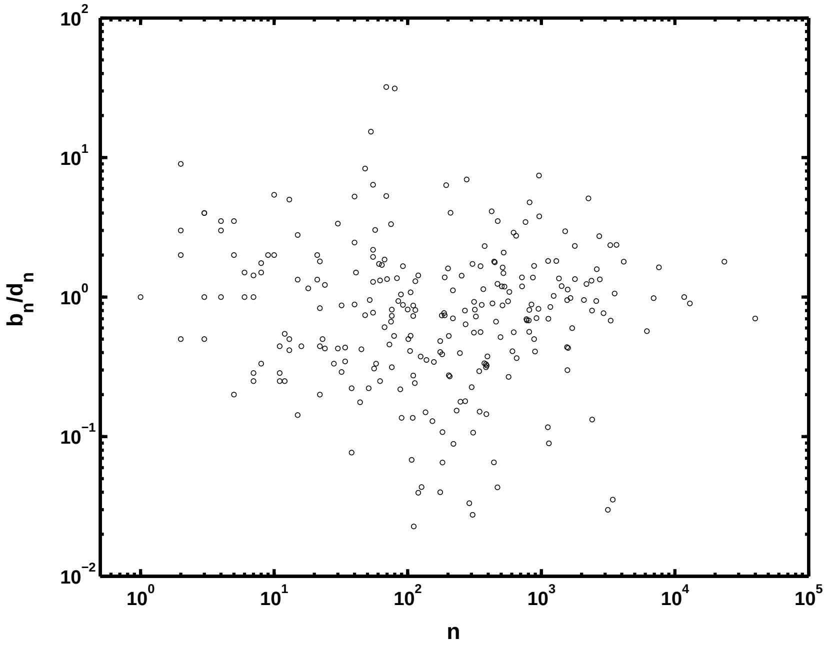

Figure 5.1: Measured value of b_n/d_n as a function of n. Data are collected over a several-years period in the Barro-Colorado island tropical forest. Figure courtesy of I.Volkov.

A first conclusion may be: the birth and death rates do not depend just on the number of individuals, but on a large number of factors that neutral theory does not take into account. Neutrality does not hold in nature and the whole theory has to be rejected.

Anyway, we saw that neutral theory can make very general and elegant predictions on distributions and patterns which are hard to obtain in other ways; it would be nice to do a kind of weak form of neutral claim, to justify the approximation without being in contrast with the observations. A reasonable way to do this is the following: obviously the birth and death rate do not depend on the population size only, but depend on a very large number of factors, and many of them may be also quite important. The parameters in the neutral theory are *effective* parameters, meaning that they take into account, in an averaged way, a lot of phenomena (like immigration, niche assembly and many other) that the theory does not include in an explicit way. In conclusion, we can express again the neutral hypothesis, saying that it is possible to "average out" all the effects that do not depend on the population size only, by means of an appropriate choice of the effective coefficients of the theory. If we take this as a definition of neutrality, we can try to extend the prediction on a larger scale and see if we obtain something meaningful.

5.2 Population dynamics on geological timescale

In Chap. 4, we saw that the b_0 and the d_0 terms play no role when one look on a very long timescale. Thus, let us assume that the populations of our species evolve according to a simple Galton-Watson process with birth rate per individual $b_1 = b$ and death rate $d_1 = d$. We already saw that neglecting b_0 and d_0 implies that the population of a species, with the condition that the species is still alive, admits as a stationary distribution the Fisher log series:

$$\langle \phi_n \rangle \propto \frac{1}{n}\alpha^n \qquad \alpha = \frac{b}{d} \tag{5.1}$$

Now, let us introduce the speciation rate per individuals σ: new species are introduced in the ecosystem at a rate σN, where N is the total population. We can also introduce a genera creation rate per individuals γ, a family creation rate and so on. The underlying idea is to try to approximate the full genealogical tree of all species with a random process of the Galton-Watson type. In some sense, our model is a hierarchic combination of Galton-Watson processes. It is clear that the biological meaning of the parameters become more and more abstract going up in this hierarchy: for example, it is well known that the speciation rate is far from being constant [64] but depends strongly on time and on the considered kind of species. Anyway, it is reasonable to do an estimate of a "canonical" speciation rate [64]; furthermore, we must recall that we are talking about effective parameters. Real taxonomic trees are far from being random trees, but we can hope that they can be roughly approximated by random trees, as far as we are interested in calculating statistical quantities.

Now, let us impose some reasonable conditions on the parameters. First of all, speciation are rare with respect to births of individuals belonging to the same species. Genera creation rates are small with respect to speciation: creation of a new genera involves strong modification of the phenotype, and this implies the overcoming of larger evolutionary barrier. This implies that there is a hierarchy also on the order of magnitude of these parameters:

$$b \ll \sigma \ll \gamma \ll \ldots \tag{5.2}$$

Another condition we must impose is that the whole system, being composed by a very large amount of individuals, should be almost critical:

$$\frac{1}{d}(b + \sigma + \gamma + \ldots) < 1 \qquad \frac{b + \sigma + \gamma + \ldots}{d} \sim 1 \tag{5.3}$$

It is also possible to introduce these parameters without introducing in an explicit way a speciation rate. Essentially, the parameters b and d are related to the typical timescale of the system (i.e. the lifetime of an individual should be of the order $\frac{1}{d}$), and the typical population size, meaning that the size of the population is of the order:

$$\langle n \rangle = \frac{\alpha}{(\alpha - 1)} \frac{1}{\log(1 - \alpha)} \qquad \alpha = \frac{b}{d} \tag{5.4}$$

These two condition are enough to determine the parameters b and d in an effective way, without any need to introduce speciation rate or any further parameter.

For simplicity, we will consider only the first two levels of this hierarchy in the following (species and genera); the results are easily generalizable to the upper levels.

We will outline in the following two very interesting consequences of these assumptions.

5.3 First consequence: lifetime distribution of species and genera

First of all, we can easily calculate the lifetime distribution of species, genera, or any grouping in the hierarchy. Since individuals do not interact in this model, the number of individuals in a genera are still distributed according to a Fisher log series:

$$g(n) = \frac{1}{n}\alpha'^{n} \qquad \alpha' = \frac{b + \sigma}{d} \tag{5.5}$$

We have already calculated the lifetime probability distribution function for this process in sec. 4.2.2. Notice that, due to the introduction of the speciation rate σ, the branching tree for the whole genera is more close to criticality than the branching tree for species, meaning that α' is more close to 1 than α. We can deduce the same phenomenon without introducing explicitly a speciation rate, simply looking at the fact that the r.h.s of Eq. 5.4 diverges when $\alpha \to 1^-$. This implies that large population sizes correspond to values of α more close to one. Fit of species abundance distributions [18] typically provide values of α around $\alpha \sim .98$. Looking at lifetimes curves, as provided by eq. 4.10, it is very hard to observe the power law regime, especially if one consider also the experimental error. In this case, the curve is much more similar to an exponential. According to our argument, genera should have an higher value of the parameter α, thus it is possible to explain the observed power law [34, 38] without referring to correlation on large scales.

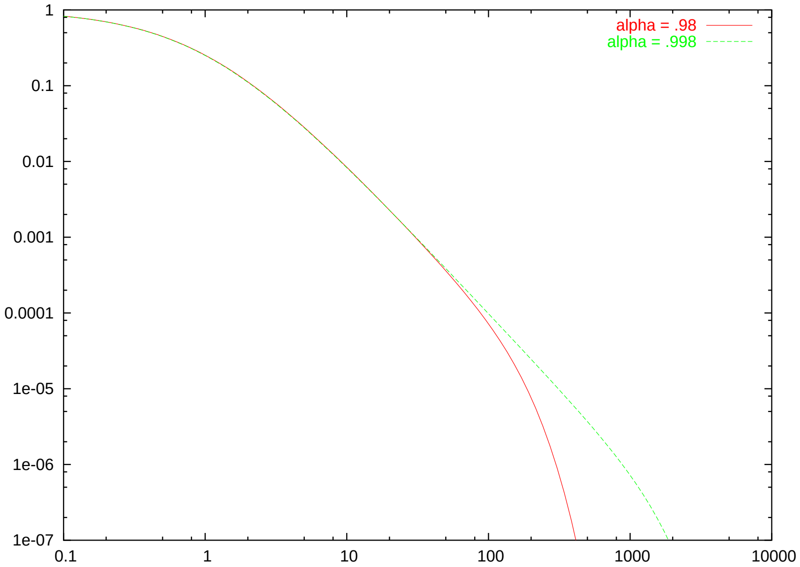

Figure 5.2: Plot of lifetime distribution (eq. 4.10) for $\alpha = .98$ and $\alpha = .998$. In the first case is very hard to distinguish the power law regime.

5.4 Second consequence: distribution of species into genera

Within this simple model, we can also calculate the genera abundance curve, i.e. the probability of having a genera with a number s of species. The problem of calculating this distribution assuming reasonable hypothesis is widely debated in the literature, from the proposal of Yule ([65], a good review with the most interesting variants of the model can be found in [66]), to more sophisticated and modern models [67, 68]. The prediction of many of these model is that also species are distributed into genera according to a Fisher log series. The simpler hypothesis to obtain this conclusion is that each species has a fixed speciation rate and extinction rates [67]. What happens is that the dynamics followed by species is the same Galton-Watson type of dynamics followed by individuals in our model. This distribution fit rather well with experimental data; however, it is preferable to explain these data starting from the population dynamics, rather than taking the species as fundamental variables.

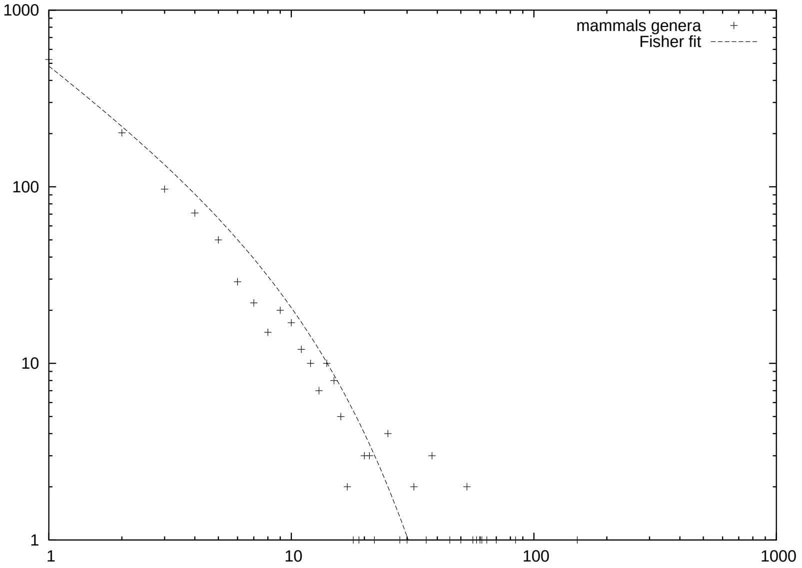

Figure 5.3: Distribution of species into genera for the Mammals. The curve is a fit according to a Fisher log series with $\alpha = 0.91, \mathcal{N} = 530$. Data taken from [69].

5.4.1 Population dynamics approach

We calculated in the previous section the probability $g(N)$ of having a genera with N individuals and the probability $f(n)$ of having a species with n individuals. Our goal is to obtain from these two distributions the probability $p(s)$ of having a genera with s species. We require that $g(N)$ should be proportional to the sum over all the possible ways of arranging any number of species with any number of individuals, with the constraint of the total number of individuals being N, weighted with the probability of the different configurations. The approximation is that typically the species i reach stationarity, even if they do not live for an infinite time. This approximation should give good results in the case of long lifetimes (rare extinction events).

The equation is:

$$g(N) = \sum_{s=1}^{\infty} p(s) \sum_{\{n_s\}} \delta(N - \sum_{i=1}^{s} n_i) \prod_{i=1}^{s} f(n_i) \tag{5.6}$$

where $\{n_s\} = \{n_1, n_2 \dots n_s\}$. Our goal is to calculate $p(s)$ by means of this equation. Let us introduce an integral representation for the Dirac delta:

$$g(N) = \frac{1}{2\pi} \sum_{s=1}^{\infty} p(s) \sum_{\{n_s\}} \int_{-\infty}^{\infty} d\omega \ \exp\left[-i\omega \left(N - \sum_{i=1}^{s} n_i\right)\right] \prod_{i=1}^{s} f(n_i) \tag{5.7}$$

Now, we can factorize each n_i:

$$g(N) = \frac{1}{2\pi} \int_{-\infty}^{\infty} d\omega \ e^{-i\omega N} \sum_{s=1}^{\infty} p(s) \sum_{\{n_s\}} \prod_{i=1}^{s} f(n_i) \exp\left(i n_i\right) \tag{5.8}$$

Introducing $\hat{f}(w)$, the Fourier transform of $f(n)$, we obtain:

$$g(N) = \int_{-\infty}^{\infty} d\omega \ e^{-i\omega N} \sum_{s=1}^{\infty} p(s) \left[\hat{f}(-\omega)\right]^{s} \tag{5.9}$$

We define now $G(x)$, the characteristic function of $p(s)$

$$G(x) = \sum_{i=1}^{\infty} p(i) \ x^{i} \tag{5.10}$$

By introducing the inverse Fourier transform of $g(N)$, we finally obtain the result:

$$\hat{g}(\omega) = -G\left[\hat{f}(\omega)\right] \tag{5.11}$$

Making an explicit Fourier transform of the Fisher Log series, we can make the substitution:

$$\hat{f}(\omega) = \frac{1-\alpha e^{-i\omega}}{1-\alpha} \qquad \hat{g}(\omega) = \frac{1-\alpha' e^{-i\omega}}{1-\alpha'} \tag{5.12}$$

This allow us to find an explicit form for $G(t)$:

$$G(t) = \frac{\log\left\{1-\frac{\alpha'}{\alpha}\left[1-(1-\alpha)^t\right]\right\}}{\log(1-\alpha')} \tag{5.13}$$

Notice that, when $1-\alpha$ is not too small, it is possible to expand the exponential in Eq. 5.13 to the first order, and recover again the Fisher log series. Thus, is species are far from criticality, the distribution of species into genera has the same form as the distribution of individuals into species. In the language of stochastic processes, the fact that species have an exponential lifetime in this regime, implies that the process is Markovian also at the species level: one can consider a speciation and extinction rate per species, without worrying about the internal structure (essentially, the number of individuals per species acts as a sort of memory). This is no more true when one looks at higher levels in this hierarchy (for example, looking at the distribution of genera into families and so on): genera do not have an exponential lifetime, and this implies that the extinction rate for a genera depends on its age.

To obtain an explicit solution from Eq. 5.13, we introduce the parameters $\gamma = (\alpha'-\alpha)/\alpha'$ and $\beta = -\log(1-\alpha)$. We can write the function $G(t)$ in this way:

$$G(t) = \frac{\log(\alpha'/\alpha) + t\log(1-\alpha) + \log\left(1-\gamma e^{\beta t}\right)}{\log(1-\alpha')} \tag{5.14}$$

The third term in the numerator allows the following Taylor expansion:

$$\log\left(1-\gamma e^{\beta t}\right) = -\gamma e^{\beta t} - \frac{\gamma^2}{2}e^{2\beta t} - \frac{\gamma^3}{3}e^{3\beta t} - \dots \tag{5.15}$$

from which we finally obtain:

$$p(s) = \frac{\beta^s}{s!\log(1-\alpha')}\sum_{n=1}^{\infty}\gamma^n n^{s-1} = \frac{\beta^s}{s!\log(1-\alpha')}Li_{(1-s)}(\gamma) \qquad s>1 \tag{5.16}$$

where $Li_{(1-k)}(x)$ is the Polylogarithmic function.

5.5 Conclusions

In this Chapter, we underline the fact that the neutral approximation, on large timescales, correspond essentially to consider species, genera, families and so on as random trees which are closer to criticality as long as one considers higher groupings in this hierarchy. We tried to guess how this approximation can be compared with experimental evidences, and found that all the predictions about lifetimes and abundance distributions are coherent with the empirical observations. It would be interesting to analyze data from higher level in the hierarchy (i.e. distribution of genera into families), to see if we are able to predict substantial deviation from the Fisher Log series.

Conclusions and perspectives

> *It was the "discovery" of the importance of the individual which lead Darwin from typological to population thinking. It was this that made him realize that the struggle for existence due to competition, so vividly described by Malthus, was a phenomenon involving individuals and not species. By introducing population thinking, Darwin produced one of the most fundamental revolution in biological thinking*
>
> Ernst Mayr, *The growth of Biological Thought* [28]

We briefly recall the results of this work:

- We introduced a neutral model based on a multiplicative stochastic process for the dynamics of the number of individuals in species belonging to the same trophic level. The result are compared with data from tropical forests, and give a good agreement.

- In a similar framework (the neutral theory of biodiversity), we calculate in an explicit way the distribution of species lifetime. This problem shows several kind of critical behaviors, depending on the parameter range. We studied these critical behaviors, as well as the scaling behavior of the solution.

- We assess the consequence of the lifetime p.d.f. and predict the expected lifetime of species and genera and the distribution of species into genera.

The main effort of this research line is to find a simple, individual-based dynamics which can be used as a zero-order model for the study of ecosystems. A deep study of these simple models can bring to simple and elegant explanation of apparently complicated, or counterintuitive, phenomena.

Let us mention a couple of example: in the model we introduced in Chap. 3, we are assuming that the species belong to the same ecological community (see Sec.

1.1). Looking at the solution of the model, there is no need to make a distinction between a community, and a metacommunity: the model is able to predict the species abundance in both cases, and the two different distribution correspond to different regimes of the parameter β: for small β, one retrieve a curve similar to a Fisher log series , which is observed in the species abundance of metacommunities [18], while for greater values of β, the distribution became bell-shaped, similar to the lognormal distribution proposed as solution for the species abundance in the communities [22].

Another example is the lifetime distribution of species and genera (Chap. 4 and 5). Here, what happens seems the opposite as the normal critical behavior from classical statistical mechanics: essentially, in critical systems, it is possible to see deviation from criticality at large scale, due to finite size effects. Here, the system on large scale is closer to the critical point that the system observed on smaller scale. The theory is able to explain this phenomenon, with simple assumptions on the parameters choice.

The advantage of population-based model is that, obviously, there is no other characteristic scale than the individual one, which is the lowest possible scale for an ecology model. Often, it is better to assume very simple hypothesis on this scale, than more complicated on the species scale. Looking at an ecosystem as an ensemble of interacting species (and not individuals) implies neglecting population dynamics; we saw how population dynamics can be very important in determining ecological patterns.

Due to the extreme simplicity, these model are amenable of several interesting generalization. A very interesting generalization is the inclusion in the model of the spatial scale. This research line seems to be very promising [24], even if it is very hard to obtain analytical results when also space is taken into account. Another crucial point is to include interactions in these models [70]. It is very hard to include in a simple model both demographic stochasticity, and organization, thought as interaction among species, without introducing too many parameters. Still, organization seems to be important in ecosystems, and a more refined ecological theory should provide also an explanation for food webs patterns [71, 72].

Appendix A

Asymptotic behavior of the exit times distribution for the one-dimensional random walk in the discrete case.

In this Appendix, we address the problem of calculating the exit times p.d.f. for a one dimensional random walk process without achieving the continuum limit. This problem may be thought as the simplest possible case of birth-death process, when the transition rates are simply constant. It has been pointed out recently [73] that for less trivial examples (like epidemics models) the approximation of studying the Fokker-Planck equation which arises as continuum limit of the process may bring to misleading results. It is thus useful to have analytic tools for dealing with these problem also in the discrete case.

In this case, we consider the birth and death equation:

$$\dot{P}_n(t) = b(n-1)P_{n-1}(t) + d(n+1)P_{n+1}(t) - (d(n) + b(n))P_n(t) \tag{A.1}$$

only for $n \geq 1$. The lifetimes distribution are proportional to minus the time derivative of $\sum_{n=1}^{\infty} P_n(t) = \mathcal{P}(t)$. We set as initial condition that the species has just one individuals:

$$P_n(0) = \delta_{n,1} \tag{A.2}$$

We introduce the Laplace transform with respect to time of the probabilities P_n:

$$\tilde{P}_n(s) = \int_0^{\infty} dt\, e^{-st} P_n(t) \tag{A.3}$$

Eq. A.1 became:

$$s\tilde{P}_n(s) = \delta_{n,1} + d(n+1)\tilde{P}_{n+1}(s) + b(n-1)\tilde{P}_{n-1}(s) - [b(n) + d(n)]\tilde{P}_n(s) \tag{A.4}$$

where, as usual, $b(n)$ and $d(n)$ are the birth and death rates as a function of the number of individuals n. Again, let us introduce the Laplace transform with respect to time of the characteristic function:

$$G(z,s) = \sum_{n=1}^{\infty} z^n \tilde{P}_n(s) \tag{A.5}$$

The function G obeys to the following equation:

$$sG(z,s) = z + \left[\left(\frac{1}{z}-1\right) d(z\partial_z) + (z-1)b(z\partial_z)\right] G(z,s) - \tilde{P}_1(s)\frac{1}{z} d(z\partial_z) z \tag{A.6}$$

From the knowledge of the function G, we can express the probabilities $\tilde{P}_n$ as a contour integral in the complex plane by means of the Cauchy integral formula:

$$\tilde{P}_n(s) = \oint_{|z|=R} \frac{dz}{2\pi i} \frac{G(z,s)}{z^{n+1}} \tag{A.7}$$

where R is such that in the circle $|z| < R$ there are no singularities of $G(z,s)$. Let us note that $G(1,s) = \mathcal{P}(s)$; from this one can show also the following relation:

$$G(1,s) = \frac{1 - d(1)\tilde{P}_1(s)}{s} \tag{A.8}$$

A.1 The random walk case

Let us solve the random walk case. By means of a time rescaling, we can set $d(n) = 1$ and $b(n) = b$ without loss of generality. Eq. A.6 gives:

$$G(z,s) = \frac{z(z - \tilde{P}_1(s))}{zs - (z-1)(bz-1)} \tag{A.9}$$

The function G has two poles $z_\pm$:

$$z_\pm = \frac{b + 1 + s \pm \sqrt{(b-1)^2 + 2s(b+1) + s^2}}{2b} \tag{A.10}$$

Since $s > 0$ the poles lie on the real axis, and are such that $0 < z_- < 1 < z_+$. We construct the following path on the complex plane, avoiding all the singularities (see fig.A.1):

$$0 = \oint_{\Gamma} G(z,s)\frac{dz}{z^{n+1}} = \oint_{\Gamma_1} G(z,s)\frac{dz}{z^{n+1}} + \oint_{\Gamma_2} G(z,s)\frac{dz}{z^{n+1}} + \oint_{|z|=\infty} G(z,s)\frac{dz}{z^{n+1}} \tag{A.11}$$

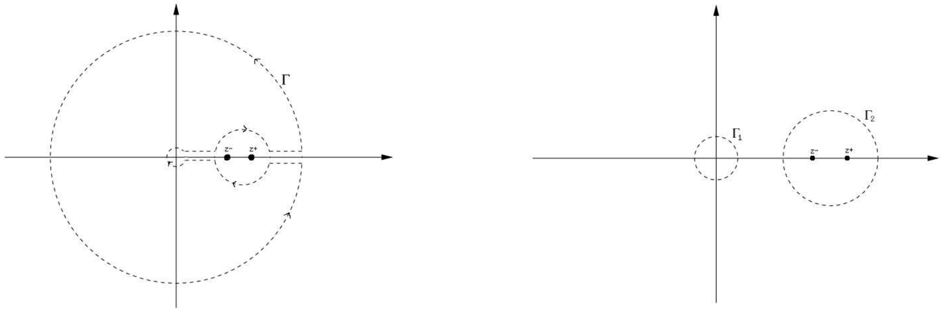

Figure A.1: Integration contour in the complex plane.

The last integral of eq.A.11 is equal to zero due to the Jordan lemma. Calculating the residues, we obtain:

$$\tilde{P}_n(s) = z_-^{-n}\frac{z_- - \tilde{P}_1(s)}{b(z_- - z_+)} + z_+^{-n}\frac{z_+ - \tilde{P}_1(s)}{b(z_+ - z_-)} \tag{A.12}$$

We expect that, for $b < 1$, $\lim_{n\to\infty} \tilde{P}_n(s) = 0$. From this follows that:

$$\begin{aligned} \tilde{P}_1(s) &= z_-(s) \\ \tilde{P}_n(s) &= \frac{z_+^{-n}}{b} \qquad n > 1 \end{aligned} \tag{A.13}$$

and, by means of A.8. we finally obtain:

$$\tilde{\mathcal{P}}(s) = \frac{1 - \tilde{P}_1(s)}{s} = \frac{1 - z_-(s)}{s} \tag{A.14}$$

Using this result, the asymptotic scaling of the lifetimes is determined by:

$$\lim_{s\to 0} \tilde{\mathcal{P}}(s) \sim \begin{cases} s^0 & b < 1 \\ s^{-1} & b > 1 \\ s^{-1/2} & b = 1 \end{cases}$$

and, by means of the Tauberian theorem:

$$\mathcal{P}(t) \sim \begin{cases} e^{-t/\tau} & b < 1 \\ const & b > 1 \\ \sqrt{t} & b = 1 \end{cases}$$

The exit times distribution is, as usual, proportional to the time derivative of $\mathcal{P}(t)$.

Appendix B

Derivation of the lifetime p. d. f. for the neutral theory

In this Appendix we would like to show the calculation to obtain the Laplace transform of the probability of being extinct at time t according to the birth and death equation 4.1:

$$\dot{P}_n(t) = b^{(n-1)} P_{n-1}(t) + d^{(n+1)} P_{n+1}(t) - (d^{(n)} + b^{(n)}) P_n(t) \tag{B.1}$$

with the birth and death coefficients being:

$$\begin{aligned} b^{(n)} &= b_0 + b_1 n \\ d^{(n)} &= d_0 + d_1 n \end{aligned} \tag{B.2}$$

As we said, we take as initial condition:

$$P_n(0) = \delta_{n,1} \tag{B.3}$$

Our goal is to calculate $p(t) \propto \partial_t P_0(t)$ in the general case $b_0 \neq d_0 \neq b_1 \neq d_1 \neq 0$. First of all, let us define the Laplace tranforms with respect to time of the probabilities $P_n(t)$:

$$\tilde{P}_n(s) = \int_0^\infty dt e^{-st} P_n(t) \tag{B.4}$$

the equation for the $\tilde{P}'s$ writes:

$$s\tilde{P}_n(s) = \delta_{n,1} + b^{(n-1)} \tilde{P}_{n-1}(s) + d^{(n+1)} \tilde{P}_{n+1}(s) - (d^{(n)} + b^{(n)}) \tilde{P}_n(s) \tag{B.5}$$

Now, we multiply the k-th equation by x^k and sum all the equations; we finally obtain an equation for $\tilde{G}(x, s)$, the laplace transform with respect to time of the generating function $G(x,t)$:

$$\begin{aligned} & [b_1 x^2 + d_1 - (b_1 + d_1)x]\, \partial_x \tilde{G}(x,s) + \\ +\frac{1}{x} \quad & [b_0 x^2 + d_0 - (b_0 + d_0 + s)x]\, [\tilde{G}(x,s) - g_0(s)] = \\ & = s g_0(s) - x \end{aligned} \tag{B.6}$$

where we defined $g_0(s) = \tilde{G}(0,s) = \tilde{P}_0(s)$. Defining $F(x,s) = \tilde{G}(x,s) - g_0(s)$ and using the fact that $g_0(s)$ do not depend on x, we obtain the following equation for $F(x,s)$:

$$\partial_x F(x,s) + p(x,s) F(x,s) = q(x,s) \tag{B.7}$$

where

$$\begin{aligned} p(x,s) &= \left[\frac{d_0}{d_1}\frac{1}{x} - \frac{b_0 d_1 - d_0 b_1}{d_1}\frac{1}{d_1 - b_1 x} - \frac{s}{(d_1 - b_1 x)(1-x)}\right] \\ q(x,s) &= \frac{s g_0(s) - x}{(d_1 - b_1 x)(1-x)} \end{aligned} \tag{B.8}$$

The solution must satisfy the conditions:

$$F(1,s) = \frac{1}{s} - g_0(s) \tag{B.9}$$

$$F(0,s) = 0 \tag{B.10}$$

Our strategy is to solve the equation B.7 with the initial condition B.9, then we will impose on the solution the condition B.10 to obtain an equation for $g_0(s)$. We will also impose $b_1 \leq d_1$; when this condition holds, one has $\lim_{t\to\infty} P_0(t) = 1$, i.e. the probability of being already extinct goes to 1 as $t \to \infty$. Since $x = 1$ is a singular value for the equation B.7, we will regularize the solution taking as initial value $x = 1 - \epsilon$ and letting $\epsilon \to 0$ at the end of the calculations. The general form of the solution is:

$$F(x,s) = \exp\left[-\int_{1-\epsilon}^{x} dx' p(x',s)\right] \left[\frac{1}{s} - g_0(s) + \int_{1-\epsilon}^{x} dx' q(x',s) \exp\left[\left[\int_{1-\epsilon}^{x'} dx'' p(x'',s)\right]\right]\right] \tag{B.11}$$

We will solve separately the case $b_0 = d_0$ from the case $b_1 < d_1$.

B.1 The critical case: $b_1 = d_1$

By means of a time rescaling, we fix $b_1 = d_1 = 1$ To make the calculation simpler, we also set $b_0 = d_0 = r$. Let us write again the coefficients:

$$\begin{aligned} p(x,s) &= \tfrac{r}{x} - \tfrac{s}{(1-x)^2} \\ q(x,s) &= \tfrac{sg_0(s)-x}{(1-x)^2} \end{aligned} \tag{B.12}$$

Now we perform the integral. Up to the leading order in ϵ, the solution is:

$$F(x,s) = \frac{e^{-\frac{s}{\epsilon}}(g_0(s) - \frac{1}{s}) + \int_{1-\epsilon}^{x} dt \frac{sg_0(s)-t}{(1-t)^2} t^r e^{-\frac{s}{1-t}}}{x^r e^{-\frac{s}{1-x}}} \tag{B.13}$$

Since the denominator diverges when $x \to 0$, in order to have $F(0,s) = 0$, we have to impose that the numerator should be equal to zero. The resulting equation for $g_0(s)$ is:

$$e^{-\frac{s}{\epsilon}}(g_0(s) - \frac{1}{s}) + \int_{1-\epsilon}^{x} dt \frac{sg_0(s) - t}{(1-t)^2} t^r e^{-\frac{s}{1-t}} = 0 \tag{B.14}$$

Now, we can take the limit $\epsilon \to 0$:

$$\int_{1}^{x} dt \frac{sg_0(s) - t}{(1-t)^2} t^r e^{-\frac{s}{1-t}} = 0 \tag{B.15}$$

Finally, we make the substitution $\frac{1}{1-t} = y$ and solve for $g_0(s)$; this brings to our main result:

$$sg_0(s) - 1 = \frac{\int_1^{\infty} \frac{dy}{y}\, e^{-sy}(1 - \frac{1}{y})^r}{\int_1^{\infty} dy\, e^{-sy}(1 - \frac{1}{y})^r} \tag{B.16}$$

In Chap. 4, we analyze in detail the scaling behavior of this solution.

B.2 The sub-critical case: $b_1 < d_1$

Let us fix again $d_1 = 1$ by a time rescaling. Performing the integral in eq. B.11, one obtains:

$$\int_{1-\epsilon}^{x} p(x', s) = \left[d_0 \log x' + (\frac{b_0}{b_1} - d_0 - \frac{s}{1-b_1}) \log(1 - b_1 x') + \frac{s}{1-b_1} \log(1 - x') \right]_{1-\epsilon}^{x} \tag{B.17}$$

We use now the same strategy of the previous section. The condition $F(0,s) = 0$ brings to the following equation:

$$\int_0^1 dt\; (1 - b_1 t)^{b_0/b_1 - d_0 - s/(1-b_1) - 1} (1-t)^{1/(1-b_1) - 1} (sg_0(s) - t) = 0 \tag{B.18}$$

Now, we substitute $y = 1 - t$ and solve for $g_0(s)$:

$$sg_0(s) - 1 = \frac{\int_0^1 dy\ (1-y)^{d_0}[1 - b_1(1-y)]^{b_0/b_1 - d_0 - s/(1-b_1) - 1}\ y^{s/(1-b_1)}}{\int_0^1 dy\ (1-y)^{d_0}[1 - b_1(1-y)]^{b_0/b_1 - d_0 - s/(1-b_1) - 1}\ y^{s/(1-b_1) - 1}} \quad \text{(B.19)}$$

The integral on the r.h.s. of the equation goes to zero linearly with s, as $s \to 0$. This means that:

$$g_0(s) = \frac{1}{s} - f(s, b_1, b_0, d_0) \quad \text{(B.20)}$$

and the function f goes to a constant when $s \to 0$. This implies that the lifetime distribution has an exponential decay.

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Acknowledgments

Chino sui tomi! Chino sui tomi!
Unknown barfly, *Osteria "I Maestri"*

It's very hard to shrink into a few lines all the people i would like to thank.

So, let's start with the "professional" acknowledgments: first of all, my supervisor, he taught me everything about how to survive in the scientific jungle. I would like to thank also Cristian, who helped me a lot in preparing my master discussion, and Matteo, who risked many times to arrive at home late for dinner due to his will to calculated everything exactly. The help of Alessandro deserves really a lot of thanks, but i will spend them later, in the next section, "top jokes". I would like to thank also Jayanth for reading very fast everything that i wrote, and Igor and Tommaso for contributing to this work with a couple of pictures.

Trieste is a cold and melancholic city and, in order to survive, one has to organize some entertainment. Among them, several funny jokes. These jokes give me the possibility to remember several people, perhaps in the best way: for example, Giacomo (friend and organizer of almost all of them), Fabio and Sara (victim of a cold-water attack under their home), Lorenzo de Leo (the same), Lorenzo Stella (bad taste joke - dance Cd at the hospital), Angelo Rosa (the lonely top model at Trieste railroad station), and last but not least Alessandro, who had a very unexpected problem with the Italian Army before moving to the USA. Thanks also to the cast of the last joke: Stefano (tenente Mario Rosati) and Luca (missing documents office).

I would like to thank also all my friends here in Trieste, starting from all my ex-house-mates (Vittoria, Claudio, Johnny, Alex, Matteo.. did I forget anybody?), to the people of SISSA soccer team (Michele, Cosma, Adriano, they are too many... this year maybe you will win something...) and all the people that came mountaineering with me (Alessandro, Jaro, il "colonnello" Casula...). Among them, Laura. She waited for me in a late morning of February, 2003, in front of the Roiano church: i was still sleeping at that time.

Going back to Rome, I need to thank also all of my friends that waited for me everytime I came back for the weekends: LaLista (people in Rome, and people scattered in all Europe), Lidia, and all the people at the university of Rome (they are too many, really).

Thank also to my parents and my brother, for everything.

October 11th, 2003