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Stochastic Foundations in Movement Ecology

Anomalous Diffusion, Front Propagation and Random Searches

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To Montse, Laura and Susana

Preface

> It was an initiation into the love of learning, of learning how to learn [. . .] as a matter of interdisciplinary cognition -that is, learning to know something by its relation to something else.
>
> Leonard Bernstein

Movement is a common feature of both living and nonliving entities, and due to its interrelations with most processes occurring in nature and life, it represents a topic of interest for many fields of research. The recent affordability of GPS technology and satellite telemetry has revolutionised the study of animal movement, allowing to follow individual animals to remote places at high spatial and temporal resolution. The emergence of highly resolved massive datasets on animal movement has raised new questions and challenges to the field, compelling the need for new methods to analyse and model movement data. It is in this context that the distinct term *movement ecology* has emerged as a cross-disciplinary research field that integrates systems biology, behavioural ecology, spatial ecology, theoretical ecology and evolutionary biology. From a quantitative and theoretical perspective, the field aims to combine mathematical modelling, statistical physics and novel methods for statistical data analysis. While it can be used in a more general context, the term *movement ecology* typically designates the study of animal motor output across a broad range of scales, in an interdisciplinary and comprehensive manner and with the focus on the mechanistic relationships between movement properties, the internal states of organisms and the environment.

A mathematical theory of movement for nonliving entities has been built along the years by physicists and applied mathematicians (from the times of Galileo, Newton or Leibniz up to present), which have given rise to the fields of classical mechanics and statistical mechanics, among others. The results and ideas from such formalisms have been subsequently taken and adapted to study movement in ecology (Brownian motion or biological diffusion represents two archetypical examples of this). Without a doubt, advances in the field of movement ecology that are to come in the forthcoming years will be reached through the close collaboration from these different communities (mathematicians/physicists and biologists/ecologists). The communication between these two worlds is then more necessary than ever, albeit this is not always easy due to the lack of tradition and the different knowledge background of each.

Within this context, the present book has been conceived by its authors as a humble contribution to help bridging the gap that still exists between these research communities. It provides an overview of essential physical models and formalisms to describe the motion of individual entities in space. Since movement of living beings often involves a high level of unpredictability or randomness, the mathematical basis of the book lies in the theory of stochastic processes. A great emphasis is put in showing that stochastic processes and stochastic dispersal models do admit several levels of description (termed here as microscopic, mesoscopic and macroscopic). Albeit its importance to understand many of the models commonly used in the literature on movement ecology, this multilevel description is relatively unknown within this field.

The present book is then intended to be of utility for a broad scientific audience within this area of knowledge. First, it would be of interest for those theoretical biologists and ecologists who want to gain insight into physical or mathematical aspects of random walks, persistence, intermittence, anomalous diffusion, front propagation, Lévy processes, random searches and many other concepts which have become relatively familiar in the biological literature. Also, we expect that graduates and novel researchers in physics and applied mathematics with interests in biology can use it as an introductory handbook to the field. We have tried in general to use a pedagogical style so the book can be used to prepare the topics for postgraduate courses on mathematical ecology, theoretical ecology or similar. With this purpose in mind, we have also included a set of problems at the end of each chapter (instructors can obtain solutions by contacting the authors).

Regarding the background level required to follow the book and also in accordance to its interdisciplinary spirit, we have tried whenever possible to provide clear and intuitive expositions, sometimes at the expense of some mathematical rigour. However, the intrinsic difficulty of some of the topics addressed makes that several parts of the book can be difficult to follow for readers without a solid mathematical background. In order to facilitate the lecture to those readers, we have decided to mark with an asterisk (*) those sections of the book where more advanced and technical topics are discussed and used, so these can be skipped without losing the essential message.

The book has been divided into three parts. The first block (Chaps. 1 and 2) is intended to provide a compilation of mathematical results and definitions necessary to understand the rest of the book. Chapter 1 provides a very elementary introduction to probability theory, while Chap. 2 introduces the concept of stochastic processes and their different levels of description: microscopic, mesoscopic and macroscopic.

The second part of the book represents its backbone and provides a comprehensive review of stochastic modelling approaches which can be used to describe ecological movement. Chapter 3 presents a selection of classical and elementary models of diffusion and dispersal while trying again to emphasise the importance of the micro-meso-macro descriptions to reach a global understanding. Chapter 4 then extends those models to consider more complex situations which arise under non-Markovian conditions, specifically with the aim to introduce the concept of anomalous diffusion. Chapter 5 considers dispersal processes coupled to reproduction, so leading mathematically to the idea of waves of advance, or fronts, through a non-occupied territory. Finally, Chap. 6 shows the essential ideas of the random search theory for animals, which is adequately contextualised within the field of animal foraging.

The third and last part of the book presents specific applications and examples of the approaches and concepts introduced previously. These three Chapters (from 7 to 9) have been conceived as a compilation of the data published in the literature on different representative topics together with a corresponding discussion. Chapter 7, for example, focuses on the analysis of individual cell trajectories and the departures that recent experimental data show from classical diffusion models, which have raised the question about the applicability of anomalous diffusion to cell motion. Chapter 8 provides examples of how dispersal and demographic experimental data can be properly analysed and parametrized for the description of actual biological invasions. Chapter 9, finally, presents several experiences and field experiments where animal random search does play a crucial role, and also provides a deep discussion on the problems and limitations one typically finds in trying to provide experimental evidences and verifications of the random search theory.

To finish, we affectionately wish to thank our collaborators and colleagues, who have shared with us so many hours of work and leisure and from whom we have learned so much. We specially acknowledge fruitful discussions with Professors Sergei Fedotov, Werner Horsthemke, Martin Krkošek, Ignacio Pagonabarraga, Gandhimohan M. Viswanathan, Ernesto Raposo, and Marcos G.E. da Luz; the wise advices over the years by Professors José Casas-Vázquez, David Jou, Josep Enric Llebot, Simon A. Levin, Ricard V. Solé, Jordi Catalan, Daniel Oro and finally to our colleagues and friends Dr. David Alonso, Dr. Luca Giuggioli, Dr. Michael Raghib, the "NIOO Movement Ecology Group", Dr. Isaac Llopis, Dr. Vicente Ortega-Cejas and Dr. Xavier Àlvarez. We also would like to thank Maite Louzao, Sepideh Bazazi, Monique de Jager, Johan van de Koppel and Aitana Oltra for helping to generate some of the figures. We also acknowledge financial support by Generalitat de Catalunya with the grant SGR 2009-164 (VM) and by Ministerio de Economía y Competitividad with the grants FIS2012-32334 (VM, DC), RyC 2009-04133 (FB) and BFU2010-22337 (FB).

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Barcelona, Spain | Vicenç Méndez
Daniel Campos
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Contents

Acronyms

CLT	Central limit theorem
CT	Continuous time
CTRW	Continuous-time random walk
DLA	Diffusion-Limited Aggregation
DT	Discrete time
ESS	Evolutionary stable strategy
FDE	Fractional diffusion equation
GME	Generalized master equation
IS	Internal State
KPP	Kolmogorov-Petrovskii-Piskunov
KRG	Kernel random generator
ODE	Ordinary differential equation
OU	Ornstein-Uhlenbeck
MFPT	Mean first-passage time
MSD	Mean square displacement
PDE	Partial differential equation
PDF	Probability density function
RMS	Root mean square
SDE	Stochastic differential equation
SS	Sensor system
WLC	Worm-like chain

Part I
Theoretical Foundations

Chapter 1
Elements of Probability Theory

The intention of this chapter is to provide a brief survey of probability theory in a very schematic way, just to present some essential concepts and results that are necessary to understand the ideas exposed throughout the rest of the book. Readers with a background in mathematical probability can skip this chapter and only revisit it occasionally when it is referred along the book.

1.1 Random Variables and Probability

The term *random variable* may sound somewhat confusing the first time a student hear about it. We are trained from our school years in solving equations, so we know that a variable x is some kind of unknown we need to determine by means of an equation. For example, I can wonder what quantity of money x I have spent during the last 3 days. I can check that my bank balance today is y and I know that 3 days ago my balance was z, so I deduce that x is a variable that must satisfy $x + y = z$. We say x is a variable because it takes different values if I just change the quantities y or z. In contrast, random variables refer to something we cannot *determine* or *solve* through an equation. Imagine that I ask you how many litres of rainwater will fall in your city tomorrow. We know the weather is (at least to some extent) unpredictable so at practice it is impossible to build an equation to provide an exact answer to this. In general, we continually find in our daily lives examples of such *random events*. Sometimes randomness may be introduced through fluctuations (we know that the train we have to take tomorrow will arrive approximately at 9:45, but we cannot predict the arrival time with an accuracy in seconds) or through some level of unpredictability (as in the case of weather), or both. So, we see that random variables must be interpreted in terms of statements like 'the probability that this will occur is ...'. In other words, one should keep in mind that a random variable does not represent a quantity, but rather a function.

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More rigorously, a random or stochastic variable X is by definition a mathematical object characterized by a set Ω (called *range*) which contains the possible outcomes $x = x_1, x_2, \ldots, x_n$ of the variable X, and a function $P_X(x)$ which assigns a probability to each element from Ω. We use here capital letters to denote random variables and small letters to denote their actual values. To be well-defined, the function $P_X(x)$ must satisfy two conditions:

1. *Positivity*: $P_X(x) \geq 0$ in the whole range Ω.
2. *Normalization*: $\sum_x P_X(x) = 1$, where the sum extends over the whole range Ω.

Assume that Ω contains a finite number of possible outcomes (i.e. n is finite). For example, if X represents the answer to the question 'Will it rain tomorrow?' or 'How many days will rain this week?' there are only two possible outcomes in the first case, or seven in the second case. Then, we will say that the stochastic variable X is *discrete*, and a probability p_i can be assigned to each of the possible outcomes, so the probability distribution $P_X(x)$ can be written as

$$P_X(x) = \begin{cases} p_1 \text{ if } x = x_1 \\ \vdots \\ p_n \text{ if } x = x_n. \end{cases} \tag{1.1}$$

On the contrary, when we ask 'How many litres of rainwater will it rain tomorrow?' then Ω involves a continuous interval of possible outcomes (from 0 to almost infinity, at practice). Then we call X a *continuous* random variable (this is the case we will mostly use throughout this book) and then $P_X(x)$ is often termed as the *probability density function* (PDF) of X. The word *density* here is not accidental, but expresses the fact that $P_X(x)$ will only represent a probability (in the colloquial sense of the word) as long as this function is integrated over an interval (because the probability to have a specific value e.g. 3.1415786 is simply 0). This is, if we define an interval (a, b) contained within Ω, then the integral

$$\int_a^b P_X(x)\mathrm{d}x \tag{1.2}$$

gives us the probability that the outcome lies within that interval. Similarly, the normalization condition expressed above takes the form, for the specific case of continuous variables, $\int_\Omega P_X(x)\mathrm{d}x = 1$. Note that this condition does not preclude $P_X(x)$ from taking values above 1 (in contrast with the discrete case, where $P_X(x) \leq 1$ is required). Again, this is because the PDF is not defined as a probability but as a probability density.
For continuous variables one typically defines the probability distribution function as the probability to find X in the interval $(-\infty, x]$. From our comments above, this yields

$$P(X \leq x) = \int_{-\infty}^{x} P_X(x)\mathrm{d}x. \tag{1.3}$$

In some contexts, $P(X \leq x)$ is better known as the *cumulative distribution function*. This function and the PDF are closely connected, since the latter is just the derivative of the former

$$P_X(x) = \frac{\partial}{\partial x} P(X \leq x). \tag{1.4}$$

From the positivity condition $P_X(x) \geq 0$, we find that $P(X \leq x)$ must be a monotonically increasing function of x and has the limiting values $P(X \leq -\infty) = 0$ and $P(X \leq +\infty) = 1$.

Let us mention now some simple (but fundamental) facts about random variables. If X and Y are random variables, the linear combination $aX + bY$ is random, and the product XY or the quotient X/Y (provided $Y \neq 0$) are also random variables. More in general, we can state that if f is a function of one (or several) random variables, then f is also a random variable. This is important since we often wish to find the PDF not for the random variable X itself but for some new transformed variable $Y = f(X)$. If the function f is invertible with inverse $X = g(Y)$, then the PDF for the new variable $P_Y(y)$ is given in terms of the PDF for the old variable $P_X(x)$ as

$$P_Y(y) = P_X(x = g(y)) \left| \frac{\mathrm{d}g(y)}{\mathrm{d}y} \right|. \tag{1.5}$$

The Example 1.1 shows how this idea would apply at practice. Also, a case of particular interest is the sum of random variables, that is useful for example to treat the joint action of many subsystems. This case will be explored in Sect. 1.6.

Example 1.1. Imagine we can deduce (experimentally, or however) that the instantaneous velocity V of a group of individuals (say microorganisms, or animals) is a random variable distributed according to a Gaussian distribution, this is,

$$P_V(v) = \frac{1}{\sigma\sqrt{2\pi}} \mathrm{e}^{-\frac{v^2}{2\sigma^2}} \tag{1.6}$$

where σ is a positive constant, and one can check that the normalization condition $\int P_V(v)\mathrm{d}v = 1$ is fulfilled. From this we can obtain the corresponding PDF for the instantaneous kinetic energy E. If we use the definition of the kinetic energy ($e_k = mv^2/2$) and invert it ($v = \sqrt{2e_k/m}$) we will apply Eq. (1.5) to obtain

$$P_E(e_k) = \frac{\mathrm{d}v}{\mathrm{d}e_k} P_V\left(v = \sqrt{2e_k/m}\right) = \frac{1}{\sigma\sqrt{2\pi}} \frac{1}{\sqrt{2me_k}} \mathrm{e}^{-\frac{e_k}{m\sigma^2}}. \tag{1.7}$$

1.2 Moments and the Characteristic Function

If we can determine the PDF $P_X(x)$ of a random variable X, then we have got all the statistical information about it. However, one might think that information is easier to capture through quantities (not through functions), and for many specific purposes this is probably true. At practice, it is possible to translate the information contained in the PDF into quantities: the moments. The moment of order n of the random variable X is defined by

$$\langle X^n \rangle = \int_\Omega x^n P_X(x) \mathrm{d}x. \tag{1.8}$$

Some of the moments have special names. The first-order moment $\langle X \rangle$ is called the *mean value*, the *average* or the *expectation value* of X. Also

$$\sigma^2 \equiv \langle X^2 \rangle - \langle X \rangle^2$$

is called the *variance* or *dispersion*, which is the square of the *standard deviation* σ. Each one of the moments has only "partial" information about the properties of the random variable. For example, the first moment (mean value) gives the position of the "center of mass" of the PDF; this should not be confused with other quantities as the most probable value (which corresponds to the maximum of the PDF) or the median (which corresponds to the specific value x for which $P(X \leq x) = 0.5$). The second moment tells us how the values are distributed around the mean value, the third moment picks up any skewness (or asymmetry) in the PDF, and the fourth moment provides information about the peakness of the distribution around the mean value. All these ideas can be easily summarized through a visual comparison of PDF's with different moment values (see Fig. 1.1).

Not all the PDF's, however, have finite moments. This happens when the integral in (1.8) does not converge; in such situations one must be very careful with some mathematical considerations. Some examples of this situation are the Lorentz or the Lévy distribution, which are discussed (among other) in the Sect. 1.3. We can also show that there is an equivalence between the statistical information of the PDF and the statistical information provided by the whole set of moments (from $n = 1$ to ∞). For this purpose we introduce the *characteristic function* $G(k)$ of a random variable X with PDF $P_X(x)$ as the complex function

$$G(k) = \langle \mathrm{e}^{\mathrm{i}kx} \rangle = \int_\Omega \mathrm{e}^{\mathrm{i}kx} P_X(x) \mathrm{d}x. \tag{1.9}$$

The relation between the characteristic function and the moments becomes evident by using the Taylor series expansion (see Appendix A.1) for the exponential function

$$\mathrm{e}^{\mathrm{i}kx} = \sum_{n=0}^{\infty} \frac{(\mathrm{i}kx)^n}{n!}.$$

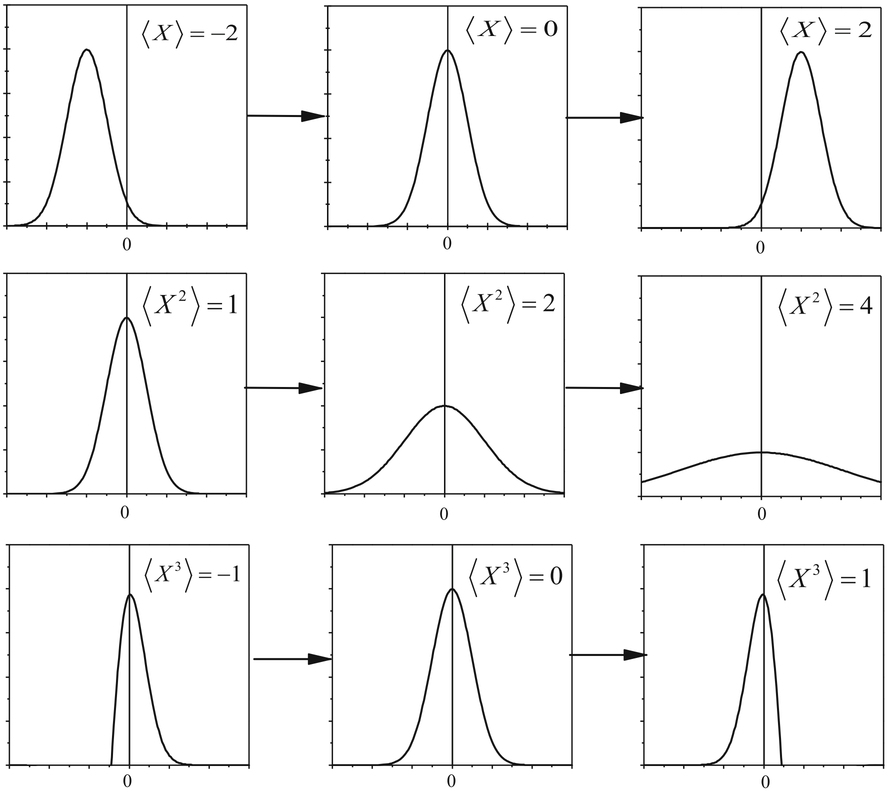

Fig. 1.1 Visual effects from changing the values of the first (*up*), second (*middle*) and third (*bottom*) order moments of a general PDF

Introducing this into (1.9) yields

$$G(k) = \sum_{n=0}^{\infty} \frac{(\mathrm{i}k)^n}{n!} \langle X^n \rangle \tag{1.10}$$

according to the definition (1.8). The series expansion in (1.10) is meaningful only if the higher-order moments are small so that the series converges. In the case $\Omega = (-\infty, \infty)$ then $G(k)$ can be regarded as the Fourier transform of $P_X(x)$ (see Appendix A.3) and the PDF can be obtained from the characteristic function by the inverse Fourier transform

$$P_X(x) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \mathrm{e}^{-\mathrm{i}kx} G(k) \mathrm{d}k.$$

Furthermore, if we know the characteristic function we can obtain the nth-order moment by differentiating

$$\langle X^n \rangle = \lim_{k \to 0} (-\mathrm{i})^n \frac{\mathrm{d}^n}{\mathrm{d}k^n} G(k), \tag{1.11}$$

as can be checked by introducing now this expression into (1.10). This finally shows the information equivalence between the characteristic function, the PDF and its moments. Since the correspondence between a function and its Fourier transform is biunivocal (in mathematical language, we would say that the Fourier transform is a bijective mapping) then the information they contain is exactly the same, and by extension the moments also fully contain this information.

1.3 Well-Known Probability Distributions

In this section we will review some common examples of probability distributions one can typically find in the literature and that will appear throughout this book.

1.3.1 Normal Distribution

A continuous random variable is said to follow a normal distribution (also called *Gaussian distribution*) if its PDF has the form

$$P_X(x) = \frac{1}{\sigma\sqrt{2\pi}} \mathrm{e}^{-\frac{(x-\langle X \rangle)^2}{2\sigma^2}} \tag{1.12}$$

or the characteristic function

$$G(k) = \int_{-\infty}^{\infty} \mathrm{e}^{\mathrm{i}kx} P_X(x) \mathrm{d}x = \mathrm{e}^{\mathrm{i}k\langle X \rangle - k^2\sigma^2/2}. \tag{1.13}$$

The PDF has finite moments which can be exactly computed. For the specific case $\langle X \rangle = 0$, for example, they take the simple form

$$\langle X^n \rangle = \int_{-\infty}^{\infty} x^n P_X(x) \mathrm{d}x = \frac{2^{n/2}\sigma^n}{\sqrt{\pi}} \Gamma\left(\frac{n+1}{2}\right) \tag{1.14}$$

for n even, or $\langle X^n \rangle = 0$ if n is odd. Here $\Gamma(\cdot)$ represents the Gamma function and we typically assume that the range of the random variable covers the whole real axis.

The Gaussian distribution is of special importance because it is a *stable* PDF . This means that a linear combination $aX + bY$ of two random Gaussian variables X and Y is also a random Gaussian variable. This property has fundamental consequences, as will be discussed in deeper detail in Sect. 1.5 and in forthcoming chapters.

Remark 1.1 (Lower-order moments of the general Gaussian distribution).

$$\langle X\rangle = \int_{-\infty}^{\infty} xP_X(x)\mathrm{d}x \tag{1.15}$$

$$\langle X^2\rangle = \int_{-\infty}^{\infty} x^2P_X(x)\mathrm{d}x = \sigma^2 + \langle X\rangle^2 \tag{1.16}$$

$$\langle X^3\rangle = \int_{-\infty}^{\infty} x^3P_X(x)\mathrm{d}x = \langle X\rangle^3 + 3\sigma^2\langle X\rangle \tag{1.17}$$

$$\langle X^4\rangle = \int_{-\infty}^{\infty} x^4P_X(x)\mathrm{d}x = \langle X\rangle^4 + 6\sigma^2\langle X\rangle^2 + 3\sigma^4. \tag{1.18}$$

1.3.2 Exponential Distribution

An exponential distribution is characterized by the PDF

$$P_X(x) = \lambda \mathrm{e}^{-\lambda x} \tag{1.19}$$

provided that the random variable X is definite positive. In case the random variable could also take negative values then (1.19) would read

$$P_X(x) = \frac{\lambda}{2}\mathrm{e}^{-\lambda|x|} \tag{1.20}$$

which has the following characteristic function

$$G(k) = \frac{\lambda^2}{\lambda^2 + k^2}. \tag{1.21}$$

The moments of this distribution are also finite and are feasible analytically. Assuming again that the range of the variable extends on the positive part of the real axis we obtain

$$\langle X^n \rangle = \frac{\Gamma(n+1)}{\lambda^n}. \tag{1.22}$$

The use of exponential distributions is widespread in many areas of physics and natural sciences (for example, in statistical mechanics or in population dynamics). This is because it satisfies a very interesting property. If X is an exponentially distributed variable that represents the time duration of a random event, then the probability that the event will occur in the interval $(x, x + \mathrm{d}x)$ (measured after a time x in which we know that the event has not occurred yet) is a constant equal to the parameter λ appearing in (1.19), independently of the value of x. This is equivalent to say that the process is *memoryless*, since the instantaneous probability that a random event will occur is always controlled by a fixed rate λ (this will be rigorously proved in Example 1.2).

1.3.3 Uniform Distribution

The uniform (or flat) distribution assigns the same probability density to any of the elements within the range Ω. So, provided the range of a random variable is defined by the continuous interval (x_1, x_2) we will say that this variable is uniformly distributed if

$$P_X(x) = \begin{cases} \frac{1}{x_2 - x_1}, & x_1 \le x \le x_2 \\ 0, & \text{otherwise} \end{cases} \tag{1.23}$$

or if it has the following characteristic function

$$G(k) = \frac{\mathrm{e}^{\mathrm{i}kx_2} - \mathrm{e}^{\mathrm{i}kx_1}}{\mathrm{i}k(x_2 - x_1)}. \tag{1.24}$$

As in the previous cases, the moments of arbitrary order can be explicitly found in this case. They read, from the definition (1.8),

$$\langle X^n \rangle = \frac{1}{n+1} \frac{x_2^{n+1} - x_1^{n+1}}{x_2 - x_1}. \tag{1.25}$$

1.3.4 Cauchy Distribution

The PDF of the Cauchy (or Lorentz) distribution is

$$P_X(x) = \frac{1}{\pi}\frac{\gamma}{x^2+\gamma^2}. \tag{1.26}$$

Its characteristic function has to be calculated by contour integration to get

$$G(k) = \mathrm{e}^{-\gamma|k|}. \tag{1.27}$$

It is easy to check that if one tries to compute the moments of this distribution

$$\langle X^n \rangle = \frac{\gamma}{\pi}\int_{-\infty}^{\infty}\frac{x^n}{x^2+\gamma^2}\mathrm{d}x, \tag{1.28}$$

then one finds that the integrand behaves as $\sim x^{n-2}$ in the limit $x \to \infty$. The integral then obviously diverges for any $n \geq 1$, so we conclude that all the moments (including the average value) of this distribution are divergent. In principle this would preclude the Cauchy distribution from being used in real processes in nature, where average values are finite. This problem is typically overcome by redefining the range of the random variable to a finite interval (a, b) where a and b would represent respectively the minimum and the maximum value of the random variable which is physically, or biologically, attainable. This idea will be further explored in forthcoming chapters.

1.3.5 Lévy Distribution

A symmetric (in x) Lévy distribution $P_X(x, \alpha)$ is a stable PDF with characteristic function given by

$$G(k, \alpha) = \mathrm{e}^{-a|k|^\alpha} \tag{1.29}$$

with $0 < \alpha < 2$. The Gaussian distribution corresponds to the particular case $\alpha = 2$, $a = \sigma^2/2$; also, the Cauchy distribution is recovered for $\alpha = 1$. The inverse Fourier transform of (1.29) yields, in the asymptotic limit $|x| \to \infty$,

$$P_X(x, \alpha) \sim \frac{a}{|x|^{1+\alpha}}. \tag{1.30}$$

The moments of this distribution are all divergent, too. Again, if we use the definition (1.8)

$$\langle X^n \rangle = \int_{-\infty}^{\infty} x^n P_X(x, \alpha)\mathrm{d}x$$

we observe that the integrand goes as $\sim x^{n-1-\alpha}$ for large x, which leads to a divergent integral for $n \geq 1$ if α takes the values specified in (1.29). Then a similar discussion to that provided for the Cauchy distribution holds.

1.3.6 Dirac Delta Distribution

The Dirac Delta PDF is very useful in different contexts, for example when we intend to analyse a discrete random variable in a context typically built for continuous variables. This distribution follows the expression

$$P_X(x) = \delta(x - x_0) \tag{1.31}$$

where $\delta(\cdot)$ represents the Dirac Delta function, whose characteristic function is $G(k) = \mathrm{e}^{\mathrm{i}kx_0}$ (see Appendix A.2 for further details on Dirac Delta function). The value of this function equals zero everywhere except at the point where the argument of the function vanishes (in the case (1.31) this would occur for $x = x_0$). At this point the function diverges (it tends to $+\infty$), but the divergence is such that the condition

$$\int_{\Omega} \delta(x - x_0)\mathrm{d}x = 1 \tag{1.32}$$

holds, provided that $x_0 \in \Omega$. So that, a Dirac Delta distribution satisfies the normalization condition like any other PDF. Another relevant condition of the Dirac Delta function is

$$\int_{\Omega} f(x)\delta(x - x_0)\mathrm{d}x = f(x_0), \tag{1.33}$$

with $f(\cdot)$ an arbitrary function. From this one can easily derive the expression for the n-order moments of the Dirac Delta PDF:

$$\langle X^n \rangle = x_0^n \tag{1.34}$$

1.3.7 Poisson Distribution

In contrast with the previous examples discussed, the Poisson probability distribution is defined for discrete random variables. The probability that the random variable takes the value x is

$$P(X = x) = \mathrm{e}^{-\lambda} \frac{\lambda^x}{x!}. \tag{1.35}$$

All the moments of the Poisson distribution are finite. Their expression can be determined from its characteristic function

$$G(k) = \mathrm{e}^{\lambda\left(\mathrm{e}^{\mathrm{i}k}-1\right)} \tag{1.36}$$

through (1.11). The Poisson distribution is closely related to the exponential distribution discussed above in this section. Consider a set of identical random events and assume that the PDF determining the duration of a single event is exponentially distributed. In that case, the probability that a number x of these events occur within an interval of duration x is given by (1.35), as we shall formally prove in Sect. 2.4.3. A classical example of this is the radioactive decay. Any particle of a radioactive sample has a probability to desintegrate, and this probability is governed by an exponential PDF. Then, the probability that a number x of desintegrations have occurred after a time x is determined by a Poisson distribution. Another well-known example of the usage of Poisson distributions is on the algorithms of generation of stochastic trajectories for reaction processes, for instance in the Gillespie algorithm [1].

1.3.8 Binomial Distribution

Consider a random variable X with only two possible outcomes; the first one is assigned a probability p, and the other one a probability $1 - p$. One can think, for instance, that we toss a tricked coin so the probability is not the same for each face. The probability that the first outcome has appeared x times after N trials (this is, after N tosses) is given by

$$P(X = x) = \frac{N!}{x!(N-x)!} p^x (1-p)^{N-x} \tag{1.37}$$

with $x = 0, 1, \cdots, N$. This is known as the binomial distribution. The moments of this PDF can also be exactly computed; however, as in the case of the Poisson distribution they cannot be explicitly written in a simple form. Instead, one can provide the corresponding characteristic function by computing the Fourier transform of (1.37)

$$G(k) = \left(1 - p + p\mathrm{e}^{\mathrm{i}k}\right)^N \tag{1.38}$$

and the moments could be now evaluated from (1.11). So, for example

$$\langle X \rangle = \lim_{k\to 0} (-\mathrm{i}) \frac{\mathrm{d}G(k)}{\mathrm{d}k} = \lim_{k\to 0} pN\mathrm{e}^{\mathrm{i}k} \left(1 - p + p\mathrm{e}^{\mathrm{i}k}\right)^{N-1} = pN. \tag{1.39}$$