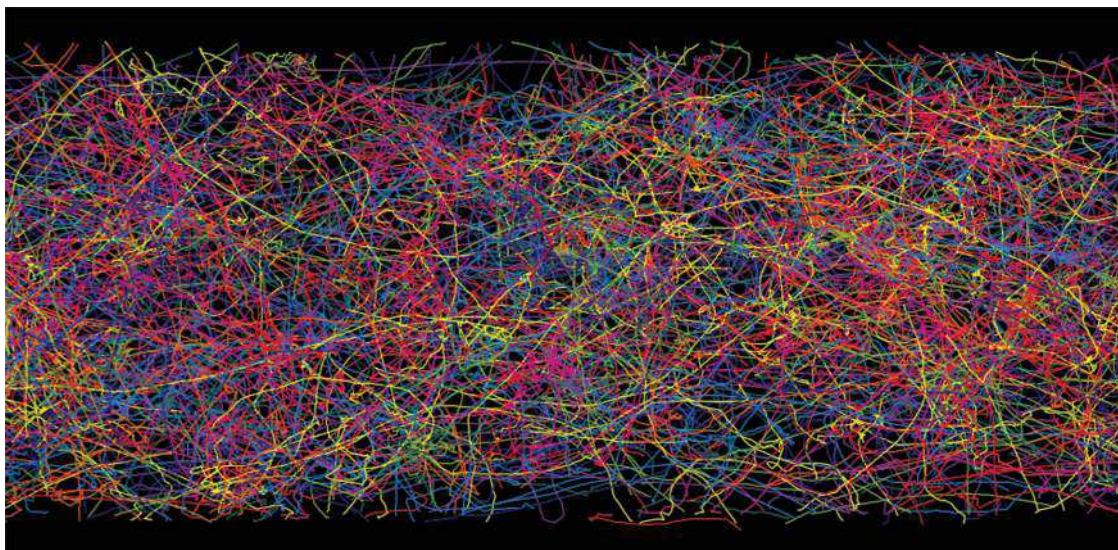# 1 | Introduction

This introductory chapter outlines the *leit-motiv* of the book – dendritic substrates for ecological interactions, chief and foremost river networks in our case, bear important consequences for a number of processes, from patterns of biodiversity to controls on the spread of waterborne disease. In this chapter we discuss important methodological aspects of spatially explicit ecology that we use throughout this book. The image that we have chosen for the heading of this introductory chapter refers to accurate measurements of the behavior of the alga *Euglena gracilis* when exposed to controlled light fields. The superposed trajectories of individuals' movements, tracked in the Laboratory of Ecohydrology at EPFL, recall a Jackson Pollock painting. Laboratory studies of mesoscopic-scale movement and reproduction support theoretical work on directional dispersal in networked environments and give important bearings for the tenet of this book, as described in this chapter. Image courtesy of Andrea Giometto

1.1 The Context

Although natural ecosystems are characterized by striking diversity in form and function, they often exhibit deep structural similarities, at times emerging across scales of space, time, and organizational complexity [2]. One angle through which such features could be considered is via the necessary linkages among macroecological "laws" [3, 4], often expressing the scale invariance of ecological patterns of abundance or trait diversity subsumed by algebraic relations (popularly dubbed power laws), intended both as functional relationships among ecologically relevant quantities and probability distributions that characterize their occurrence [5]. Clearly, not all ecological patterns exhibit scale-invariant properties; many well-defined characteristic scales exist in a broad spectrum of ecosystem dynamics. Yet many do, and there scaling theory offers a powerful tool to make way for coherent, unified descriptions capturing the essence of a process. In this chapter we introduce our main theme (highlighting the role of river networks viewed as ecological corridors that shape species and population distributions) in the context of spatially explicit ecological modeling.

One example, discussed in this chapter, concerns species' numbers and their abundance and size emerging in relation to broad ecosystem features like the topology of the substrate for ecological interactions [6–10].

1

We shall observe how emerging features, such as the distribution of species' persistence times at observation sites [9], are controlled more by the nature of the landscape where interactions occur than by many detailed features specific to the underlying ecosystem. A large body of empirical [9, 11] and laboratory [12–16] evidence is quoted to support such a view. We argue that dispersal constrained by specific habitat structures is a major determinant of the observed diversity patterns at both species and genetic levels [6, 8, 14, 17–20]. This result, a rather far-reaching one, is well captured by spatially explicit ecological approaches that we introduce in this chapter (Sections 1.2 and 1.3).

We contend that, within an ecohydrological framework, river network structures and their embedded hydrologic dynamics play an important role [21]. First, they provide supporting landscapes for ecological processes, many of which are essential to human life and societies. Historically, human settlements followed the river networks for the necessary water resources [22]; river networks are home to (and provide hierarchical habitat features for) freshwater fish [6–8] and stream ecology in general [23, 24] as well as pathways to life-threatening waterborne human diseases and zoonoses, that is, for human and animal hosts alike [25]. River networks may be also seen as meta-ecosystems that affect the metabolism of terrestrial organic carbon in freshwater ecosystems, an important part of the global carbon cycle [23, 26], and the amount of nutrients removed from streams and reservoirs affected by network structure and stream ecology therein [24, 27].

A broad research field exists where signatures of the hydrologic, ecologic, and geomorphologic dynamics of river basins coexist. This field has proved its importance by furthering our understanding of spatially explicit epidemiology and ecology (Chapters 2 and 3). Our ultimate goal is a comprehensive theory of how dendritic structures, their associated features, and interactions with external forcings (chiefly, hydrological stochasticity) shape emergent properties of various ecosystems. Such theory would help us address a wide variety of important questions: from conservation plans for freshwater ecosystems to optimal control for containing waterborne disease epidemics to proper inclusion of riparian systems into large-scale resource management [21, 28]. Understanding and control of biological invasions is also part of this scheme. While providing what we believe is a useful review, the novelty of this book lies in envisioning a research area where hydrology, ecology, and geomorphology intersect. We feel that important

advances will be made in this area in the near future. This book is by no means intended to provide closure on the role of river networks as ecological corridors; rather, it is a blueprint for future developments. Throughout its material, in fact, we suggest specific areas or open problems that appear to us to be particularly promising.

Incorporating ecological dynamics into riverine systems is not an easy task, given the variety of the taxa involved, their trophic positions, and the interactions between the different organisms ranging from competition to predation to parasitism. Very frequently, if the aim is to investigate population dynamics, the analysis is restricted to one or a few species or functional groups. This is what has been done, for example, when exploring zebra mussel invasions [29] or cholera dynamics [30]. If instead the aim is to investigate general patterns of biodiversity, one considers specific taxa or groups usually sharing the same trophic level, for example, fish or phytoplankton or riparian vegetation. In such a case, the main operating ecological interaction is interspecific competition, either indirect (e.g., exploitation of common food resources or nutrients) or direct (e.g., via interference). Available data usually comprise lists of presence/absence of species, possibly complemented by their relative abundances, the latter being averaged over time or simply measured in a given year. If the identity of the particular species is neglected, it is possible to derive species-abundance distributions, namely, the number of species that have a certain abundance or a certain abundance rank. Static models of species-abundance relations have long been proposed to achieve that goal (see, e.g., [31] for an excellent review). Dynamic models in which the observed relation is obtained as the long-term equilibrium of a model containing the basic time-dependent processes that shape community biodiversity are more recent. The processes shaping the maintenance of biodiversity are four fold [32]: selection, namely, the differences in the species fitnesses and therefore in their competitive ability, which operates in both ecological and evolutionary time; drift, namely, the inherent stochasticity that brings species to extinction and operates on an ecological timescale only when the size of the community is rather small; speciation, which counters drift and selection over evolutionary timescales; and dispersal, which counters local species extinction via the movement of organisms across space and acts on ecological timescales. Caswell's seminal paper on the related dynamic models [33] borrowed concepts of neutral molecular evolution and applied them to the ecological context. The organic development of a neutral

theory of biodiversity was presented in a unified way only later [34]. The main tenet therein assumes that selection (i.e., differences in competitive ability, stated otherwise) is not operating, while drift is countered by speciation or dispersal. Concerning this last point, it is important to remark that almost all neutral theories are spatially implicit in that they consider either an isolated community whose survival is thus guaranteed by speciation, or a local nonisolated community whose survival is guaranteed by immigration from a "background" metacommunity. A coherent theory that considers all four processes in a space-explicit framework distinguishing between ecological and evolutionary timescales is still lacking (but see [35] for a notable attempt). This book aims at partially filling this gap by presenting a series of models that are always space explicit and suited to specifically describing the peculiar structure (and thus connectivity) of river basins. We proceed step by step, first including the dendritic substrate of river basins into the neutral paradigm of biodiversity, then breaking perfect neutrality by adding either space-dependent carrying capacities of local communities or elevational niche apportionment. Species invasion and disease spread are subsequently investigated by paying greater attention to realistic details, though with a species-specific focus and within fluvial ecological substrates.

To set the context, we start with an example of the simplest dynamic model of biodiversity, the neutral one [34], which assumes that all species are competitively equivalent at a per capita level. It should be noted that some unrealistic assumptions of the neutral theory have attracted much criticism [36–38], for example, in terms of timescales, testability, and robustness; also, the neutral theory overlooks much species-specific ecological information, which is required when studying the dynamics of the system or of a set of particular species and the interactions among them [39] (Box 1.1). However, the neutral model has the advantage of letting us introduce the biodiversity-shaping processes one by one; in fact, the neutral theory switches off all the differences between species and all the interactions with the exception of strong competition for space (both intra- and interspecies), as we shall recall below. Being focused on competition for space, it is thus particularly suited to testing the fundamental differences between the spatial structure of river basins and 2D isotropic landscapes. Our first approach thus focuses on the quantitative assessment of the role of directionality and network structure on ecological organization, in particular on patterns of diversity distribution. We show, in particular, how the implemen-

tation of the neutral theory behaves in 2D lattices or 2D space-filling trees imposing directional dispersal [21, 40]. The investigation of the differences between the two substrates (the common name for the ecosystem landscape where interactions occur) proved important to later developments, chiefly laboratory ones (Section 1.2).

1.1.1 Neutral Theory of Biodiversity in a Nutshell

The neutral theory of biodiversity (NTB) was originally proposed [33] in complete analogy with the neutral theory of molecular evolution [41, 42], which assumes that gene mutations are selectively neutral, namely, that new genes are demographically equivalent to old genes, as they do not confer any advantage in terms of decreased mortality and/or increased fertility. The main advocate of NTB was Hubbell [34, 43], who greatly developed these ideas starting from his work on tropical forests, which typically display very high biodiversity. In NTB, genes are replaced by species, which all have the same demographic fitness. Mutations are replaced by the occurrence of new species. It is worth noting that in genetics, neutrality is rooted in specific biochemical mechanisms, for example, that different sequences of three nucleotides (codons) may code for the same amino acid. In ecology, instead, we do know that all species are different and have differential ecological functions and abilities. Moreover, in genetics, neutral theory is not advocated as the theory that can explain the whole of genetic diversity but as a theory that can explain the evolution of specific genes. Even the neutralists do not deny the importance of Darwinian selection in the origin of adaptations, although they think that most of the molecular diversity can be explained by random genetic drift, that is, the neutral model. In any case, neutral models in ecology may be seen as a limit approximation. The theory might hold when dealing with biodiversity within communities characterized by species with similar traits, for instance, those belonging to the same functional group or, more generally, the same guild. In these cases, in fact, we may conceive that the differences in demographic rates are not very large.

Neutral models and the pertaining theory have been fully developed by statisticians and population geneticists [41, 44–46] and blended into a coherent theory of biodiversity by Hubbell [34]. Thus, all the basic results of NTB can be found in the population genetics literature: just replace genotypes with species and mutants with new species. Neutral models are not space explicit and are traditionally phrased according to two possible

paradigms: (1) biodiversity is studied at the regional scale, and the arrival of new species is due to immigration from outside the region; (2) biodiversity is analyzed at the continental level, and a new species can only arise via speciation. Clearly the two paradigms imply not only a different spatial scale but also a different timescale, because speciation is much rarer than the arrival of a new species from the surrounding regions, especially if the region is not very large. The extension of NTB to a space-explicit paradigm in riverine networks is actually one of the goals of the present book. In this section, we summarize the results of the space-implicit approach.

In NTB, abundances of all species fluctuate at random according to a birth–death stochastic process. The process may obey different rules (see below), but the most popular is the one in which the total number of individuals (no matter of what species) is constant across generations and equal to N. We might think of this situation as the one arising when considering territorial organisms, each occupying a fixed portion of the landscape, which is made up of N territories. At each time step a randomly chosen individual dies and is replaced by another individual, which may be the progeny of individuals belonging to a species already present in the community or an individual of a new species. It is often stated that NTB implies no interaction between species. This is not completely true: competition (of the so-called contest type) is actually quite strong, because each individual excludes any other individual from its own territory. However, neutrality is due to the assumption that intraspecific competition and interspecific competition have the same strength: no species has any advantage over another species in the process of replacing a dead individual.

The assumption of a constant number of individuals allows the derivation of the dynamics of a simple biodiversity index in the following manner (reported in [36]). Let f_t be the probability at generation t that two individuals of the community belong to the same species. We assume that the N individuals, before dying, produce progeny. The frequency of the progeny of each parent is $1/N$ because we assume neutrality, namely, that the fertility of each individual is the same independently of the species. Then each territory will be occupied at generation $t + 1$ by one individual chosen at random among all the progenies. However, with probability γ, this individual may be replaced by an individual of a new species (this might occur because of either mutation or immigration). Now, pick two individuals at random at generation $t + 1$. If they are the progeny of the same parent in the previous generation (which occurs with

probability $1/N$), then the probability that they belong to the same species is 1. If they are the progeny of different parents (which occurs with probability $1 - 1/N$), then the probability that they are of the same species is f_t. Also, with probability $(1 - \gamma)^2$, neither of the two individuals picked at random belongs to a new species. Therefore, one finally obtains

$$f_{t+1} = (1-\gamma)^2 \left(\frac{1}{N} + \left(1 - \frac{1}{N} \right) f_t \right). \tag{1.1}$$

In the long run, f_t will approach the following equilibrium:

$$\bar{f} = \frac{(1-\gamma)^2}{N - (N-1)(1-\gamma)^2},$$

which, by assuming that γ is very small, N is very large, and $N\gamma$ is finite, is well approximated by

$$\bar{f} \approx \frac{1}{1 + 2N\gamma}. \tag{1.2}$$

The quantity $2N\gamma$ is termed the fundamental biodiversity number θ. In fact, it is related to one of the most used biodiversity indices, Simpson's diversity index H. This is defined as the probability that two individuals of the same community belong to different species [47]. Thus, at equilibrium, Simpson's index of a neutral community is given by

$$H = 1 - \bar{f} = \frac{2N\gamma}{1 + 2N\gamma} = \frac{\theta}{1 + \theta}.$$

Most of the discussion around NTB is, however, focused not on a single biodiversity index but rather on the whole distribution of abundances defined as the distribution of the number of species $n_j(t)$ in the ecological community containing exactly j individuals at time t. As the abundances vary according to a birth–death stochastic process, $n_j(t)$ varies stochastically, of course. Under appropriate conditions, the values of $n_j(t)$ converge (in distribution) to a steady state for $t \to \infty$. This is termed the expected distribution of species abundance, say, ϕ_j, often used to fit empirical data. One can then compute the average of n_j, $E[n_j]$. Of course, data come from a sample of the community that does not presumably include all the N individuals of the community and all the S species. The assumption is made that the community has reached equilibrium, and the sample is so large as to justify the fact that the sampled n_j is close to the theoretical expected value of n_j, namely, ϕ_j (but see [46] for how to deal with small samples).

It is often stated that NTB implies that ϕ_j is the logarithmic series proposed by [48], so that the

logarithmic series would be a sort of fingerprint of neutrality. However, this claim is not true in general. Three remarks are worthwhile before briefly going into the details: (1) depending on the rules of the stochastic process that governs the NTB model, different functions for ϕ_j can be obtained, one of which is the logseries; (2) numerous different mechanisms, other than NTB, can lead to the logseries distribution, and therefore, as clearly stated by [31], "an empirical species-abundance distribution cannot by itself give evidence on how to choose among them;" (3) many empirical species-abundance distributions have been examined since the 1940s, and, depending on the dataset, sometimes the best fit was the lognormal distribution, sometimes the geometric series, sometimes the logseries, and so on [47]. Therefore, researchers should refrain from using the logseries as a yardstick for neutral theory.

Let us now discuss how ϕ_j can be obtained. A key paper [45] set the problem within a wide context. The paper considers a model with Malthusian demography and a model in which the total size of the community is constant and equal to N. Here, we illustrate and discuss both.

Box 1.1 Deriving Species Abundance Distributions from Malthusian Models

First, consider the case of a Malthusian demography with constant birthrate β, constant death rate μ, and constant rate of demographic increase $r = \beta - \mu$. Neutrality implies that birth and death rates are equal across species. Each new species arises according to a Poisson process, with a constant arrival rate ν. The times between arrivals are independent, exponentially distributed with mean $1/\nu$. The only possible transitions of a certain species abundance j ($j = 1, 2, ..$) in an element of time dt are from j to $j - 1$, j or $j + 1$, and the transition rules are as follows: from j to $j - 1$ with probability $j\mu dt$, from j to $j + 1$ with probability $j\beta dt$, from j to j with probability $1 - j(\beta + \mu)dt$. If $j = 0$ (which is true for a candidate new species), the only possible transitions in time dt are from 0 to 0 or 1, the transition probabilities being as follows: from 0 to 1 with probability $j\nu dt$, from 0 to 0 with probability $1 - j\nu dt$. It should be clear that in Karlin and McGregor's approach the number of species $S(t)$ is not fixed *a priori* because there is a continuous turnover of species due to migration or speciation. This should be contrasted with, for example, the somewhat simpler approach of [49], in which the number of species S is fixed *a priori*. Each of the S species can become extinct and then start again owing to migration or speciation.

It is useful to recapitulate some properties of the simple birth–death Malthusian process [44]. Let $P_j(t)$ be the probability that a population started with one individual at time 0 contains j individuals at time t. Then $P_j(t)$ is a geometric series with a modified zero term:

$$P_0(t) = \frac{\mu(\exp(rt) - 1)}{\beta \exp(rt) - \mu}$$
$$P_j(t) = (1 - P_0(t))(1 - u(t))u(t)^{j-1}, \quad \text{with } u(t) = \frac{\beta(\exp(rt) - 1)}{\beta \exp(rt) - \mu}. \tag{1.3}$$

Note that $P_0(t)$ is nothing but the probability of extinction at time t. By letting t go to ∞, one obtains that eventual extinction is certain if $\beta \leq \mu$, while eventual extinction occurs with probability μ/β if $\beta > \mu$. It is easy to prove that the expected value of the abundance j varies as $\exp(rt)$. For this reason, the case $\beta > \mu$ is discarded because the expected value of the abundance of each species increases exponentially with time, which is clearly quite unrealistic. As for the average time to extinction for $\beta \leq \mu$, it is easy to prove (by integrating over time $1 - P_0(t)$, which is the probability that the time to extinction is less than t) that it is given by

$$t_{ext} = \frac{1}{\beta}(\ln \mu - \ln(\mu - \beta)). \tag{1.4}$$

Therefore, the time to extinction is infinite if $\beta = \mu, r = 0$.

Box 1.1 *Continued*

As the expected value of the abundance of each species is constant if $\beta = \mu, r = 0$, this first case seemed a good starting point for [45] and [46] as well as for [33]. Actually, it is possible to prove [45, 46] that in this case the number of species $n_j(t)$ containing exactly j individuals at time t has a Poisson distribution with expected value given by

$$E\left[n_j(t)\right] = \frac{\nu}{j\beta}\left(\frac{\beta t}{1 + \beta t}\right)^j. \tag{1.5}$$

This is exactly the expected distribution ϕ_j of species abundance at time t and is a logseries of the kind advocated by [48]: $\alpha \lambda^j / j$, provided that one sets $\alpha = \nu/\beta$ and $\lambda = \frac{\beta t}{1 + \beta t}$. Problems arise, however: (1) the mean of the total size N of the community (sum of the abundances of all the species) can be shown to increase linearly with time ($E[N(t)] = \nu t$); (2) the mean of the total number of species S increases logarithmically with time ($E[S(t)] = \frac{\nu}{\beta} ln(1 + \beta t)$). This seems to be a sort of paradox, given that the probability of extinction is 1 for all species, but it can be explained as follows: the expected number of species grows to infinity because the average lifetime of each species is infinite even if each species becomes ultimately extinct. Therefore, the case $r = 0$ of the Malthusian model describes an ever-increasing community in both the total number of individuals and the total number of species, which is somewhat unrealistic. Also, if we let $t \to \infty$ in expression (1.5), we get for the species-abundance distribution

$$\phi_j = \frac{\nu}{j\beta} = \alpha/j,$$

that is, a hyperbolic distribution with just one parameter, which would be unable to fit most observed species-abundance distributions. The way out, advocated by [46] and [33], is to calculate the species-abundance distribution conditional on a fixed size N of the community; [46] has proved that it is given by

$$E\left[n_j | N\right] = \frac{\nu}{\beta j}\left(\begin{array}{c} \nu/\beta + N - j - 1 \\ N - j \end{array}\right)\Bigg/\left(\begin{array}{c} \nu/\beta + N - 1 \\ N \end{array}\right). \tag{1.6}$$

Actually, it is this functional form and not the logseries that has been used by [33] to compare the patterns of species abundance generated by NTB against those generated by other traditional models, such as the broken-stick and the lognormal models.

The second case considered for the Malthusian model is $\beta < \mu$. If it is so, extinction is still certain, but the average extinction time t_{ext} is finite and given by Equation (1.4):

$$t_{ext} = -\frac{1}{\beta} \ln\left(1 - \frac{\beta}{\mu}\right),$$

in which $\beta/\mu < 1$. One should note that t_{ext} is also the average lifetime of each species. Thus, it is easy to understand [45] that the average number of species $E[S(t)]$ will converge to an equilibrium $E[S]$, which is simply given by the product of the arrival rate ν times the average lifetime of each species t_{ext}. Therefore, in this case, the mean number of species of the community is finite and given by

$$E[S] = -\frac{\nu}{\beta} \ln\left(1 - \frac{\beta}{\mu}\right).$$

Box 1.1 *Continued*

We can now somehow suspect that the logseries is involved because the right-hand side of this equation is nothing but the sum of the following logarithmic series:

$$\sum_{j=1}^{\infty} \frac{\nu}{\beta j} \left(\frac{\beta}{\mu} \right)^j.$$

In fact, [45] have proved that the probability distribution of $n_j(t)$ converges for $t \to \infty$ to a Poisson distribution whose expected value is

$$E\left[n_j \right] = \nu \int_0^{\infty} P_j(t) dt.$$

After some boring calculations, based on the previous formulas for $P_j(t)$ (Equation (1.3)), we obtain

$$E\left[n_j \right] = \phi_j = \frac{\nu}{\beta j} \left(\frac{\beta}{\mu} \right)^j. \tag{1.7}$$

Thus the logseries is the expected value of the species-abundance distribution. Also, one can easily obtain the average size of the community,

$$E[N] = \sum_{j=1}^{\infty} j \frac{\nu}{\beta j} \left(\frac{\beta}{\mu} \right)^j = \frac{\nu}{\beta} \frac{\frac{\nu}{\beta}}{1 - \frac{\nu}{\beta}},$$

which closes our derivations.

Karlin and McGregor's approach [45] allows the calculation of the expected number of species (which are not always the same but have a continuous turnover) on the basis of the three fundamental rates: birth β, death μ, arrival or speciation ν (Equation (1.7)). Actually, the species-abundance distribution, the number of species, and the total number of individuals in the community depend on just two parameters: the ratios ν/β and β/μ. The logseries has also been obtained by a slightly different model [49]. They have assumed that there exists a given number S of potential species in the community. Each of these species may become extinct according to the above described birth–death process. Once extinct, it may be replaced by another species at a rate of occurrence ν_0. Therefore, the rate of arrival (*sensu* [45]) of a new species (no matter which) in the whole community is $\nu_0 S P_0$, where P_0 is the probability of extinction at equilibrium (which may be equated to the fraction of the S species that are extinct at equilibrium). As a matter of fact, the logseries obtained by [49] coincides with that obtained by [45], provided one sets $\nu = \nu_0 S P_0$.

The problem with this model (in both versions, by [45, 49]) is that it relies on β/μ being a number smaller than 1. However, β/μ is nothing but the average size of the progeny produced by one parent in the whole lifetime, namely, the fitness of each species (remember that because of neutrality, all the species have the same fitness). This immediately points out the weakness of the Malthusian model with $\beta < \mu$. Although the results are very elegant and lead to the logseries distribution, the theory relies on assuming that the ecological community consists of species that are all unfit. Such a community would be easily invaded by a new species with a fitness even slightly larger than unity at low density. As a matter of fact, a more realistic NTB model would require consideration of a community of non-Malthusian species exhibiting some sort of density dependence. Fitness can be assumed to be larger than unity for low abundance, declining with increasing abundance and smaller than unity above a carrying capacity. This would guarantee that all the species are equally fit, they do not increase or decrease disproportionately, and their time to extinction is finite (see, e.g., [50]), not infinite as in the Malthusian models with $\beta \geq \mu$. Obviously, the resulting expected value of the species-abundance distribution is no longer a logseries if one assumes density dependence. As far

as we know, there is no simple function describing the distribution even for prototypical models of density dependence, such as the logistic model. However, this does not imply that the NTB assumption cannot be used. Very simply, expected distributions can be derived by extensive simulation of density-dependent models and compared with data.

The model that is most used in NTB, however, is the one in which the total community size is constant. This approach was pioneered by [45]. They basically assume a mechanism similar to the one that was illustrated with reference to Equation (1.1). However, they consider time units that are so small that at most one event can take place: one of the N individuals dies at random and is replaced by one individual of the same species or by one individual of another species with probability proportional to the relative abundance of each species. Then, with probability ρ, the replacing individual may mutate into another species. In practice, if $n_j(t) = N_j$, $j = 1, 2, \ldots r$, $\sum_{j=1}^{r} N_j = N$ (r being the number of possible species) and the transition is from species k to species i, then $n_k(t+1) = N_k - 1, n_i(t+1) = N_i + 1$. The species i may be one of the species already present in the community or a new species. Obviously, k may coincide with i, and in this case, nothing changes after one time unit. The number of species r is considered to be very large because it includes not only the species that are actually present in the community but also those that might arise because of speciation or immigration (of course, these latter species are characterized by $n_j(t) = 0$ and $n_j(t+1) = 1$ if t is the time of speciation immigration). Karlin and McGregor [45] have found that for $t \to \infty$ and $r \to \infty$ the expected species abundance distribution $\phi_j = E\left[n_j\right], j \geq 1$ is given by

$$\phi_j = \frac{1}{j}\frac{N\rho}{1-\rho}\left(\begin{array}{c} \frac{N}{1-\rho} - j - 1 \\ N - j \end{array} \right)\Big/\left(\begin{array}{c} \frac{N}{1-\rho} - 1 \\ N \end{array} \right). \qquad \textbf{(1.8)}$$

It is interesting to observe that Equation (1.8) formally coincides with Equation (1.6) of Box 1.1 if one sets $\nu/\beta = \rho N/(1-\rho)$. Note that Equation (1.6) was obtained from a time-continuous stochastic process in which ν is the instantaneous rate of new species arrival in the whole community. Since $1/\beta = 1/\mu$ is the average generation time of each species, the quantity ν/β is the average number of new species arriving in the community per generation. Instead, Equation (1.8) derives from a time-discrete stochastic model in which ρ is the speciation probability per individual in a time unit. In any case, expressions (1.6) and (1.8) are equivalent in terms of data

fitting because they have the same form as a function of the abundance j.

Using Equation (1.8) [45], one obtains the probability that two individuals are of the same species. It turns out to be given by $1/(1 + N\rho - \rho)$, which for small speciation probability ρ, large N, and finite $N\rho$ is very well approximated by

$$\bar{f} = \frac{1}{1 + N\rho}.$$

This expression is the same as Equation (1.2), provided one sets $2\gamma = \rho$. The factor 2 is simply due to the fact that Equation (1.1) was obtained by assuming that two individuals may mutate at the same time, while [45] assume that at most one individual can mutate in each time unit.

1.2 Neutral Individual-Based Models on Networks (and Beyond)

One example, and an early suggestion that was instrumental in directing our thinking, stems from an application of the neutral model of biodiversity [34]. It deals with the quantitative assessment of the role of directionality and network structure on ecological organization. A word of caution is in order, as the exercise that we present here might be somewhat misleading. In fact, many factors other than network configuration and transport anisotropy are operating in nature, playing different but obviously relevant roles. However, inclusion of all factors, no matter how detailed and realistic, hardly seemed a good starting point for the pursuit of any generalizable signatures like the one we are taking on at this point [21]. Here, in fact, we first show results from a baseline, rather abstract theoretical model that focuses on the fundamental differences between the topology of river basins and 2D landscapes. The neutral theory offers the elements for a basic dynamics capable of maintaining biodiversity. Despite its bold (and in many cases unrealistic) assumptions, the neutral model has produced many important results, even after having been tested extensively against empirical data – many features shown by real systems do not require a more complicated model [51]. Patterns predicted by the neutral theory can also arise from nonneutral interspecific dynamics in the presence of some stochasticity and high species richness, thus widening the range of applicability of the theory. Despite its success, it is crucial to recognize that the neutral theory overlooks much ecological information,

for example, species-specific information that is required when studying the dynamics of the system or of particular species and the interactions among them [39]. In any event, employing the neutral theory is generally justified as long as steady state biodiversity patterns are addressed (but see [39]). Here, we show how the implementation of the neutral theory behaves in 2D lattices or 2D space-filling trees imposing directional dispersal [21, 40]. Two different frameworks, namely, an individual-based model and a metacommunity model, are introduced to that end. Contact models are introduced much later, in Section 3.2.3.

Box 1.2 Species Diversity in Neutral Metacommunities

The main tenet of the unified neutral theory of biodiversity [34] assumes that selection, in this context the difference in competitive ability of species, is turned off in the making of species diversity, and – a bold statement indeed – that all species' vital rates are equivalent at a *per capita* level. The main ecosystem-forming processes are therefore simply drift, countered by speciation or dispersal. It should be noted here that originally all neutral theories were meant to be spatially implicit, in that they considered isolated communities whose survival depended on speciation, or a local connected community, whose survival was guaranteed by immigration from some background metacommunity providing immigration rates and their composition.

The neutral theory of biodiversity [34], with its minimal set of assumptions and parameters, has been the subject of a lively debate that peaked about 10 years ago, proving both influential [49, 51–53] and controversial [54–57] as an explanation of biodiversity patterns. Here, we are interested in testing and exploiting the theory (as in [8]) across ecosystems, not simply in two-dimensional landscapes or in mean-field contexts, to which other spatial aspects contribute only weakly [34, 49, 52, 57, 58]. This book, in fact, focuses on the search for implications of hydrologic controls placed by river networks functioning as ecological corridors, a highly constraining *milieu* where landscape effects matter decisively.

The overall context that we need to explore here shares the concerns of the early biogeographers: what conditions are to be met for a species to occupy a site and maintain a population there? In this context, three factors matter: dispersal ability, habitat suitability, and susceptibility to biotic filtering [59]. In words, a species must be capable to reach the site by accessing the region and disperse therein; the climatic drivers and, more generally, the abiotic environmental conditions must be ecophysiologically suitable for the species; and the biotic environment, the whole of the relevant biological interactions, must meet a minimum of species' needs. Dispersal capacity from areas where the species is endemic (or simply exists) is key. Its nature includes the biogeographic natural history of the species embedding all factors limiting its spread from the places where they first originated. This, naturally, includes barriers to migration, the roles of biotic and abiotic dispersal vectors, and the suitability of the landing site from all biological viewpoints [59] – in brief, all it takes in terms of the environmental conditions that a species needs to settle, grow, and maintain a viable population. If landscape effects are key, lesser importance lies in biotic interactions with other organisms, either favorable (like mutualism and commensalism) or unfavorable (like predation and competition), in shaping local communities. Biotic interactions may or may not include environmental constraints on communities, such as the concept that whole communities (and ecosystems thereof) may experience species composition limited by environmental carrying capacities or defining roles of ecosystem engineer species that manipulate their environment favoring other species [59]. Pinpointing the relative importance of the various effects is case specific and primarily requires examining ecological patterns along geographic and environmental gradients (Sections 2.2, 2.4, and 2.5). Moreover, the

Box 1.2 *Continued*

examination of specific population dynamics (Chapter 3) will explore whether individual populations of a species may persist in suboptimal conditions and, in such a case, what factors affect the intrinsic vital rates (say, growth and death rates), determining ultimately their steady state abundances. Fluctuations induced by population dynamics that prompt environmentally suitable sites to become unoccupied may also be a factor, ofter blurring a clear-cut interpretation of species–environment relations [59]. Despite stochastic fluctuations, however, species distributions in space are most often expected to respond to major features, perhaps not simply local environmental determinism [59], that control their potential and realized ecological niches (Box 2.9). Cases where this does not happen would be such that fluctuations in demography and the strength of biotic interactions are so large that species–environment relations would be clouded. While this is obviously not excluded in real ecosystems, the general aim of this book prevents inclusive efforts in that direction.

The threefold influence of dispersal, niche, and biotic interactions shapes species distributions in space (say, within specific dendritic and dendrite-derived landscapes in our case). It may be deconstructed in many cases of interest, viewing their components as separate entities treated like specific boundary conditions [59], and yet suitable conditions for a species lie at the intersection of the ensemble of factors that determine the individual suitabilities. Also, one must consider that obviously a species may not colonize a site for reasons other the the ones accounted for above. In particular, human disturbances, so as to say, may prevent the establishment of virtually any species, inasmuch as – accepting, for example, the idea that the size of the largest species surviving in an ecosystem is related to the ecosystem's size [60, 61] – habitat fragmentation has a long-term impact that may have long-established endemic species go locally extinct. However, once locally extinct, one may assess whether the species might be capable of recolonizing the same site once again, possibly because of dispersal [34] (see also Section 1.3).

How and where species have emerged from evolutionary processes may explain patterns of biodiversity at any scale. Speciation causes, whether allopatric (where geographic barriers split the range of ancestor species disrupting gene flow between the separated populations and ultimately leading to distinct species or subspecies) or sympatric (where divergence is due to ecological specialization), are known to be numerous (see, e.g., [62]). For the limited purposes of this book, it is sufficient to acknowledge that geographic or ecological speciation processes have occurred, and continue to occur at a slow pace (Section 1.3), because our focus is firmly placed on how speciation may shape future patterns of species distribution in complex landscapes shaped (or constituted) by fluvial processes. Rather than questioning whether (and how) species resulting from specific speciation processes would result in more/less specialized features, we shall sample a large number of neutral traits on noninteracting species and observe landscape effects under the null model provided by the neutral theory of biodiversity – with a few nonneutral ingredients at times selectively added to zoom in on the network perspective we pursue. It is also a matter of scale, of course. At continental scales, biogeographical history and dispersal limitation predominate, and environmental suitability plays secondary roles in explaining the geography of a focus species [59]. This perspective will have to be extended when studying biological invasions in networked environments (Chapter 3), because the effects of niche changes (Box 2.9) between native and invaded ranges may pitch in loudly when considering whether biological invasions are at all possible.