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Andrea Rinaldo , Marino Gatto , Ignacio Rodriguez-Iturbe
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River Networks as Ecological Corridors

River networks are critically important ecosystems. This interdisciplinary book provides an integrated ecohydrological framework blending laboratory, field, and theoretical evidence that changes our understanding of river networks as ecological corridors. It describes how the physical structure of the river environment impacts biodiversity, species invasions, population dynamics, and the spread of waterborne disease. State-of-the-art research on the ecological roles of the structure of river networks is summarized, including important studies on the spread and control of waterborne diseases, biodiversity loss due to water resource management, and invasions by non-native species. Practical implications of this research are illustrated with numerous examples throughout. This is an invaluable go-to reference for graduate students and researchers interested in river ecology and hydrology, and the links between the two. Describing new related research on spatially-explicit modeling of the spread of waterborne disease, this book will also be of great interest to epidemiologists and public health managers.

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River Networks as Ecological Corridors

Species, Populations, Pathogens

By

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Non quia difficilia sunt non audemus,
sed quia non audemus difficilia sunt

Not because things are difficult that we do not dare,
but because we do not dare they are difficult

Seneca, Letter to Lucilius (194,26)

Ἄριστον μὲν ὕδωρ
Greatest indeed is water

Pindar, Olymp. 1,1

It's all in the water

Mary Knapp Parlange

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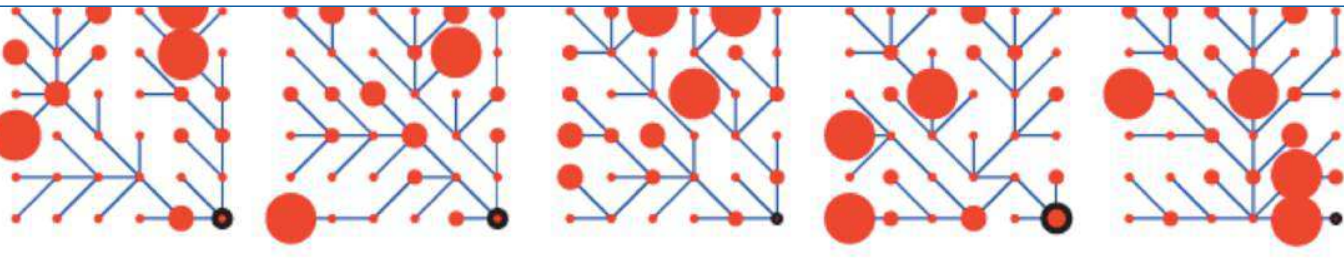

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Preface

This book draws together several lines of argument to suggest that an integrated ecohydrological framework that blends laboratory, field, and theoretical evidence focused on hydrologic controls on biota has contributed substantially to our understanding of the function of river networks as ecological corridors. This function is relevant to a number of key ecological processes. Jointly with other determinants that this book will discuss, these processes control the spatial ecology of species and biodiversity in the river basin, the population dynamics and biological invasions along waterways, and the spread of waterborne disease. As revealing examples, here we describe metapopulation persistence in fluvial ecosystems, metacommunity predictions of fish diversity patterns in large river basins, geomorphic controls imposed by the fluvial landscape on elevational gradients of species' richness, zebra mussel invasions of an iconic river network, and the spread of proliferative kidney disease in salmonid fish. Our main tenet is that ecological processes in the fluvial landscape are constrained by hydrology and by the matrix for ecological interactions (notably, the directional dispersal embedded in fluvial and host/pathogen mobility networks). Accounting for these drivers requires spatial descriptions that have produced a remarkably broad range of results that are worth being recapped in a book illustrating the coherent framework that produced them. In brief, this book investigates how the physical structure of the environment affects biodiversity, species invasions, survival and extinction, and waterborne disease spread, from the (somewhat narrow, yet, in our view, significant) perspective of ecosystems produced by fluvial processes and forms whose origins and features have long been a focus of study.

As we began exploring somewhat systematically the possible ramifications of these interests, either theoretical or grounded in relevant field or laboratory evidence, we realized that drawing together much scattered work would require a synoptic account of what ties the various topics together. This proved to be a trying task, however, especially given the pace with which novel and exciting contributions were (and are) emerging in supposedly disparate fields. It was thus necessary to conclude the writing of this book even in the face of continual changes in the field. However, this book is timely. We believe that it meets its initial aim, described in a nutshell in the introductory paragraph. More importantly, perhaps, our survey of the current cultural landscape of the discipline highlights key research questions that remain to be addressed, of which there are many. Although the material presented here is prone to aging quickly, owing to the broad interest that the topics are currently attracting, we think that showing the basic unity of the topics, at least from a conceptual viewpoint, is worth the effort, as this unity is largely overlooked in the literature to date. From the synoptic view given here, our line of thought should appear in its full coherence, if not in its perceived generality – or so, of course, we hope.

Over the course of several years, we have contributed to defining the field of ecohydrology which describes hydrologic controls on biological systems. Early examples were soil moisture dynamics controlling (when limiting, of course) plant growth in a semiarid landscape and flow distributions acting as the master variable of stream ecology. We sought to investigate how the very texture and fabric of river networks define the corridors for species biodiversity, population migration, and the spread of disease. We hoped to define general rules, because we have learned much in recent years about recurrent hydrologic properties that hold regardless of climate, vegetation, or exposed lithology – the universality of the geometry of nature in shaping the scale-free structure of the river basin. Thus we began constructing models of ecosystems in which these universal characters would feature explicitly. In early models, which we describe in the beginning of this book, each node in the model represented a metacommunity or a small ecosystem. Dissecting its behavior served us well, no less than simulating the ever-changing fish populations in the Mississippi–Missouri river network, finding that variable river runoff influences fish dispersal, habitat size, and metacommunity dynamics, ultimately affecting biodiversity. Regardless of whether the model was realistic, the patterns derived from a minimalist model – fed by a proper geometrical substrate for interactions – intrigued us. So, together with several collaborators over the years, such as groups developed at EPFL, Padova, Princeton, and Milano, at times collectively, we turned our attention to population migrations, using as a pivotal example the

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American westward migration of the nineteenth century. The finding that a diffusion model of migration, in which migrants diffuse isotropically through space, could not adequately explain the rates of westward expansion gave us pause. In times in which freedom of migration was at stake, our interest grew by the day. A simple assumption that colonizers moved strictly along river networks showed a key improvement in modeling the speed of the migration wave. Remarkably, laboratory experimentation supported the theoretical and empirical result: directional dispersal has a life of its own and in turn defines key biodiversity properties.

Attention to spatial models of a different type of population migration (a waterborne disease epidemic) was the next logical step. Together with our collaborators, we published in 2008 the first spatially explicit model of cholera epidemics. In a January 2011 paper, our team used the model to predict the spread of cholera in Haiti following the devastating 2010 earthquake. The model proved prescient. From there, we focused progressively on better and more robust tools to assimilate data in real time to predict how the intertwined processes of pathogen transport via waterways and via human mobility affect the epidemiological connection of nodes – the human settlements where disease can develop and diffuse – and thus drive the dynamics of an infection.

This book was born out of a review paper that we wrote for the fiftieth anniversary issue of *Advances in Water Resources*. The material has been substantially expanded, however, especially from a methodological viewpoint. Methodological detours have largely been inserted into the main text as boxes, which, we hope, will help to maintain the flow of the presentation.

The motivations for writing this book extend further. The boy from Bangladesh shown in the cover photograph drank the water of the mighty Meghna River to convince one of us (AR) that no harm would result. This happened a few hundred meters away from the largest hospital in the world devoted to the treatment of diarrheal diseases, in a region with one of the highest endemicities of cholera (and where the pathogen originally evolved to irradiate globally). As it turns out, predicting such a simple outcome (will the boy get cholera?) is plagued by so much uncertainty – given the unknown concentration of the possible leakages or spillovers from the hospital's sewers, the rates of decay of bacteria in open waters, the hydrodynamic dispersion that commands the point concentration of pathogens in time (relevant because the threshold for infection is dose dependent), to name a few factors – that the resulting weakness of our predictions is a permanent liability affecting our capability to put a price tag on ecosystem services (in this case, safe drinking water). This is a key point of our reflection.

In fact, an emerging literature, largely referred to as environmental economics, integrates development and environmental thinking by focusing on economic evaluation and on the development of the proper notion of sustainable development. An idea recently put forth, by Partha Dasgupta in particular, is that it is now clear that by "economic growth," we should mean growth in wealth – the social worth of an economy's entire set of capital assets, including its natural capital and hence the ecosystem services embedded in it – not only growth in gross domestic product (GDP) or the many ad hoc indicators of human development that have been proposed in recent years. Dasgupta writes that the very concept of wealth invites us to extend the notion of capital assets and the idea of investment well beyond conventional usage. As such, by "sustainable development," we should mean development in which wealth (per capita) adjusted for distribution does not decline in time. This has radical implications for the way in which national accounts are prepared and interpreted. ("These are still early days in the measurement of the wealth of nations, but both theory and the few empirical studies we now have at our disposal should substantially alter the way we interpret the progress and regress of nations" – excerpted from Dasgupta's "*The Nature of Economic Development and the Economic Development of Nature*" [1].)

As a matter of fact, we all seem still to be – so as to say – under the spell of Kuznets's paradigm, that is, the one suggesting that the growth in standard economic indicators would mirror a systematic reduction of social inequalities. More precisely, he said that inequality rises first, to be followed later with more capital accumulation by inequality reductions. To be fair, Kuznets was very cautious in defining the range of validity of his theory to hold only under special circumstances, and yet the main point that came across is that a stronger economy would lead to a better society – or so, of course, we thought, in the spirit of the liberalism inspired by the towering figure of the distinguished expatriate economist. Enter Thomas Piketty and his analysis of *Capital in the XXI Century*, following economists like Sen, Barbier, Fisher, and Turner, and the fake Kuznetsian world collapses, as it is clear (empirically and factually) that growth in wealth indicators does not correlate with reduction in inequalities; on the contrary, inequalities tend to be exacerbated. Wealth inevitably follows a power law distribution in a steady state of the dynamics of any economy implying

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that often (the percentage would depend on the scaling exponent, in fact) 80 percent of the wealth is in the hands of the richest 20 percent of the population. Piketty convincingly argues that the data upon which Kuznets's tenet was established are an artifact of the conditions faced by rapidly recovering societies post–World War II, and a reanalysis based on current data – including the original data – shows strikingly different results.

Why does all this matter for our book? Economic indicators that omit the depletion and degradation of natural resources and ecosystems are at best misleading – we must account for the depreciation of natural capital in appraising the wealth and poverty of nations. Natural capital must include the value of net losses to natural resources inflicted by the societies shaped by development thinking, that is, stacked against nature *sensu* Dasgupta, as opposed to those shaped by environmental thinking. Natural capital assets include minerals, fossil fuels, forests and similar sources of material and energy inputs, and – critically – those of all ecosystem services often impaired by purely economic development. If one views ecosystem services as incomes, that is, flows as opposed to reservoirs, one may see whole ecosystems as a capital asset. In any case, if we use up more natural capital to produce economic output today, then we have less for production tomorrow. At the same time, we are also squandering valuable natural capital – ecosystems provide important goods and services to the economy, such as recreation, flood protection, nutrient uptake, erosion control, water purification, carbon sequestration, and clear water to protect against waterborne disease. By converting and degrading ecosystems, we are depreciating important ecological capital endowments.

Economic indicators change dramatically when the depletion and degradation of natural resources and ecosystem services are accounted for. Unfortunately, natural capital tends to be undervalued because it is unique, hard to put a price tag on, poorly understood, and difficult to measure. Consider one example touched upon in Chapter 4 of this book: the case of schistosomiasis spread and water resources development. Schistosomiasis is a chronic parasitic waterborne disease that affects an estimated 779 million people at risk of contracting the disease, of whom 106 million (or 13.6 percent) live either in contexts where irrigation schemes have been constructed or in close proximity to large or small dam reservoirs. Compelling evidence has been gathered by studies that examined the relation between water resources development projects and the spread of schistosomiasis, primarily in sub-Saharan African settings, where a stunning 90 percent of the world's burden is concentrated. This is clearly related to the expansion of the range of the obligatory intermediate host for the parasite (some species of freshwater snails) and by the reduced mean distance of human settlements from the nearest water body – infection occurs through direct contact with water through skin penetration of the parasite. As an illustration, one of our students doing fieldwork on the disease in Burkina Faso became infected because once, and only once, he had removed his protective gloves to pick up a pair of scissors that had fallen into water at the test site. It is beyond doubt that the development and management of water resources are important risk factors for schistosomiasis, and hence strategies to mitigate negative effects should become integral to planning, implementing, and operating future water projects.

But how? While the impact of improved agriculture is perceived immediately and directly by, say, the GDP of the region implementing the water resources use scheme, the social and economic costs of the increased burden of the disease are hard to quantify, let alone predict. A debilitating disease, schistosomiasis is a poverty-reinforcing neglected disease owing to its low mortality and impact on the poorest alone. While contemporary economics is considering the proper manner in which to account for the social and economic costs of future loss of the workforce, immaterial factors weigh in, and an assessment seems unlikely anytime soon. Pricing is key in some circles. A price tag means discounting the environment, and pricing is necessary inasmuch as declaring that some good cannot be priced is tantamount to assuming that its worth is next to nothing. Others contend that price is not value, and accepting that it is impossible to price all ecosystem services may be way toward giving them nonmonetary value. Material and immaterial values should then be considered in their own units (say, the number of species rescued from extinction or the number of cases avoided in epidemics). Not surprisingly, therefore, pricing biodiversity and ecosystem services has been termed the "never-ending story."

Key to all the above is our capability to assess and reliably predict the spread of the disease under different scenarios – economic and water development; human mobility and awareness of the mechanisms of infection (hinging on proper educational systems); improved or worsening water, sanitation, and hygiene conditions. In this sense, this book, focused as it is on the prediction power of spatially explicit epidemiology and centered on the robustness of the structure of waterways acting as a

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substrate for ecological interactions, provides, we hope, significant account of the progress recently made. Such progress, it is the authors' belief, is ready to be used for the betterment of society at large and to help in assessing the wealth or poverty of nations.

As an economy's GDP could be made to grow, and its related societal indicators made to improve for a time, by mining natural capital (say, by decimating forests, damaging soil, destroying key ecosystem services by depleting renewable resources or reducing biodiversity), there is no excuse for not using what we have learned to assess the true costs and benefits of development thinking and to rethink distributive justice, where a large share of the basis for environmental thinking could be made quantitative. This is the case, in our view, for river networks as ecological corridors. Will future large-scale water resources management plans include a reduction in the loss of biodiversity across scales in river basins? Could the structure of river networks be a template for the large-scale spread of waterborne disease? Are we capable of making a compelling economic argument for preventing water development schemes in light of the social and economic costs of the predicted increased burdens of disease they would bring? Do biological invasions, including historic population migrations that shaped human community compositions as we see them now, depend on the topology of river networks as the substrate for their dispersal? The answers to these questions are largely positive in our view, as the reader will gather from her reading, and at the heart of the future development of ecohydrology, a recent field of growing importance. Social discounting applied to public policies concerning the preservation of natural capital needs quantitative assessment and thus an "engineering" capable of producing reliable scenarios. Evaluations of the effects of learning-impairing disabilities brought by neglected waterborne diseases are not ethical primitives, nor do they have observable market value like the return rates on an investment. They need reliable projections, evaluations of management alternatives, and proper cost–benefit analyses. This is only possible if we are capable of evaluating material/immaterial and present/future commodities. Our ignorance of the true economic value of natural capital is often an unsurmountable barrier to proper policy analysis. Contributing to lifting this veil of ignorance seems like a worthwhile endeavor because no economy can survive without natural capital. In the case of the ecosystem services provided by the river basin, we show that the time is ripe for retooling our decision-making basis.

Large-scale water management plans currently do not consider protection of biodiversity. Why? Because bioversity protection has been perceived as mission impossible. Instead, we show that explicitly accounting for the constraining role of river networks acting as the substrate for the relevant processes and interactions makes a substantial step toward much improved predictability of quantitative evaluations. This is central to contemporary thought centered on how a society develops a collective consciousness of the meaning of the fair distribution of water, and thus of material and immaterial resources and ecosystem services, across different individuals and events of various natures across Time (capitalized, as Proust would have it).

A word of caution is in order at this point. We ask the reader to be forgiving, for, in this book, we have often resorted to using boxes, at times quite long but clearly highlighted. This stems from the fact that technical detours can distract from the main flow of the scientific discourse, which we believe shows a notable coherence. Some of these boxes are indeed highly technical and could be skipped, unless the reader is interested in replicating results or desires an in-depth understanding of a topic. We wondered whether it would be worthwhile to write much of the material at a somewhat lower technical level, as not many upper undergraduate courses exist on these topics. We have decided against doing so, but we also agreed to add road maps, especially in the openings of boxes aimed at more technical material, warning the reader about the difficulty of their contents. A few boxes are technical but kept at a fairly elementary level and, we hope, are self-contained: we placed them on purpose to encourage less specialized audiences to access most of the material contained in this book. Typically, they explain some of the basic background methodology not just for advanced undergraduates but also ideally for graduate students and researchers who may need a brush-up or are entering the field from different disciplines. They would be most welcome, in fact: we love contamination of different genres, as will become apparent to the reader.

In terms of audience, we believe that our target is mainly graduate students and researchers in earth and environmental sciences, in particular, in ecology and hydrology (and their meeting point, ecohydrology, i.e., water controls on living communities). All in all, we expect this book to appear on recommended reading lists for advanced undergraduate courses at a few universities that might have professors interested in these topics and in the peculiar synthesis of disciplines hitherto unconnected provided by the areas where this book has

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developed. We also wish to warn the reader that the diversity of phenomena described in this book, many of them pertaining to different disciplines with their own typical symbolic notations, made it impossible even to attempt a normalization of notation throughout the book. Thus we apologize that in different contexts, we allow ourselves to use the same symbol for different meanings. As an example, we beg the reader to tolerate that the symbol ρ is used in Chapter 3 for denoting the density of an invading species, whereas it denotes the rate of loss of acquired immunity in Chapter 4. These are standard notations in the as yet unconnected fields of biological invasion in rivers and epidemiology of water-related disease.

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Obviously, we leave it to the reader to judge the strength and coherence of our arguments, which seem quite compelling to us. Regardless of the outcome, putting this book together has been a very rewarding journey, both personally and intellectually.

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