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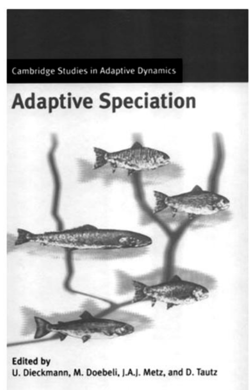
Book Review

DIECKMANN, U., M. DEOBELI, J. A. J. METZ & D. TAUTZ, 2004. Adaptive speciation. Cambridge University Press, *xii* + 476 p., 15.5 × 23.5 cm, hardback, US$100.00, ISBN 0-521-82842-2.

Evolutionary processes result in two major outcomes, the evolution of adaptive traits within existing species and the formation of new species via speciation. Although adaptation proceeds by natural selection, speciation may or may not involve a role for selection. Speciation driven by natural selection is of inherent interest to biologists, because it provides a bridge between the study of microevolution within species and the study of macroevolutionary diversification. Interest in the role of selection in speciation dates back to Darwin (1859) and to the modern synthesis (Mayr, 1947; 1963; Dobzhansky, 1951), but has received renewed interest in the last decade (Funk, 1998; Schluter, 2000; Gavrilets, 2004). This resurgence has been accompanied by a reclassification of models of speciation from geographic to process-oriented ones, although the two are certainly not independent.

Due to the preponderance of the biological species concept (Mayr, 1963), speciation research has primarily been concerned with the evolution of barriers to gene exchange between diverging taxa (*i.e.*, reproductive isolation; see Coyne & Orr, 2004). Amongst most biologists, reproductive isolation is thought to arise indirectly as a 'by-product' of genetic differences that evolve between geographically-separated populations. The book *Adaptive Speciation* by Dieckmann, Deobeli, Metz and Tautz challenges this paradigm.



Briefly put, this book considers speciation processes whereby divergence is an adaptive response to disruptive selection caused by frequency-dependent biological interactions. Thus adaptive speciation, by definition, occurs under conditions of geographic contact rather than geographic isolation. To the extent that challenging existing paradigms promotes scientific progress (Kuhn, 1962), this book may come to represent an important contribution.

A brief review of the history of speciation research is likely to illuminate the other ways in which this book is useful. Contrary to a currently popular belief, thinking about speciation dates back to Darwin, who is often criticized for not discussing speciation and for being ambiguous about the nature and reality of species (*e.g.*, Coyne & Orr, 2004; but see Mallet, 2005 for an alternative view). Although Darwin's ideas about speciation were understandably less-developed than those of current evolutionists, both these criticisms are at least somewhat unfounded.

First, in the Origin of Species (1859) Darwin visualized a role for natural selection in population divergence and speciation "the principle of benefit derived from divergence of character ... will generally lead to the most divergent variations ... being preserved and accumulated by natural selection ... until a sufficient amount of variation has been accumulated to form it into a well-marked variety" (pp. 117, note Darwin considered species as nothing more than such 'well-marked varieties', a thesis with ramifying implications). Moreover, he discusses how such divergence could be driven by disruptive selection such that "the most distinct varieties ... have the best chance of succeeding" (pp. 155).

Second, as a naturalist Darwin knew that species could be recognized and demarcated. He did not think that species lacked boundaries, stating that "species come to be tolerably well-defined objects, and do not ... present an inextricable chaos of varying and intermediate links" (pp. 177). Instead, he preferred to view all evolution, including speciation, to arise from divergence of character in response to selection. Species were delimited from varieties, but only with respect to the magnitude of divergence, "these forms may still be only...varieties; but we have only to suppose the steps of modification to be more numerous or greater in amount, to convert these forms into species...thus ... species are multiplied" (pp. 122). Darwin did not attach as much importance to reproductive isolation as did the founders of the modern synthesis, although he certainly did consider it (*e.g.*, in his discussions of hybrid sterility). Instead, Darwin focused on divergence via selection and thought speciation could arise in the absence of complete geographic isolation.

The modern evolutionary synthesis of the mid 20th century saw the emergence of the biological species concept and the idea that reproductive isolation was essential to, and a defining characteristic of, speciation (Mayr, 1963). Gene flow between taxa prevented speciation and new species were thought to arise simply as a 'by-product' of changes that occurred in allopatry, by selection, by random genetic drift, or by a combination of these factors. Interest in both the mechanisms and the geography of speciation waned. Given geographic isolation and enough time, speciation was seen as inevitable and it was rarely, if ever, seen as adaptive.

In contrast, much recent work on the process of speciation has focused on whether and how selection accelerates the rate at which reproductive isolation evolves (*e.g.*, Funk, 1998; Schluter, 2000). However, opposing camps still exist. In the monumental, timely and exhaustively researched book *Speciation*, Coyne and Orr (2004) explicitly espouse the views of the modern synthesis; speciation is argued to occur primarily in allopatry as a by-product of genetic changes (albeit there is increased recognition of the role of selection). The book *Adaptive Speciation* questions this dogma and openly challenges the idea that reproductive isolation is usually a 'by-product' of allopatric divergence. By focusing on the role of population interactions and selection in sympatry, and on the concept that divergence itself can be adaptive, it represents a movement towards a more Darwinian view of speciation (a chapter by Will Provine provides a more complete historical summary). This clear shift in focus sets *Adaptive Speciation* apart from Coyne and Orr's book on speciation published the same year.

The book itself is organized into three components: 1) theories of speciation, 2) ecological mechanisms of speciation, and 3) patterns of speciation. The basic tenets of adaptive speciation are outlined in the first section. It is argued that frequency-dependent interactions among individuals generate disruptive selection, which splits a single population into two even when resource distributions are unimodal (see Gourbiere & Mallet, 2005 for a critique of adaptive dynamics). These ideas are nicely rounded out by two chapters on more 'traditional' theories of speciation in sympatry (by T. Kawecki) and para/allopatry (S. Gavrilets). Chapter 7, by Doebeli and Dieckmann, is perhaps the most thought provoking and is referred to throughout the book. It examines the effects of spatial structure on speciation and argues that parapatric range distributions actually arise from interactions occurring in sympatry, such that current day ranges cannot be used to support allopatric speciation. Overall, the fist section, theory section, is excellent. One criticism is the weak treatment of speciation arising from selection to avoid maladaptive hybridization (*i.e.*, reinforcement, Dobzhansky, 1951). Reinforcement can be viewed as adaptive speciation because it involves selection, requires geographic contact between taxa, and is frequency-dependent such that greater encounter rates between heterospecifics can facilitate divergence (Noor, 1995; Kirkpatrick, 2000; Nosil *et al.*, 2003). Perhaps it was downplayed because it is a legacy of the modern synthesis (Dobzhansky, 1951).

The second section deals with ecological mechanisms of speciation and provides useful and clear summaries of empirical studies of speciation in cichlids, sticklebacks and other freshwater fishes, phytophagous insects, agricultural pests, flowering plants and experimental bacterial populations. The third section deals with patterns of speciation and, once again, provides summaries of speciation work in *Anolis* lizards, montane plants and fishes in Mesozoic rift lakes. Attempts are made to determine whether empirical results support, or refute, adaptive speciation.

Each of the three sections of the book are, on their own, excellent. However, where the book falls short is in forging links among the separate sections. In fact, even the two empirical sections, on process and pattern respectively, appear disconnected. In defense, generating clear associations between pattern and process is not easy. Moreover, the studies in the empirical sections were not explicitly designed to test adaptive speciation theory, making a union between theory and data especially difficult.

To conclude, despite sounding negative at times, the utility of this book is great. It provides an overview of speciation theory from several points of view and provides summaries of some of the best empirical research programs on speciation. The book provides fresh ideas and the chapters dealing explicitly with adaptive dynamics challenge the views of the modern synthesis. Ultimately, this book will be useful to anyone interested in speciation. In particular, it should be read by those interested in ideas on speciation that differ, be they right or wrong, from the dominant views espoused since the 1940's. My view after reading four recent books on speciation (Schluter, 2000, Coyne & Orr, 2004; Gavrilets, 2004; Dieckmann *et al.*, 2004) is that when it comes to the process and geography of speciation, the verdict is still out.

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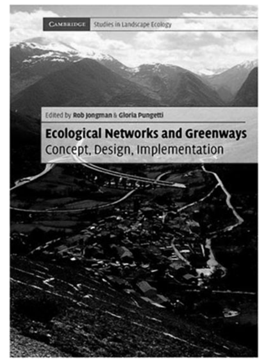

JONGMAN, R. & G. PUNGETTI (eds.), 2004. Ecological Networks and Greenways: Concept, Design, Implementation. Cambridge University Press, *xxi* + 345 p., 17.5 × 24.5 cm, paperback, US$50.00, ISBN 0-521-53502-6.

World population is projected to grow by 1.83 billion people between 2003 and 2030 – all in urban areas and most (85%) in less developed regions of the world (United Nations, 2004). As people spread over the globe, their cities, roads, and farms fragment remaining undeveloped areas, jeopardizing many other species. There is increasing recognition that biodiversity conservation cannot afford to ignore developed landscapes and that more integrated approaches to planning and development are needed.

Against this backdrop, *Ecological Networks and Greenways* fits nicely into an emerging vision of a world in which core protected areas and the surrounding developed lands function synergistically to support vibrant ecological and human communities. In the introductory chapter, Jongman and Pungetti describe how ecological networks – which include core protected areas, buffer zones, and corridors linking these components – arose from efforts to conserve biodiversity. Greenways arose from efforts to create connections for people, allowing them to access the countryside and providing links between urban and rural lands. The lines are not drawn sharply, and both terms have evolved to embrace multiple purposes consistent with sustainable land use.

Ecological Networks and Greenways, the second offering in the *Cambridge Studies in Landscape Ecology* series, contains 16 contributed chapters that explore these conservation tools in some breadth and depth. The focus is on "...how ecological networks and greenways can be developed on the ground after the theoretical basis has been established (p. *xviii*)" and the book is aimed at scientific, design, and planning audiences. The contributions are generally well written, though the tone changes markedly from chapter to chapter – not unexpected for an edited volume. Less excusable, several maps have poor resolution, indistinguishable shades of gray, or confusing legends. A number of the graphs contain unnecessary clutter (the kind that Excel software generates by default) and the choice of legends could have been better in some. Some standardization among chapters could have improved the graphs and maps.

The volume presents many aspects of ecological networks and greenways in Europe and the Americas, including scientific concepts and theories, planning and design considerations, and the policy dimensions, broad collaboration and public participation needed for successful implementation. The first three chapters define ecological networks and greenways and place them in historical context. They are somewhat duplicative in technical content, but it is worth reading them all to experience the differences between European and American history and perspectives. The following 12 chapters present examples with varying degrees of conceptual, technical, policy, and implementation detail. The concepts and examples presented range from individual greenways, through citywide greenway systems, to regional, multi-national, and continental ecological networks. The editors summarize the issues and challenges in the final chapter.

Common threads permeate the book: the importance of designing networks for explicit functional goals; the need to consider networks from the perspective of the species that will occupy them; the need to resolve conflicts between human and green infrastructure (*e.g.*, the ecological "black spots" where roads and ecological networks meet); the tension between designing networks for multiple uses and avoiding conflicts among uses; the reality that "... no single theory, no single scientific or planning concept can be taken as universally applicable (p. 292)"; and the notion that political challenges to implementing ecological networks and greenways are currently greater than technical challenges.

Perhaps the most important thread is an explicit recognition that "nature conservation and land use planning are social actions (p. *xix*)". Consequently, a major theme that emerges is the importance of social context and networks to success. Simply put, the (re)creation of functional ecological networks depends on the development of collaborative networks among a broad array of people, including scientists, policymakers, transportation planners, open space planners, land developers, and, perhaps most importantly, the public at large. This is indeed an arena of great opportunity and formidable challenges. For example, Chapter 13 describes an ecological network in Florida, USA, that will include some 30% of the state's land. It has grown out of collaboration among environmental and transportation forces, has broad political and public support, and is extremely well funded. Yet, efforts to complete the network face considerable challenges from groups that support private property rights and the privatization of resources, and an economy based increasingly on land development. In Argentina, collaborative efforts to protect conservation land in the Yungas ecoregion are confronted by massive land use change (to agriculture), sharp socioeconomic disparities, high unemployment rates, and social unrest (Chapter 14).

In the final analysis, *Ecological Networks and Greenways* is an excellent volume for anyone interested in learning more about ecological networks and greenways. It would be a great book to read and discuss in a semester-long graduate seminar, or as part of just about any graduate course dealing with landscape ecology, conservation biology, environmental policy, or sustainable development. I can easily imagine individual chapters showing up on the reading lists of more specialized courses in a variety of disciplines. The contributors' inspiring visions and examples of a world in which people and institutions collaborate in the name of conservation are sure to incite readers to think outside the box.

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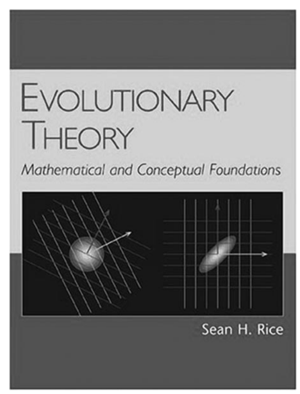
RICE, S. H., 2004. Evolutionary Theory: Mathematical and Conceptual Foundations. Sinauer Associates, *xiv* + 370 p., softcover, 15 × 22.5 cm, US$49.95, ISBN 0-87893-702-1.

With all the controversies, small and large, about the status of the "theory of evolution", it is refreshing to read a book that not only unabashedly takes a theoretical stance, but one that can give even experienced theorists a new insight into what they do. Like all theories, evolutionary theory explores the consequences of a particular set of assumptions, and, like most theories, uses mathematics to pursue those consequences beyond the reach of our intuition.

The traditional approach is "bottom-up", telling a story about genes (including mutation, selection, and drift) and deducing the observable outcomes. Rice does an elegant job of laying out this approach in the first five chapters of this surprising compact book, leading us from one and two-locus models of selection, through descriptions of drift and effective population size, to the integrative approach of diffusion theory (including the cleanest derivation of the Kolmogorov backward equation that I have seen).

Only after laying out this foundation does the book turn in what clearly is the author's true direction: the derivation of Price's theorem. I found two aspects of this presentation remarkable. First, the philosophical distinction between the "gene-based" approaches of classical population genetics and the "phenotype-based" approach summarized in Price's theorem can be thought to exemplify one of my favorite sayings (and one loathed by almost all of my students) that "it is smart to be stupid". One can think of gene-based theories as clever abstractions of what we are often really interested in (the phenotype). What Price achieved, as Rice shows, is taking on the problem of change over time at the level of phenotype "stupidly", by looking directly at the change of observables.

Second, Rice shows, in a way I had not imagined, that Price's theorem really does subsume gene-based approaches. His development of the theory of genetic drift was the clincher. I had a verbal understanding that Price's approach is driven by covariance between phenotype and fitness, and thus assumed that the model was only a model of selection. On the contrary, if one derives the variance of the covariance (an abstract-sounding but real object), and thinks of it as the degree to which predictability (selection) is unpredictable (drift), one can use the Price framework to study drift itself. To both the mathematician and the biologist in me, that's a beautiful unification.



Who is this book for? Certainly not for the mathematically timid, even though Rice assures us that it is for biology graduate students who "know a bit of evolutionary biology and a bit of mathematics". Like most books with substantial mathematical content, the casual reader will not get more out of this one than a sense of the possibilities of the approach. I must confess that I got pretty lost in Rice's discussion of developmental evolution, where the matrices involved in the usual theory are exalted into the rather more ethereal world of tensors. I look forward to enlightenment, as will likely occur as that branch of theory develops.

What's in it for the ecologist? Again, only the most mathematically determined ecologist would make it all the way through this book, even though some of the most relevant applications appear at the end. Rice presents a fairly standard chapter on evolutionary game theory at the end, and leaves out the more technical derivations of the methods of adaptive dynamics. Not surprisingly, the final chapter on multilevel selection, long the playground of Price equation aficionado, is clear, bold and illuminating. Rice minces no words in castigating those who refuse to understand that kin selection is a form of group selection, or who use a flawed derivation of Hamilton's rule to buttress evolutionary arguments.

Although the writing is always clear, a few more figures would have helped in following the arguments. For those who can weather the mathematics, the book is both a powerful overarching view of modeling evolution, and is full of gems of insight. If you wish to see how balancing selection can be thought of as migration or what the coalescent has to do with effective population size, this book is well worth the time and effort. As an ecologist, I find the approach more inviting than that of more narrowly defined population genetics books, and look forward to using these methods in my own work.

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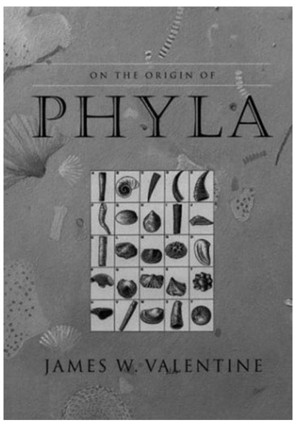

Valentine, J. W., 2004. On the Origin of Phyla. University of Chicago Press, *xxiv* + 614 p., 18.5 × 26 cm, hardcover, US$55.00, ISBN 0-226-84548-6.

It is a confident man who takes a blank sheet of paper and writes "On the Origin of Phyla" at the top. But confidence has been built into the human psyche by natural selection (see Johnson, 2004). Valentine writes that his title pays homage to Darwin, but he knows as well as anyone that it invites comparison between his book and the greatest book ever written on biology.

Valentine first lays out the framework within which we seek to understand the origins of phyla. In less than 200 pages he gives a masterly overview of classification, animal structure from cell to organism, development and its genomic underpinning, and the tension between molecular and anatomical data in seeking to define phylogeny. Another 50 pages summarize the nature of the fossil record, and describe the special difficulties that surround the apparently sudden appearance of metazoan phyla at or near the beginning of the Cambrian period.

The middle section of the book takes 200 pages to describe those attributes of metazoan phyla that may provide important evidence about their origins. These pages stress basic anatomy and development; adaptive diversity and ecology are downplayed because they are largely phenomena of the deployment of phyla, rather than their origin.

In the third section, Valentine looks at the data of the fossil record that relates to diversity and the reasons for its variation through time, essentially to argue that the patterns of the Cambrian are probably as real as those seen later: there is no need to appeal to extraordinary processes as we view the origin of phyla.

Finally, in the last 50 pages Valentine faces the question of the origin of phyla. He has led his 10,000 readers across mountains of data, avoiding swamps of superfluous facts and arid wastelands of useless argument. But we don't see the sea ahead: we see apparently endless hills of hypotheses. The reader looks in vain for the grand resolution that would cap this book. Valentine's last section is titled, "Why are problems of metazoan evolution so hard?"

Of course, no-one else has answered the question either. Valentine's effort did not fail for lack of scholarship or clear thinking. The major part of this book is a model of distilled information, expressed in terse, spare, clear English. No-one else has given us such a beautifully interwoven summary of the anatomy and development of the animal phyla, set in the modern framework of multidisciplinary, integrative biology. Valentine allows us to see clearly the problems of the origin of phyla, but can't help us to answer them.

I suspect the problem lies in Valentine's choice of input. Of course, all the data he synthesizes are vital to any answer. But those data are all descriptive and analytical. They describe and define metazoans, but in themselves cannot explain why they evolved: even the new data on genomes describe but do not explain. Natural selection acts on whole organisms, not on their anatomy, not on their developmental pathways, not even on their genes. Natural selection plays out in behavior, locomotion, physiology, and ecology as the animal operates in its environment.

Therefore it is a surprise that Valentine does not pay much attention to the physical conditions on Earth around the Cambrian period. Valentine has made many stellar contributions to paleoecology both before and after his seminal book (1973), yet his comments on the functional ecology of early metazoans are brief and scattered here and there in the book.

For example, there is no reference to Logan's suggestion that the invention of "guts" changed the pathways of nutrients in the ocean by sequestering them in fecal pellets and fast-forwarding them to the seafloor (Logan *et al.,* 1995). When did suspension-feeders (benthic or planktonic) clear the surface waters of murky particles dead and alive, extending the photosynthetic realm deeper into the ocean and thereby changing all oceanic ecosystems? What generated the phosphorite deposits around the base of the Cambrian and do they reflect some important change in the marine biota (compare Schulz & Schulz, 2005)? Was "Snowball Earth" a vital precursor to the origin of phyla? (I don't think so, but the question should be asked.)

Valentine's effort offers a challenge. Why is the question apparently intractable? (There have been many hypotheses.) If Valentine cannot synthesize a plausible scenario, or testable hypotheses, who can, and how? There is only one Earth, and metazoan phyla evolved on it in only one history: what was that history?

So let us change the title of this book (in our minds) to "*Valentine's Challenge*". Readers of *Ecoscience* are precisely the scientists who could offer potential solutions to the questions posed by the origin of phyla (of course, you have to read the book first).

But one word of warning, this is not going to be an easy task. It would require an effort of scholarship at least as arduous as the one Valentine undertook. Columbus did not reach India, Moses did not reach the Promised Land, and Valentine's book does not match Darwin's. Nevertheless, I would not be in the least surprised if Jim Valentine is sitting at his desk with a blank sheet of paper in front of him, on which he has just written, "On the Origin of Ecosystems."

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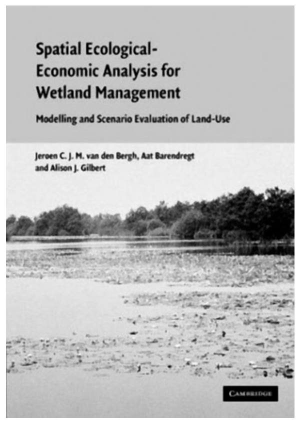
VAN DEN BERGH, J. C. J. M., A. BARENDREGT & A. J. GILBERT, 2004. Spatial Ecological-Economic Analysis for Wetland Management. Modelling and Scenario Evaluation of Land-Use. Cambridge University Press, *xiv* + 239 p., 17.5 × 25 cm, hardcover, US$120.00, ISBN 0-521-82230-0.

In recent years we have seen a number of studies evaluating the impacts of land use scenarios that bridge the natural and social sciences and acknowledge spatial heterogeneity of the area under consideration. This book presents a detailed account of an earlier published (van den Bergh *et al.,* 2001) integrated research applied to wetland ecosystems, combining hydrology, ecology and economics, while using spatial modeling and evaluation techniques.



The first chapter describes the threats facing wetlands, indicates that the underlying processes range from ecology, hydrology to socio-economy and puts forward the claim that any solution requires integration of these scientific disciplines. Chapter two provides reviews on wetland hydrology, ecology and environmental economics. The third chapter discusses existing approaches to integrated and spatial modeling, techniques for monetary valuation and reviews indicators to evaluate model performance.

Chapters four to nine describe the set up of the study, which was carried out in freshwater lake and polder ecosystems in the Vecht area, the Netherlands. A theoretical framework for the study (Chapter five) is followed (Chapter six) by a description of history, land use and policy in relation to conflicts between agriculture, nature conservation and recreation. Next, four scenarios are defined to manage land and water: business as usual *versus* stimulation of agriculture, recreation and nature respectively. Chapter seven and eight describe the models used to forecast the biophysical and socio-economic impacts of these four scenarios while Chapter nine introduces the performance indicators used to evaluate them. The various scenarios are compared and evaluated in Chapter ten. The book concludes with a chapter on implications for policy and research.

The biophysical part of the study was based on logistic regression models implemented in a GIS environment to predict change in plant species distribution in response to changes in hydrological conditions caused by the four scenarios. The authors motivate this choice while stressing shortcomings of alternative methods. However, the chosen models assume equilibrium and reversibility, assumptions which unfortunately did not receive any further attention while answering the justifiable question raised by the authors (p. 127) whether "it is feasible to model a wetland ecosystem".

The explicit attention to the spatial dimension should be highly appreciated in this work. The book rightly states that space is an overlooked dimension in economics. The spatial-economic model in chapter eight separates the economic valuation from the environmental assessment. This separation prevents the "*problem of double-counting*" (p. 129-130) and ensures a transparent insight into the trade-offs between the economic and the environmental impacts. The method employed for the valuation of the impacts of the various scenarios is basically a simple effect-on-production technique combined with an opportunity costs approach. The use of spatial equity as a criterion to evaluate the scenarios is interesting, but less relevant in the context of the current study.

The book successfully takes up the challenge of bringing together the natural and social sciences in spatially explicit scenario evaluation. It suggests that such information would be useful to spatial planning and water management at national, regional and local levels (p. 88). The question remains to what extent such integrated modeling would be used by the actual institutions and decision-making bodies involved. Water management and land use planning in the Netherlands are characterized by a long tradition of negotiations and stakeholder involvement and opposing interests among the various stakeholders.

For which target group has this book been written? Is the book about wetlands and wetland management, a suggestion emerging after reading the first chapters, or about methods for integrated modeling and assessment? The book is stronger and more generic in the latter field. It is recommended to those interested in spatial planning and spatially explicit integrated assessments.

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