THE MARRIAGE OF INVASION ECOLOGY AND ECOLOGICAL THEORY


Key words: alien species; community ecology; ecological theory; exotics; invasive species; models; population dynamics.

Can ecological theory inform our understanding of biological invasions? Can the study of biological invasions inform our understanding of ecological theory? Indeed, are biological invasions a unique ecological phenomenon deserving of recognition as a distinct subdiscipline? These questions have reverberated through the literature on invasions since Darwin used biological invasions in constructing his argument for natural selection in The origin of species. They have often been implicit rather than explicit in discussions of both ecological and evolutionary theory and in invasion-related research. This new book is the first in a series intended to make these questions central to invasion ecology, and in the process, to help define and differentiate the field.

The subject of biological invasions is typically introduced in terms of its significance for conservation and ecosystem integrity. Indeed, papers that describe the magnitude and scope of environmental damage ascribed to invasions are typically used to justify further funding for research into the ecological determinants of invasion. A cogent issue that emerges from such a perspective is the relevance of theory to practice: can ecological theory provide the increase in understanding of invasions needed to “solve” the problem of invasions and the environmental damage ascribed to them? This new book directly addresses this question by assembling a set of papers that explore this set of intersections among theoretical, experimental, and observational ecology, “pure” and “applied” ecology, and theory and policy.

Cadotte et al. take an approach that is explicitly based on population and community ecology. In their introduction, they set the stage by defining the elements of a theory of biological invasions as the interactions of intrinsic population growth rates, competition, extinction, mutualisms, and dispersal. The chapters that follow address these components of population and community ecology in considerable detail. Indeed, the book might have been titled “theoretical population and community ecology and biological invasions: reciprocal interactions,” as this is its overwhelming focus. All chapters, in some way, focus on the species, whether in terms of language and conceptualization of the basic ecological problem, the mathematics of population dynamics and population interactions, or larger-scale issues such as biogeography.

The book begins with two comprehensive reviews of the conceptual basis of invasion ecology, starting before Darwin and going up through 2005. Cadotte, in a thoughtful and provocative review of the early history of both ecological thinking and invasion biology, addresses the perceived dissociation of ecology and invasion biology. He juxtaposes thinkers who emphasize understanding the factors that structure ecological communities in general with thinkers, epitomized by Charles Elton, who emphasized “invasion ecology” as the study of damaging impacts of non-indigenous species. Cadotte reviews the work and conceptual approach of early ecologists, such as Warming, Clements, Grinnell, Lotka, and Volterra, among others, and points out that although they may have used non-native species dynamics to illuminate succession, competition, population growth, etc., they did not conceptualize “invasion ecology” as a separate subject. Davis, in an equally detailed and thought-provoking chapter, reviews the more recent history of thinking about invasion biology, highlighting important papers and books, and contrasting the perspective of Elton, who emphasized the foreign-ness and impact of what we now call invasive species with the more dispassionate approach in H. G. Baker and L. Stebbins’ classic book (1965). The genetics of colonizing species. Academic Press, New York). Both authors distinguish “invasion ecology” as specifically addressing conservation and environmental impact as central components of the topic from research that uses species invasions as studies for theoretical questions in ecology and evolution. However, neither author acknowledges that the discipline of ecology as a whole has evolved dramatically over the past several decades. As recently as the 1970s there was a much sharper distinction between “pure” theoretical ecology and “applied” science, reflecting the way in which science itself was conceptualized—and assigned value—in universities. All branches of ecology now integrate theoretical and applied aspects more or less seamlessly, and there is nothing now “second-class,” as there had been, in making environmental degradation a legitimate topic for ecological research.

The book is divided into four sections. The first, the introductory section, includes both the historical reviews of Cadotte and Davis, and a very stimulating discussion by Murphy et al. of the welter of terms used to describe invasive species and invasions. In an interesting attempt to deal with the confusion of classification schemes that have been proposed in recent years, these authors use information from the literature on the biotic characteristics of 95 species in Canada to explicitly test the validity of different classification schemes. They conclude that none really works well, that “the search for operational definitions of terminology in invasion ecology remains elusive,” and that a population-based approach might be more useful than one that categorizes species. Their suggestions will undoubtedly stimulate much discussion and debate.

The next three sections include one that emphasizes population dynamics (five papers), one that emphasizes species interactions (seven papers), and one that looks at large-scale patterns of populations and communities (four papers). The individual contributions vary greatly in their success at integrating invasion biology and theoretical ecology. Some, such as those by Murrell and by Satake et al., only briefly relate model development to invasions; others, such as those by Courchamp and Caut, and Gilbert, clearly integrate concepts and models in theoretical ecology with invasion processes in ways that illuminate both components. Many of the chapters are mathematically intensive; most chapters require familiarity and comfort with the mathematics of population and community dynamics. Even the final summary chapter by the editors uses a metapopulation model to conclude that invasions at different scales can be understood through an analysis of the population
intrinsic rate of increase ($r$). There is a rough inverse correlation between analysis of invasion data and modeling intensity. However, the chapters emphasizing mathematical model development will certainly provide a rich resource for ecologists studying relevant aspects of invasion ecology to explore in the future. It may be that the relative failure of some of the papers to effectively provide a bridge from theory to invasion ecology may reflect the young state of the science. Their inclusion in the book is thus likely to provide a stimulus for greater integration of population and community modeling with invasion ecology.

Does the book succeed, overall, in its attempt to integrate ecological theory and the study of invasions? Yes: in its strong emphasis on population and community modeling, it certainly provides the basis for an emerging integration at this level of ecology. Many of the chapters will, undoubtedly, stimulate a substantial improvement of the degree of integration of these fields. No: in its relatively narrow focus on one branch of ecological theory, it leaves many components of both theoretical ecology and invasion ecology as yet unintegrated. But this is not bad—it leaves room for the series of books to grow in many directions, which will benefit both the study of ecology and the understanding of invasions.

A couple of technical notes: (1) it would have been helpful to ask each of the authors presenting substantial mathematical material to have included a table of parameter symbols as an appendix to each chapter, as terminologies and model parameters vary in their representation from chapter to chapter; (2) there are a surprising number of typographical and proofreading errors throughout the book.

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**ADVANCING ISLAND BIOGEOGRAPHY WITH THE STUDY OF CONTINENTAL ISLANDS**


Key words: colonization; evolution; extinction; incidence functions; island biogeography.

Colonization, extinction, species number and turnover, assembly rules, and incidence functions are major themes of island biogeography. Martin Cody’s twenty-plus year study of plant distributions on over 200 islands in Barkley Sound, British Columbia provides a rich context for exploring them. The islands studied are land-bridge islands, ones that became isolated from the “mainland” of Vancouver Island as sea level rose since the last glacial maximum. Because of their close proximity and former connection to the mainland, these islands provide a powerful explanatory lens for a variety of questions that are difficult to study with more isolated, oceanic islands—the classic focus of island biogeography studies.

Ecologists, biogeographers, and conservation biologists will find this book to be valuable, not just for its observations and conclusions, but also for its innovative methods and analytical approaches—ones that have equal value for ecological research, planning the design of reserves, and evaluating the success of restoration efforts. Given its advanced and specialized subject matter, this book is unlikely to be used as the sole basis for an undergraduate or graduate course; it would, however, provide an excellent reading contribution for a course on island biogeography or reserve design. The book presents the analysis and synthesis of a *tour de force* study comprising census data on the vascular flora of about 300 species, across 217 islands, over 22 years, with 14 survey periods. It is complemented throughout with thorough, but brief, discussions of relevant work from other island biogeography studies, and with complementary information on animal distributions. Its topics are approachable, with sufficient background provided to allow issues to be easily understood. The book is clearly written, free of obvious typographical errors, and possesses high quality figures and illustrations. The book is reminiscent in many ways of *A new island biogeography of the Sea of Cortés* edited by Ted Case, Martin Cody, and Exequiel Ezcurra (2002. Oxford University Press, New York), which was similar in providing a thorough study of an island archipelago. Like the preceding book, this one also provides an excellent set of appendices that will undoubtedly provide the data needed for many subsequent publications. The principal differences between these books, besides the different geographical setting, is the focus here on a single taxonomic group, vascular plants, and a more unified presentation, typical of sole-authored work.

The book is comprised of nine chapters. Following the introduction, Chapter 2 explores the physical and biotic setting for the work. One of the more interesting aspects of this chapter is the development of “island phyllogenies,” whereby the relationships among individual islands are plotted like species on a phylogenetic tree, showing the history of isolation among islands through time as sea level rose and large continuous areas were split into increasingly smaller and more fragmented ones. Another highlight of this chapter is the development of an index that integrates the contribution of multiple potential source populations in measures of island isolation. Chapter 3 is a useful review and exploration of island biogeography theory, with a focus on plants in Barkley Sound. I found the conceptual figures in this chapter to be extremely useful and clear, particularly the ones illustrating the relative influence of long-term and short-term extinction dynamics on species richness of islands.

The majority of data analysis and synthesis occurs in Chapters 4–7, which explore species richness, nestedness, assembly rules, species turnover, dispersal syndromes, and incidence functions. The last of these, incidence functions, which examine the pattern and predictability of species distributions across islands, are particularly well described. These analyses are intriguing because they are generally unavailable for plant species. The author is able to conduct these analyses, (1) because many species in this archipelago are
providing compelling evidence that recent increases in alien
Ireland. xiv

impact colonisation events in differentiating island floras over time. Perhaps most
impressive is the interpretative power his site-specific knowledge
in differentiating island floras over time. Perhaps most
examine the relative importance of chance colonization events
islands with similar physical characteristics, histories of
explores shifts in animal characteristics, particularly in their
occurs over so long a
time. The author has gained familiarity with individual
inhabitants and natural systems, face new and growing
ambitious discourse in four parts: 1) "The global context," 2)
keenly focused on the subject of alien plant species
conservation principles and practices. As the title indicates, this
occurrences have happened at the expense of reduced native
conservation movement, and setting up the conflict in ethics that
gave rise to the forum upon which the book is based. Lavigne's
brief history of conservation is perhaps too brief; he covers the
development of the conservation ethic, from Bacon's utilitarianism
to the emergence of progressive conservation and
protectionist conservation, through the Wise Use Movement
(WUM), in fewer than eight pages. He is particularly alarmed
about the growing credibility the WUM advocates have
developed using less-than-credible analyses, as illustrated by
and insinuation of their agenda into conservation policies such as
the Convention on International Trade in Endangered Species of
Wild Fauna and Flora (CITES). This book is a normative work,
collected to persuade the reader that there are real problems in
the world, that the source of many of these problems is unfettered
exploitation of wildlife as resources, and that these problems can
be addressed to some degree through the application of
conservation principles and practices. As the title indicates, this
is intended to be an optimistic work, even a prescriptive guide.

The organization of the book into four parts brings some
structure to this otherwise arrhythmic collection of essays. Part
I, "The global context," is composed of four essays describing in
varying levels of detail the emergence and condition of the
conservation movement. These essays include a detailed
documentary of the history of the conservation movement
(Martin Willison), a historical critique on the importance and
influence of the agricultural (Neolithic) age to the current
human condition (Ward Chesworth), a historic/philosophical
discourse on sustainability (Sidney Holt), and the impact of free
market forces on conservation practices and policies around the
world (Sharon Beder). Holt's essay is the longest in the book
(40 pages), and is the most introspective, though a bit rambling.
Beder’s chapter includes an extensive description of the strategy of The Nature Conservancy as a model of successful implementation of conservation principles.

Part II, “Modern examples of sustainable use,” begins with a couple of essays on sustainability of fisheries and ocean management (Jeffrey Hutchings, Vassili Papastavrou, and Justin Cooke, respectively). Terrestrial conservation challenges in Africa are addressed in essays that attempt to debunk the utility of commoditization of wildlife in the ivory trade (Ashok Kumar and Vivek Menon) and the bushmeat crisis to better understand the failure of development policies in protecting wildlife (Heather Eves). Eves argues that the community infrastructure necessary for conservation to succeed is predominately absent in Africa. The final two essays in this part explore the utility of ecotourism in wildlife management. The Ugandan experience with ecotourism is explored as a case study (Arthur Mugisha and Lilly Ajarova); they define a set of shortcomings in ecotourism that include lack of security, health concerns, seasonality, remoteness, and lack of standards or safeguards. Whale watching as ecotourism is explored by Peter Corkeron, using a peculiarly interesting compositional framework based upon the Book of Job. His point is clear—the future of whales depends on the establishment of an iconographic ethic about whales among the peoples of the world.

Part III, “Factors at play,” is composed of five essays that explore why wildlife conservation is failing in the world. These are the most compelling essays in the book, as they explore the root causes of failures of conservation policies developed over the past two decades. The sociologic aspects of conservation are addressed in the first two essays. The attitudes, values, and objectives of wildlife conservation (Vivek Menon and David Lavigne) and the relationship between science and economics (William Lynn) begin to get to the heart of the matter. As Captain Jacques Yves Cousteau famously said, “people protect what they love.” The final three essays in this part address problems with the economic commodification of wildlife, including an argument against conventional economic logic as a mechanism to protect biodiversity (William Rees), the failure of subsidies to protect European fisheries (Michael Earle), and a persuasive argument that willful human behavior (un-coerced) will not support sustainable practices (Ronald Brooks). This part is part admonition and part critique.

The final part of this collection, “The way forward: putting theory into practice,” is the longest of the book, with 10 essays. The first five of these include essays on changing public opinions and attitudes (Robert Worcester and John Oates, respectively), an essay lauding the North American model of wildlife management (Valerius Geist), a framework for assessing the sustainability of bushmeat hunting (E. Milner-Gulland), and an analysis of the failures of fisheries and wildlife management from an engineering perspective (William de le Mare). The remaining five essays are general policy analyses and presentation of conceptual frameworks for sustainable wildlife conservation. These include the precautionary principle in Canada (Michelle Campbell and Vernon Thomas), the need for a “steady-state revolution” (Brian Czech), a proposed new architecture of wildlife management in the developing world (Atherton Martin), a rather radical argument that the “greens” are preventing implementation of the sort of revolutionary practices necessary for ecological sustainability (Stephen Best), and a concluding chapter by editor David Lavigne that calls for a “reinventing” of wildlife conservation for the 21st Century. Developing a common voice in edited collections is always problematic and often impossible. This book has many voices, and Lavigne wisely chose to let them sing out. The voices in Gaining Ground include sociology, ecology, policy, ecology, and economics. This cacophony risks chaos, but in the end harmonizes like a street choir. There is roughness, disagreement, and even error, but these differences enhance the importance of the areas of agreement, as articulated by O’Regan in the Forward. The collection fails in its goal to provide an optimistic tone. However, even in the fatalism that emerges from these pages, Lavigne highlights the nobility in the struggle to develop sustainable policies and practices. This is not a polished polemic, nor a scholarly investigation; it is more accurately a discourse among passionate professionals about the most critical issue of our generation—preserving a viable ecosystem for future generations. This book therefore represents a valuable contribution to the ecological sustainability literature.

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INTRODUCING POPULATION ECOLOGY: KEY CONCEPTS AND CURRENT RESEARCH DIRECTIONS


Although species clearly do not exist in isolation, a great deal of insight into ecological systems can potentially be gained by starting from a population perspective. Much of the research in ecology is oriented from a population perspective, examining single species population dynamics, with the ultimate aim of integrating these into broader evolutionary and community perspectives. This work has had notable successes, for example, the understanding of the way that density-dependence regulates populations, the recognition of the existence of nonlinear population dynamics, the use of stochastic models in population management and PVA, as well as the development and application of metapopulation models in a conservation framework. Population ecology is a coherent subdiscipline spanning taxonomic groups including plants, animals, and microbes, and the basis for a large proportion of this work are

Key words: density-dependence; evolutionary biology; population dynamics; population interactions; population model.
mathematical models linked to data. The two new volumes by Rockwood and Ranta et al. are written in this vein, using models of various types to illustrate, predict, and understand the dynamics of ecological systems.

The two books are very different in their focus. Rockwood’s book is a strong introduction to population ecology aimed at an undergraduate or early postgraduate audience, whereas the monograph by Ranta et al. is a summary of recent research, particularly highlighting recent contributions by the authors. What I felt was a strength of both books was that they both stress the wider relevance of population ecology for a broader understanding of ecological systems. This includes extensions to understanding evolutionary biology and life-histories, conservation, and community ecology. Although it is not entirely clear that all large-scale ecological problems can be tackled with a bottom-up approach, scaling from population dynamics (macroecological studies often take a different approach, for instance), both volumes present many good examples of how this can work.

Dealing with Rockwood’s introductory textbook first, the book is organized into two sections, the first dealing with single-species, the second with multi-species systems (typically two-species interactions). One of the key aims of the book is to achieve a combination of topic coverage and mathematical rigor, and I think this is achieved very well. Simple mathematical models are used throughout the text in order to illustrate the concepts and, importantly, how data can be analysed to test model predictions. The book has a number of novel inclusions for a book of this level, including the use of stochastic models at several points (although the emphasis is on deterministic models) and the inclusion of metapopulation ideas throughout. These are both welcome additions, particularly the former: the simple idea that the geometric mean population growth rate is the appropriate predictor of population growth is missing from many textbooks that introduce population dynamics, yet is a concept fundamental to understanding population models in real stochastic environments.

In the first section of the book, Chapters 1–3 are mainly concerned with population dynamics and fundamental issues in population modelling. The subject matter here is largely common to most introductory textbooks, although as mentioned above, the inclusion of stochastic models is novel. The discussion of different density-dependent models, and the relationships among them is also good and very useful. Chapter 4 introduces age-structured population dynamics, concentrating on age-structured matrices, but also mentioning stage-structured models. I suspect the material here may be a little difficult for many biology undergraduates, although the inclusion of an appendix summarizing the key relevant matrix theory is useful. Chapters 5 and 6 are interesting and stimulating extensions, dealing with metapopulation theories and life-history strategy. These are a good conclusion to the first section as they make clear how population biology can be put to wider use.

The second section of Introduction to population ecology considers a suite of interactions, including interspecific competition (Chapter 7), mutualism (Chapter 8), host–parasites (Chapter 9), predator–prey (Chapter 10) and finally plant–herbivores (Chapter 11). The chapter on mutualisms is a welcome addition, and one that particularly caught my eye as this has been a lamentably under-explored area from the population modelling perspective. Sadly however, this chapter is only five pages long, to some extent reflecting the lack of attention by modellers to mutualisms, although I felt that several studies from recent years that use population models to explore the evolution and ecology of mutualistic interactions could have been covered.

As a textbook for teaching and learning, Rockwood’s book is clearly written and well laid out. Chapters are preceded by a clear outline of the subject matter, and end with a summary of the main take-home message. The coverage of the literature is generally good and up to date. As a general point, having trained in plant ecology I felt that although plant populations are by no means ignored, examples are largely zoological. As an example, discussion of the law of constant final yield appears to be in error (the plot of mean size against density has a slope of –0.71, indicating undercompensating density-dependence). Also the discussion of thinning laws in plants seems to confuse intra- and inter-specific thinning, which are different processes. Not specifically restricted to plants, I also thought that the section outlining tests for density-dependence was dangerously naive, and did not cite the many cautions about using regressions of population growth on density as a test for density-dependence. However, having said this, these criticisms are minor and should not detract from what I think is an excellent and comprehensive first text on population ecology.

Ecology of populations by Ranta et al. is a summary of recent research and has a very different target audience, being aimed at researchers at the post-graduate level and above. The focus of the monograph is on spatio-temporal dynamics and is written from a modelling perspective, providing an overview of a series of mathematical and simulation models. The details of the models are largely summarized and omitted, and are available in the primary literature, the aim being that the work should be accessible to a wide audience. In the introduction, the authors state a series of aims, but I would say that the strengths of the book lie primarily in its accessibility and proximity to the cutting edge of population ecology research.

The coverage of the volume is wide. The first six chapters deal with population dynamics, starting with basic theory (Chapter 1, an overview; Chapter 2, “Population renewal”), three chapters on spatio-temporal dynamics (Chapter 3, “Population dynamics in space”; Chapter 4, “Synchronicity”; Chapter 5, “Order-disorder in space and time”), and concluding with Chapter 6 on structured populations. The initial chapters do a good job of introducing the basic tools required to perform the type of analysis the authors use for time-series analysis. These include the use of cross-correlation functions, detrending, power spectra and autocorrelation analysis. Although for any rigorous application of the methods a more detailed text would be required, the authors do a good job of outlining the methods and why they should be used. Applications of the methods throughout these six chapters illustrate nicely how the methods can be used.

Of these initial chapters, I found Chapter 5 particularly stimulating. This deals with the relationship between local and global population dynamics, and how spatial patterns may emerge as a function of different underlying processes. For instance, local host–parasitoid dynamics may be cyclic, but because of localized dispersal, different parts of a global range may be in different phases of population growth. Because of this, the global dynamics may appear more stable than the local population dynamics. However, this is only half of the story; examination of maps of population density reveal distinct spatial patterns in the population with waves of high and low densities travelling through the habitat. The lesson is that local temporal data are not enough to understand population dynamics—an explicit spatial context is also required. This lesson is illustrated with comprehensive examples including voles in Finland, measles in the U.K., and Canadian lynx. These examples (literally) add another dimension to classic problems in the synchronicity of population dynamics (also covered in Chapter 4).

Chapters 7, 8, and 9 are to varying degrees applied chapters, dealing with “Biodiversity and community structure” (Chapter 7), “Habitat loss” (Chapter 8) and “Population harvesting and management” (Chapter 9). Chapter 7 is somewhat of a departure as it considers the dynamics of interacting competing
populations within the community (where the community contains lots of species, not just two species as is usually the case when inter-specific interactions are dealt with in a population framework). The approach taken is actually not so different (multi-species extensions of the Ricker model are explored) and leads to some interesting outcomes, such as community closure, whereby once it has become stochastically extinct from a community a species is often unable to reinvade. This was a stimulating chapter; however I felt that perhaps the authors in trying to be comprehensive had not quite done justice to this topic—having said that, stochastic spatial models of community assembly could easily constitute another monograph!

Chapters 8 and 9 on habitat loss and harvesting fit in much more logically with Chapters 1–6 and the authors show clearly how the modelling techniques and lessons from the opening chapters may be applied to real-world problems. Some examples of habitat loss effects are given, such as the effects of habitat loss on cycling of vole populations; however, the chapter on harvesting would have benefited from more concrete examples as all of the figures in this chapter are from simulations.

For the final three chapters, Ranta et al. switch focus and consider behavioral and evolutionary problems, looking at “Resource matching” (Chapter 10), “Spatial games” (Chapter 11), and “Evolutionary population dynamics” (Chapter 12). These are again stimulating chapters: the main interest for ecologists is that these chapters have taken the population dynamic models developed in the early chapters from the book and applied them to these rather different scales. In the main these three chapters are theoretical, without detailed case studies and comparison with field studies. As a reader this is disappointing, although perhaps understandable given that the work described is comparatively novel.

In all, and as can be seen from the preceding description of its contents, Ecology of populations is an ambitious volume, attempting to cover almost the whole of population ecology and its potential applications and extensions. I found it to be an interesting and stimulating volume—by no means does it provide all of the answers or give a comprehensive review of the field but, to be fair, the authors point out in the introduction this is not what they were trying to achieve. In several places (particularly the chapter on community dynamics) the treatment of some topics may be somewhat too brief. I took a great deal from this book, and I think that there is much of value for anyone working in population dynamics contained within it. I would certainly recommend it to young researchers in the field as it makes important theoretical ideas and techniques accessible and understandable.

These two volumes are very useful contributions in their different ways. Both will benefit population ecologists in the early stages of their careers, the first in introducing the key concepts, the second in introducing research-active areas, problems, and techniques. The common emphasis is on mathematically sound theory, underpinned by data as well as the application of population ecological theory to wider problems, and for this the authors of both volumes are to be commended.

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**Spotlight**

**RECENT PUBLICATIONS OF PARTICULAR INTEREST**

Hayes, Richard, and Daniel Grossman. 2006. *A scientist’s guide to talking with the media: practical advice from the Union of Concerned Scientists*. Rutgers University Press, New Brunswick, New Jersey. xv + 200 p. $18.95, ISBN: 978-0-8135-3858-7 (alk. paper). At one time or another, many of us have been dismayed at how our comments have been used by journalists. This book, authored by a media director and a journalist, seeks to help scientists “use the media to raise awareness of scientific research and thought.”

Stewart, Paul D. 2007. *Galápagos: the islands that changed the world*. Yale University Press, New Haven, Connecticut. 240 p. $29.95, ISBN: 978-0-300-12230-5. Want to visit the Galápagos Islands, but haven’t managed it yet? This book, with its beautiful pictures and interesting text, will either make you think you’ve been there or make you arrange your plane tickets.