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Pinus is a remarkable genus comprising at least 111 tree species with a very large distribution range in the northern hemisphere. Where they occur, pines usually form the dominant vegetation cover and are extremely important components of ecosystems. They also provide a wide range of products for human use. In many cases exploitation and other human pressures are threatening the survival of natural pine forests, although pines are now also widely grown in commercial plantations, both within and outside their natural ranges. This book presents a definitive review of pine ecology and biogeography written by forty of the world's leading authorities on this important genus. In the face of increasing human pressure and global climate change, it provides an essential source of reference for all those concerned with the management of natural and planted pine forests.

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Ecology and Biogeography of *Pinus*

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Ecology and Biogeography of *Pinus*

Edited by **David M. Richardson**
Institute for Plant Conservation, University of Cape Town, South Africa

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PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK http://www.cup.cam.ac.uk
40 West 20th Street, New York, NY 10011-4211, USA http://www.cup.org
10 Stamford Road, Oakleigh, Melbourne 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain

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First published 1998
First paperback edition 2000

Typeface 8.5/11.5pt Swift Regular *System* QuarkXPress® [SE]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Ecology and biogeography of *Pinus*/edited by David M. Richardson.
p. cm.
Includes bibliographical references and index.
ISBN 0 521 55176 5 (hb)
1. Pine–Ecology. 2. Pine–Geographical distribution.
I. Richardson, D. M. (David M.), 1958– .
QK494.5.P66E27 1998
585′.217–dc21 97-11056 CIP

ISBN 0 521 55176 5 hardback
ISBN 0 521 78910 9 paperback

Transferred to digital printing 2004

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This volume is dedicated to the memory of William Burke Critchfield (1923–1989) and Nicholas Tiho Mirov (1893–1980), whose dedication to thorough studies on various aspects of pines greatly improved our knowledge of this remarkable genus. Their influence lives on in this book.

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Preface and acknowledgements

The main aim of this book is to provide, within the confines of one manageable volume, an informative overview of the current understanding of the ecology and biogeography of the genus *Pinus*. This is clearly a very ambitious objective.

The idea of compiling this book first came to me about a decade ago but for several years I was unable to devote time to the project. Also, I felt that it would be rather presumptuous for a South African ecologist with very little first-hand experience of pines in their natural habitats to initiate a synthesis of the kind that I felt was needed. At that time, my knowledge of pines was that of a forestry graduate with training in the silviculture of pines as exotics, and of a researcher with an interest in the ecology and management of pines as invasive alien species in South African fynbos. My experience of pines in their natural range was confined to brief encounters with a handful of species in the Mediterranean Basin. My infatuation with pines came about rather differently to that of any other 'pinophile' that I know. Since this has influenced how I approached the compilation of this volume, it may be of interest to readers.

My work on pines as invaders first led me to explore the literature on life-history adaptations of pines – my quest being to discover what traits equipped pines to be such tenacious persisters and aggressive colonizers in South African fynbos, and what could be done to contain their rampant spread. My readings on the subject also led me to examine the conditions that caused range changes within the natural distribution of pines. I also explored the various interactions between disturbance and pine dynamics. Searching for other insights, I scrutinized the palaeoecological literature and was fascinated to find clues to the current range limits of pines in reconstructions of pine migrations following deglaciation. At this time, my colleague William Bond was busy with his PhD studies at the University of California at Los Angeles. One product of his North American sojourn was his seminal paper entitled 'The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence' (Bond 1989). I was intrigued by Bond's findings, as they appeared to explain (or at least provide a framework for understanding) so much of the dynamics of the recent range changes that I had been studying. Soon after his return to South Africa, we collaborated in a study of the determinants of pine distribution based on many published accounts of range changes from numerous localities in the natural range of pines, and in areas where they were invading new habitats (Richardson & Bond 1991). Our main conclusion was that interactions between pine seedlings and various biotic factors in the regeneration niche were fundamentally important in defining range limits. This gave me a new perspective for reflecting on a wide range of topics in the vast literature on pines.

In 1990, I spent a few months in Australia, and was interested to see *Pinus radiata*, which I knew well as an invader of South African fynbos, invading eucalypt forests. Invasions at sites such as Black Mountain in Canberra seemed to be driven by a different suite of factors to those I had identified as being important in pine invasions in South Africa. I started comparing the behaviour of this and other pine species as invaders in different parts of the southern hemisphere. This research forced me to read widely on various aspects of pine ecology. I was totally fascinated by the wealth of information available, but frustrated by the lack of a thorough synthesis. There was a treasure chest of information, but the facts were so scattered that forming clear pictures was difficult.

As I delved deeper into the huge literature on pines, I began corresponding with pine authorities in various fields from many parts of the world. For several years I corresponded with the late Bill Critchfield. His carefully

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formulated replies to my miscellaneous queries, for example on the evolution of serotiny in pines, reinforced my preoccupation with *Pinus*; it seemed to be the model genus for exploring all sorts of fascinating ecological and evolutionary questions. I was also riveted by the rich information base concerning the impacts of various types of land use on pine dynamics, especially in the Mediterranean Basin and the American Southwest. For the Mediterranean Basin, my interest was fuelled by regular contact with ecologists from various parts of the region at several MEDECOS conferences, and particularly by two visits to the Centre d'Ecologie Fonctionelle et Evolutive in Montpellier in France. For the American Southwest, my curiosity was whetted by accounts in the literature on range management, and by the scientific and popular writings of, and correspondence with, Ronald Lanner, then Professor of Forest Resources at Utah State University.

In several parts of the world, pine taxa are facing extinction as a result of growing human pressure on forests. This is extremely obvious and worrying in parts of Mexico and Central America, and in northern Asia – regions which together store two-thirds of the genetic diversity in *Pinus*. Even very widespread species in more affluent regions have been decimated. This escalating attrition of genetic diversity has untold implications for the future, for example by annulling many options for selective breeding to enhance productivity and disease resistance of pines for human utility. The selective clearing of pines in certain habitats, notably low-altitude sites, has unexplored ramifications for the future of pine forests in the face of global climate change.

The need for a synthesis of the current knowledge on pine ecology and biogeography was obvious. Nicholas Mirov's volume on *The Genus Pinus*, published in 1967, served this function reasonably well, but is now seriously out of date in many aspects. Certainly, Mirov's book did not provide answers to many questions I was asking about pines. There has been enormous progress in virtually every aspect of pine ecology since the 1960s. Given this, it soon became clear that a single-author account that would do justice to emerging perspectives in all fields would be an impossible task. The answer seemed to lie in a carefully planned, multi-author volume. In 1992 I cautiously started compiling an outline for this book. I consulted hundreds of publications and scores of authorities in numerous fields. The final list of chapters and authors (40 contributors from nine countries) was completed after more than three years of correspondence and deliberation.

The book comprises 22 chapters, divided into six parts. The first chapter introduces the volume by placing the genus *Pinus* in perspective. Part Two contains a chapter on phylogeny and systematics, and one on the early evolution of pines. The next part consists of four chapters that detail the historical biogeography of pines in the four major pine regions of the world: northern Asia, Europe, northern North America, and Mexico and Central America. Part Four deals with more recent biogeography for two regions, the Mediterranean Basin and the American Southwest. Also included in this section is an account of the macroecology of pine distribution and abundance. Nine chapters (11–19) are grouped together in a section on Ecological Themes. Although many of the chapters in others sections touch on the role of humans in shaping pine biogeography, three chapters are grouped in the final section on Pines and Humans. This section provides a global review of pines in cultivation, a separate chapter on one remarkable species, *P. radiata*, and an overview of the newest 'pine rise': the rampant spread of invasive pines from sites of cultivation in the southern hemisphere.

A problem confronting the contributors to this volume was the enormous size of the literature on pines. One author complained that reviewing his particular subject was like 'taking hold of an elephant'. Another protested that 'it is like painting a large bridge – by the time you finish, the first part needs painting all over again!' Most authors faced the major problem of deciding what to leave out. It is inevitable that some readers will judge us to have erred in selecting what to include and what to omit. Although the combined reference list for this volume contains about 3000 titles, there are many others that probably deserved mention. I am resigned to the fact that the literature on pines is so huge and rapidly expanding that it will never be possible to tell the whole story in one volume. Nevertheless, I hope that this book will prove to be a useful guide to the most significant literature and a valuable synthesis of current knowledge.

Many people have helped in many ways to bring this book to publication. In the early stages of planning, Phil Rundel (University of California, Los Angeles) and Paul Zedler (San Diego State University) were especially supportive, as was Alan Crowden of Cambridge University Press. During the final stages of editing the book Phil Rundel was a superb 'guide' on a 'pine safari' through the great forests of the Sierra Nevada and the arid South West. During this trip we scrawled the first draft of the introductory chapter and pondered many aspects of pine ecology. His hospitality, enthusiasm, and breadth of knowledge was a great source of inspiration to me. Dick Mack of Washington State University in Pullman is also thanked for his hospitality and for sharing with me his knowledge of the conifer forests of Washington and Idaho. A special word of thanks is due to Richard Cowling who, as Director of the Institute for Plant Conservation at the University of Cape Town, allowed me to take on this time-consuming project when so many other matters required my attention. The late Derek Donald, lecturer and then professor of Silviculture at the University of Stellenbosch, South Africa, from 1960 until his death in 1993 was the source of much information and helpful advice. The following colleagues at the now-defunct South African Forestry Research Institute are thanked for help and

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support in many ways over the years: Fred Kruger, David Le Maitre, Richard Poynton and Brian van Wilgen.

I am very grateful to the following friends, colleagues and associates for reviewing chapters, providing advice, and helping in various other ways: H. John B. Birks (Botanical Institute, Bergen, Norway; and Environmental Change Research Centre, University College, London, UK), Robert A. Blanchette (Department of Plant Pathology, University of Minnesota, St Paul, Minnesota, USA), Robert A. Boardman (Primary Industries of South Australia, Adelaide, Australia), William J. Bond (Botany Department, University of Cape Town, South Africa), John W. Duffield (Shelton, Washington, USA), William S. Dvorak (CAMCORE, North Carolina State University, Raleigh, North Carolina, USA), Martin V. Fey (Department of Geological Sciences, University of Cape Town, South Africa), Johann G. Goldammer (Fire Ecology and Biomass Burning Research Group, Max Planck Institute for Chemistry, University of Freiburg, Germany), John H. Hoffmann (Department of Zoology, University of Cape Town, South Africa), Henry F. Howe (Department of Biological Sciences, University of Illinois at Chicago, USA), Michael Huston (Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA), Harry E. Hutchins (Itasca Community College, Minnesota, USA), Dale Johnson (Biological Sciences Center, Desert Research Institute, Reno, Nevada USA), Fred J. Kruger (CSIR Division of Water, Environment and Forestry Technology, Pretoria, South Africa), Glen M. MacDonald (Department of Geography, UCLA, California, USA), Jeremy J. Midgley (Botany Department, University of Cape Town, South Africa), Jacques Lepart (CNRS, Centre d'Ecologie Fonctionelle et Evolutive, Montpellier, France), Fernando Ojeda (Departamento de Biologia Vegetal y Ecologia, Universidad de Sevilla, Spain), Phil W. Rundel (Department of Biology, UCLA, Los Angeles, California, USA), Costas A. Thanos (Department of Botany, University of Athens, Greece), Geoff D. Tribe (Plant Protection Research Institute, Rosebank, South Africa), Brian W. van Wilgen (CSIR Division of Water, Environment and Forestry Technology, Stellenbosch, South Africa), Robert D. Westfall (USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA), Kathy Willis (Department of Plant Sciences, University of Cambridge, Cambridge, UK) and Costas Zachariades (Institute for Plant Conservation, University of Cape Town, South Africa).

Thanks to the magic of e-mail and the Internet it was possible to communicate regularly with most of the contributors to this volume and with the reviewers. I doubt whether it would have been possible to finish the task of compiling the volume without this tool. I thank all the contributors and reviewers for responding rapidly to my numerous requests and queries.

Thanks are due to the following publishers for granting permission to reproduce material from their publications: Botanical Society of America (*American Journal of Botany*); California Botanical Society (*Madroño*), Columbia University Press; Ecological Society of America (*Ecology*); Duckworth Publishing; Kluwer Academic Press; Macmillan Magazines Ltd (*Nature*); Missouri Botanical Garden (*Annals of the Missouri Botanical Garden*); Sigma XI, The Scientific Research Society (*American Scientist*); South African Association of Botanists (*South African Journal of Botany*) and Timber Press.

Nalini Dickson, who is Librarian at the Institute for Commercial Forestry Research at the University of Natal in Pietermaritzburg, was wonderfully helpful and did numerous literature searches which were extremely helpful in filling various gaps. The staff at the Forestry Faculty and G.S. Gericke libraries at the University of Stellenbosch were also very supportive. My wife, Corlia, helped in countless ways for which I am immensely grateful (I doubt whether she will ever get over the overdose of pines on our 1996 trip to the USA). Craig Benkman, John Birks, Steffan Eggenberg, Diane Erwin, Greg Forsyth, Johann Goldammer, Colin Hughes, Bill Libby, Glen MacDonald, Jose Moreno, Fernando Ojeda, Phil Rundel, Melissa Savage, Diana Tomback and Willy Stock kindly helped in locating photographs to fill various gaps. Jessica Kemper is thanked for her meticulous and cheerful assistance in final checking of the manuscript and proof reading. Thanks to Wendy Paisley, secretary at the Institute for Plant Conservation, for general assistance.

I am extremely grateful to the team at Cambridge University Press, especially Maria Murphy, Jane Bulleid, Ian Sherratt, Alan Crowden and Stephanie Thelwell.

Compiling and editing this book has been a great adventure. I sincerely hope that the insights included here will be of value to students of pine ecology and that they will help in the formulation of strategies for the wise management of these forests in the future.

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October 1996

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