Island Colonization

New or recently sterilized islands (for example through volcanic activity) provide ecologists with natural experiments in which to study colonization, development and establishment of new biological communities. Studies carried out on islands like this have provided answers to fundamental questions as to what general principles are involved in the ecology of communities and what processes underlie and maintain the basic structure of ecosystems. These studies are vital for conservation biology, especially when evolutionary processes need to be maintained in systems in order to maintain biodiversity. The major themes are how animal and plant communities establish, particularly on 'new land' or following extirpations by volcanic activity. This book comprises a broad review of island colonization, bringing together succession models and general principles, case studies in which Professor Ian Thornton was intimately involved, and a synthesis of ideas, concluding with a look to the future for similar studies.

Professor IAN THORNTON (La Trobe University, Melbourne) who was one of the world's leading island biogeographers, working primarily on the volcanic islands of the Pacific, died in 2002. Amongst the papers he left behind was the manuscript of this book, with an express wish that should anything happen to him, his friend and colleague, Professor TIM NEW (also La Trobe University) would finish the book for him, which he has done.

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Island Colonization

The Origin and Development of Island Communities

IAN THORNTON Formerly of La Trobe University, Melbourne

Edited by

TIM NEW La Trobe University, Melbourne



CAMBRIDGE UNIVERSITY PRESS Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521854849

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First published 2007

Printed in the United Kingdom at the University Press, Cambridge

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

ISBN-13 978-0-521-85484-9 hardback ISBN-13 978-0-521-67106-4 paperback

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Contents

Editorial preface	page ix
Acknowledgements	xiii
PART I Theoretical and experimental studies	1
1 Introduction	3
Types of islands	7
2 Theoretical and experimental colonization	10
Theoretical models	10
Experimental islands in the laboratory	12
Experimental islands in nature	14
The equilibrium theory of island biogeography	15
The mangrove islet experiments	25
PART II Natural recolonization after devastation	27
3 A clean slate?	29
Volcanic effects on living communities	29
Local survival	37
4 Life returns: primary colonization of devastated surfaces	42
Nitrogen	45
Colonization of lava flows	47
Colonization of ash fields and tephra deposits	48
Extrinsic energy	49
PART III The recolonization of devastated islands	57
Islands as areas for the study of community assembly	59
Organic flotsam	60
5 Recovering island biotas: Volcano and Bárcena	61
Volcano Island, Lake Taal, Philippines, 1911	61
San Benedicto (Bárcena I), Mexican Pacific, 1952	65
6 Thera, Santorini Group, Mediterranean	72
The pre-eruption environment	76
The 'Minoan' eruption	79

vi contents

	The effect of the Theran eruption on Crete	81
	The Great Date Debate: when did the 'Minoan' eruption occur?	88
	Biological recolonization of Thera	93
7	Long and Ritter Islands, Bismarck Sea	95
	The Bismarck volcanic arc	95
	Long Island's eruptive history and the last eruption	97
	The Ritter Island event	101
	Biological recolonization of Long Island	104
	The nature of the colonists	115
	A tighter focus	119
8	Krakatau, Sunda Strait	120
	The pre-1883 biota	121
	The first colonists	123
PA	RT IV Assembly of biotas on new islands	133
	Starting points	135
9	Lake Wisdom: a new island of fresh water	137
10	New islands in the sea	142
	Sand cays in the Coral Sea and on the Puerto Rico Bank	142
	Palea Kameni and Nea Kameni (Santorini), b. 197 BC	142
	Tuluman, Admiralty Group, Bismarck Sea, b. 1953	146
11	Anak Krakatau, Krakatau's child, b. 1933	148
	Birth and early physical development	148
	Rate of establishment of biota	149
	Pioneers exploiting extrinsic energy sources	150
	Successional mosaics	151
12	Surtsey, Island of Surtur, b. 1963	157
	Emergence and development of Surtsey	157
	Scientific research on Surtsey	159
	Surtsey and the Krakataus	160
	The course of colonization	162
	Dispersal to Surtsey	175
	Earliest associations and communities of species	180
	Differences from the colonization of the Krakataus	182
	Lessons from Iceland	183
13	Motmot: an emergent island in fresh water	185
	Birth and physical development	185
	The colonization of Motmot	186
	Colonization by Ficus species	195
	Motmot's food chain	196
	Absences from Motmot	198

Cambridge University Press
978-0-521-85484-9 - Island Colonization: The Origin and Development of Island Communities
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More information

	Generalist pioneers	199
	Comparisons	199
PART V Colonization and assembly		203
14	Dispersal	205
	Constraints on the dispersal of animals	207
	The frequency of arrivals	214
15	Stepping stone islands: the case of Sebesi	218
	The theoretical importance of stepping stones	218
	The Sunda Strait islands	220
	Types of evidence of stepping stone function	221
	The comparison with Panaitan	232
	Asynchronous environmental change on Sebesi and Krakatau	236
	Conclusion	238
16	Learning from nature's lessons	239
	Community development	239
	Rakata and Anak Krakatau	242
	Anak Krakatau and Surtsey	242
	Repetitions of the colonization process	243
	Conclusions from comparisons, including other colonizations	244
	Chance and determinism	246
	Summary of the colonization process	256
	Light spots	257
References		260
Index		281

CONTENTS

vii

Editorial preface

Ian Walter Boothroyd Thornton, Emeritus Professor of Zoology at La Trobe University, Melbourne, died in Bangkok on 1 October 2002, on his way home from Laos, where he had been advising the Laos National University on science course development. Among his papers he left an incomplete initial draft of a book he had long planned to write on the development of island communities – an interest he had pursued vigorously for much of his academic life. Ian had discussed aspects of his book with me, and other colleagues, and had expressed the wish to his wife, Ann, that should anything happen to prevent him from finishing it himself, I might be able to complete the work and see it through to publication. As anyone who has attempted any similar task will know, such an exercise is daunting in both scope and responsibility! Although we had debated a number of the themes included, and I had participated in extensive field expeditions (including four trips to Krakatau) with Ian over some 30 years, our perspectives sometimes differed considerably.

The dilemmas of editing a close colleague and friend's posthumous work have been summarized admirably (and, coincidentally, in the autobiography of another distinguished Pacific region entomologist, Robert Usinger), and I have tried to follow the spirit of the perspective given there by Gorton Linsley and Lin Gressitt (1972). They noted that their subject could have no opportunity to read and edit the final manuscript, and that they wished to retain his words in their original form. They therefore opted to limit editorial effort to verification of facts, correction of errors and obvious 'lapsi' (*sic*), but otherwise simply sought to improve the format whilst preserving the original text. Most of the words in this book are indeed Ian's, and some chapters have been changed little from his files. More revision and augmentation has been needed for others, together with illustrations and tables (as guided by the text), some later material and references. I have attempted to make my limited additions both seamless and in accord with Thornton's views.

Reviewers of an early draft suggested that the then extensive 'cultural content' of the book should be reduced somewhat, to increase its primary relevance to ecology. I have done this, but retained some flavour of the effects of volcanism on humanity. However, much of this aspect has been dealt with in a very

X EDITORIAL PREFACE

readable recent account by de Boer and Sanders (2002), so that the intriguing questions of the wider influences of the Theran and Krakatau eruptions that Thornton had treated extensively in his draft are now largely redundant. Winchester's (2003) book on Krakatau also provides much background on broader effects on people. Again from reviewers, I was asked to consider two options for how the work might be developed. First, to present it with limited augmentation as Ian Thornton's creation and a summary of his thoughts on some important ecological themes as developed during a long period of practical investigation. Second, to modify and enlarge it far more extensively as a co-author, a path that one reviewer considered to be more valuable. I opted for the first of these, in the belief that further development would introduce the likelihood of submerging the personal perspective that is the core of the book, and lessen Thornton's impact by introducing alternative views: analytical biogeography is a controversial topic! For the same reason, I have included only minimal references to papers published after 2002.

The book comprises several distinct parts, each of several chapters. The first part introduces the themes discussed and provides some of the historical and theoretical background that biologists have used to study island communities. Part II deals with the processes of recolonization after devastation by volcanic activity, with Part III following this with appraisals of specific islands, some of which have been studied in considerable detail. The later trends of assembly from these foundation communities are treated in Part IV, with broader integration (using the same cases) presented in Part V. Finally, Ian looks forward from this discourse to endorse and evaluate the importance of such studies in understanding and sustaining Earth's biota. This is not a textbook. Rather, it presents a chosen suite of ideas, perspective and reasoning by a leading Pacificregion biogeographer, together with diversions on the wider effects of volcanic eruptions on humanity, and how both natural communities and human civilization may develop subsequently. It is founded in the ideas and conflicts of island biogeography, and the biological and other information relevant to Ian's themes is documented succinctly. The final 'message', of the importance of understanding community development in order to conserve both natural communities and the underlying processes that sustain them, is one with which few biologists would disagree. He also raises the important topic of 'what we don't know', and ecologists seeking fruitful ideas will find much to stimulate their minds, and to challenge their ingenuity.

Ian Thornton was passionate about islands: a true 'islomaniac' in Schoener's (1988) sense of having 'a powerful attraction to islands'; and his enthusiasm was infectious. Early in his academic career, he spent a sabbatical period in the Hawaiian Islands, where his studies on the remarkable endemic radiations of Psocoptera of the archipelago illuminated patterns of speciation on such isolated islands. Later, he pursued similar studies in the Galapagos, and a book

EDITORIAL PREFACE xi

resulting from that trip (Thornton 1971) is a classic in the literature of that intriguing archipelago. However, these early studies founded in post-colonization events on islands and clarifying patterns of insect evolution and distribution whetted Ian's appetite for larger questions, leading him to investigate and consider the more general origins of island faunas and the extents to which their communities are structured or 'determined' in some way.

In many ways, and as noted above, this is a very personal book. Following from his imposing synthesis of Krakatau (Thornton 1996a) and later studies on Long Island (resulting from a strenuous expedition he organized and led whilst in his 70s: Thornton 2001), he brings together his experiences and previous studies, together with those of a number of his friends and colleagues, to address issues of fundamental evolutionary and biogeographical interest. Thus, John Edwards (whose studies on Mount St Helens are discussed here) visited Krakatau with Ian, and was his major collaborator on Long Island; Sturla Fridriksson (whose magisterial studies of Surtsey Ian recognized as one of the closest parallels to Anak Krakatau) also visited Krakatau and Ian, Surtsey. Rob Whittaker's group at Oxford and our group at La Trobe enjoyed much intellectual controversy over our mutual interests in Krakatau - and Ian revelled in controversy! He continually sought the intellectual input of colleagues versed in those fields of biology with which he was less familiar; he enjoyed encouraging young people, and many recent graduates and graduate students were enthusiastic participants in his expeditions - which were pivotal experiences in their development. As Ian wrote in his acknowledgments to Krakatau: 'Although my Indonesian colleagues flatter me with the saying "naga tua, tenada muda" ("old dragon, young power"), in recent years the need for auxiliary, really young power has increased.' However, his enthusiasms and drive never diminished.

Ian would, I suspect, have made his major acknowledgement in this book to Ann, with whom he first viewed Krakatau in 1982 (a sighting that was to prove pivotal in focusing his studies on island community development) and to whom he dedicated his book on Krakatau. I would echo this acknowledgment in thanking Ann for making his draft available, and for entrusting me with trying to bring it to fruition. Some of his many colleagues and correspondents, participants or collaborators in expeditions, sounding boards for Ian's speculations, or critics of his written drafts, are cited in context in the book and it would be presumptuous of me to list them here in any order of priority. However, a list of his major co-authors and collaborators from the expeditions and suites of papers from recent expeditions provide a partial summary of the debts he would assuredly acknowledge. I regret that these thanks must be incomplete: the accumulation of a lifetime debt of acknowledgement is not easy for anyone else to appraise properly. But, many times in meeting Ian in the departmental corridor up to a decade after his formal (but nominal) retirement from the Department of Zoology, he would make some comment along the lines of

xii EDITORIAL PREFACE

'I've just heard from so-and-so. He/she reckons that What do you think?' The unconscious assimilation of such inputs is part of the intellectual development of any scientist; but the depth and breadth of Ian Thornton's interests and the generosity with which he would respond with constructive (and, often, original) comment was typical of the man, and of the regard in which his scientific work is held.

Tim New Melbourne, February 2006

Biographical memoir

New, T. R., Smithers, C. N. and Marshall, A. T. (2005). Ian Walter Boothroyd Thornton 1926–2002. *Historical Records of Australian Science* 16, 91–106.

Acknowledgements

The following editors and publishers are thanked for granting permission to reproduce or modify tabular or illustrative material: Blackwell Science, Oxford; Ecological Society of America, Washington DC; Elsevier Science, Oxford; The Royal Society, London; Springer Science and Business Media, Heidelberg; Professor Junichi Kojima (*Japanese Journal of Entomology*); Professors Osamu Tadauchi and Junichi Yukawa (*Esakia*). Every effort has been made to obtain permissions for such use, and the publishers would welcome news of any unintended oversights.

I would also like to thank Professor Hideo Tagawa, Kagoshima University, Japan for his invaluable compilation of the 46 scientific papers resulting from his team's extensive research on the Krakatau archipelago (Tagawa 2005), bringing together papers that were previously highly scattered and, some, difficult to access. Dr Borgthór Magnússon has generously sent me recent papers on Surtsey.

I appreciate very much the enthusiasm of Ward Cooper, through whom this book was submitted to Cambridge University Press, and the constructive comments made by reviewers of that earlier draft. His successor at Cambridge, Dominic Lewis, has been very patient in awaiting the completed book.

The impeccable copy-editing by Anna Hodson has enhanced the quality of the manuscript markedly, and I greatly appreciate her perceptive comments and advice.

The cover photograph, of Anak Krakatau erupting in 1993, is by Igan S. Sutawidjaja.