SCOPE 37

Biological Invasions

A Global Perspective

Edited by

J. A. Drake
Department of Zoology and Graduate Program in Ecology, University of Tennessee, Knoxville, USA

H. A. Mooney
Department of Biological Sciences, Stanford University, Stanford, USA

F. di Castri
CNRS-Centre L. Emeberger, Route de Mende-BP 5051, 34033 Montpellier Cedex, France

R. H. Groves
CSIRO Division of Plant Industry, GPO Box 1600, Canberra ACT 2601, Australia

F. J. Kruger
South African Forestry Research Unit, PO Box 727, Pretoria 0001, Republic of South Africa

M. Rejmánek
Department of Botany, University of California, Davis, California 95616, USA

and

M. Williamson
Department of Biology, University of York, York Y01 5DD

Published on behalf of the
Scientific Committee on Problems of the Environment (SCOPE)
of the
International Council of Scientific Unions (ICSU)

by

JOHN WILEY & SONS
Chichester · New York · Brisbane · Toronto · Singapore
Contents

Contributors xix

Preface xxiii

Chapter 1 History of Biological Invasions with Special Emphasis on the Old World 1
Francesco di Castri
1.1 Introduction 1
1.2 The relevance of an historical background to understanding trends and patterns of biological invasions 3
1.3 Peculiarities of the Old World as related to the invasion potential of its species 7
1.4 Biological invasions into Old World ecosystems 13
1.5 Human-history driving forces in the Old World as related to biological invasions 17
1.6 Conclusions 26

Chapter 2 Patterns, Extents and Modes of Invasions by Terrestrial Plants 31
Vernon H. Heywood
2.1 Introduction 31
2.2 Taxonomic patterns: names and numbers 33
2.3 The extent of invasions 40
2.3.1 North temperate regions 41
2.3.2 Mediterranean-climate regions 42
2.3.3 Grasslands and pastures 43
2.3.4 Tropical forests 44
2.3.5 A pattern of islands 45
2.4 Modes of invasions 46
2.4.1 The early historical and aboriginal phases 47
2.4.2 The European/colonial phase 48
2.4.3 The role of the botanic gardens 49
2.4.4 Recent changes in the spread and decline of invaders 51
2.5 Summary and conclusions 51
Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.2.4</td>
<td>Invasion stages</td>
<td>117</td>
</tr>
<tr>
<td>6.2.5</td>
<td>Why are some invasions successful while others are not?</td>
<td>121</td>
</tr>
<tr>
<td>6.2.6</td>
<td>Why are some environments vulnerable while others are not?</td>
<td>123</td>
</tr>
<tr>
<td>6.3</td>
<td>Attributes of invading species</td>
<td>124</td>
</tr>
<tr>
<td>6.3.1</td>
<td>Life forms and growth characteristics</td>
<td>124</td>
</tr>
<tr>
<td>6.3.2</td>
<td>Morphological plasticity and the importance of rapid vegetative growth</td>
<td>127</td>
</tr>
<tr>
<td>6.3.3</td>
<td>Responses to environmental cues</td>
<td>129</td>
</tr>
<tr>
<td>6.3.4</td>
<td>Competitive ability in the 'struggle for dominance'</td>
<td>129</td>
</tr>
<tr>
<td>6.3.5</td>
<td>Survival during unfavourable periods</td>
<td>130</td>
</tr>
<tr>
<td>6.3.6</td>
<td>Mechanisms facilitating intra- and inter-system transfer</td>
<td>132</td>
</tr>
<tr>
<td>6.3.7</td>
<td>The 'perfect invader'—does it exist?</td>
<td>133</td>
</tr>
<tr>
<td>6.4</td>
<td>The management of invasive aquatic plants</td>
<td>133</td>
</tr>
<tr>
<td>6.4.1</td>
<td>Available options</td>
<td>134</td>
</tr>
<tr>
<td>6.4.2</td>
<td>Eradication versus control and the costs of inaction</td>
<td>136</td>
</tr>
<tr>
<td>6.4.3</td>
<td>Successful control programmes—why did they succeed?</td>
<td>137</td>
</tr>
<tr>
<td>6.4.4</td>
<td>Unsuccessful control programmes—why did they fail?</td>
<td>141</td>
</tr>
<tr>
<td>6.4.5</td>
<td>Can programme success be predicted?</td>
<td>144</td>
</tr>
<tr>
<td>6.4.6</td>
<td>The role of legislation</td>
<td>145</td>
</tr>
<tr>
<td>6.4.7</td>
<td>Integrated control strategies</td>
<td>146</td>
</tr>
<tr>
<td>6.5</td>
<td>Conclusions</td>
<td>147</td>
</tr>
</tbody>
</table>

Chapter 7  Temperate Grasslands Vulnerable to Plant Invasions: Characteristics and Consequences  155
Richard N. Mack

7.1 Introduction  155
7.2 Temperate grasslands vulnerable to plant invasion: the characteristics  156
7.2.1 The lack of large, hooved, congregating mammals  157
7.2.2 The dominance of caespitose grasses  157
7.3 Temperate grasslands vulnerable to invasion: the consequences  159
7.3.1 The temperate grasslands of South America  160
7.3.1.1 The invasion of 'European cardoon and a tall thistle'  160
7.3.1.2 Farming brings new invasions  161
7.3.2 Grasslands in the Intermountain West of North America  163
7.3.3 Grasslands in the Central Valley of California  164
7.3.4 Australian temperate grasslands  167
7.4 New potential hazards  170
7.5 Summary and conclusions  173

Chapter 8 The Characteristics of Invaded Mediterranean-climate Regions  181
Fred. J. Kruger, G. J. Breytenbach, Ian A. W. Macdonald, and D. M. Richardson

8.1 Introduction  181
8.2 Patterns of invasion in different mediterranean ecosystems  181
8.2.1 Degrees and patterns of invasion in the different regions  181
Chapter 9 Wildlife Conservation and the Invasion of Nature Reserves by Introduced Species: a Global Perspective

Ian A. W. Macdonald, Lloyd L. Loope, Michael B. Usher, and O. Hamann

9.1 Introduction

9.2 The extent of the invasion of nature reserves by introduced species

9.3 Some effects of introduced species on ecosystem function in nature reserves

9.3.1 Acceleration of soil erosion rates

9.3.2 Alteration of other geomorphological processes

9.3.3 Alteration of biogeochemical cycling

9.3.4 Alteration of hydrological cycles

9.3.5 Alteration of fire regimes

9.3.6 Prevention of recruitment of native species

9.3.7 Concluding comment on the effect of invaders on ecosystem function

9.4 Some effects of alien species on ecosystem structure in nature reserves

9.4.1 Acceleration of local and global extinction rates

9.4.1.1 Extinction of oceanic island birds

9.4.1.2 Other island extinctions

9.4.1.3 Extinctions in continental ecosystems

9.4.1.4 Continental nature reserves—the significance of introduced plant pathogens

9.4.1.5 Continental nature reserves—the significance of introduced insect herbivores

9.4.1.6 Future risks, arising through 'trophic cascades'

9.4.2 Genetic effects of introduced species

9.5 Control of invaders in nature reserves

9.5.1 Controlling plant invaders

9.5.2 Controlling introduced animals in nature reserves

9.6 Summary and conclusions
## Chapter 10 Characteristics of Invaded Islands, with Special Reference to Hawaii

*Lloyd L. Loope and Dieter Mueller-Dombois*

10.1 Introduction 257
10.2 Characteristics of islands: an overview 257
10.3 Characteristics and invasions of the Hawaiian Islands 260
10.4 Why do invaders of island ecosystems have such a high rate of success? 262
10.4.1 Evolution of island organisms in isolation 262
10.4.2 Modification of island environments by humans 265
10.4.3 Invasibility of island ecosystems 266
10.4.4 Reduced aggressiveness and vulnerability to extinction of island biotas 268
10.5 Island invasions and conservation 273
10.6 Summary and conclusions 274

## Chapter 11 Ecosystem-level Processes and the Consequences of Biological Invasions

*P. S. Ramakrishnan and Peter M. Vitousek*

11.1 Introduction 281
11.2 Invasions of intact ecosystems 282
11.3 Invasions of primary succession 283
11.4 Invasions of secondary succession 284
11.5 Invasions and shifting cultivation—a case study 284
11.5.1 Shifting agriculture and secondary succession 285
11.5.2 Weed potential under shifting agriculture 286
11.6 Adaptive strategies of natives versus exotics: system-level consequences 287
11.6.1 Allocation and establishment 287
11.6.2 C₃/C₄ strategy and microdistribution 291
11.6.3 Nutrient conservation by exotic species 293
11.6.4 Weed extinction 294
11.7 Conclusion 296

## Chapter 12 Attributes of Invaders and the Invading Process: Terrestrial and Vascular Plants

*Ian R. Noble*

12.1 Introduction 301
12.2 The ideal invader 302
12.3 Plant strategies 303
12.4 Functional groups 304
12.5 Summary and conclusions 310

## Chapter 13 Attributes of Invaders and the Invading Processes: Vertebrates

*Paul R. Ehrlich*

13.1 Introduction 315
13.2 What is an invader?
13.3 Paired comparisons 316
13.4 Are some species just naturally good colonizers 317
13.5 Characteristics of good invaders 318
13.6 Size of the introduction: frequency of attempts 321
13.7 Invasibility 322
13.8 What controls the success of invasions? 324
13.9 Conclusions 325

Chapter 14 Mathematical Models of Invasion 329
Mark Williamson
14.1 Introduction 329
14.2 Arrival and establishment 330
14.2.1 Minimum viable population size 331
14.2.2 The parameters of establishment 332
14.2.3 Models of epidemics 337
14.3 Spread 338
14.4 Models of equilibrium state 340
14.4.1 The number of parameters 340
14.4.2 Simplified models of communities 341
14.4.3 Food webs 343
14.5 Conclusions 345

Chapter 15 Theories of Predicting Success and Impact of Introduced Species 351
Stuart L. Pimm
15.1 Introduction 351
15.2 The problems of small populations 351
15.2.1 Theory 352
15.2.2 Empirical tests 1: island birds 353
15.2.3 Empirical tests 2: island insects 354
15.2.4 Empirical tests 3: Hawaiian vertebrates 354
15.3 Community structure and chance of invasion 355
15.3.1 Models of community assembly 355
15.3.2 Details of community resistance 358
15.3.2.1 Competitors 358
15.3.2.2 Predators 358
15.3.3 Empirical studies 1: the role of competition 359
15.3.3.1 Hawaiian birds 359
15.3.3.2 The application to other taxa 360
15.3.4 Empirical studies 2: the role of predation 360
15.3.5 Empirical studies 3: community assembly 361
15.4 What determines the impact of an introduced species? 362
15.5 Can we anticipate the effect of an introduced species? 363
15.6 Conclusions 365

Chapter 16 Invasibility of Plant Communities 369
Marcel Rejmánek
16.1 Introduction 369
16.2 Species richness versus invasibility 370
16.3 Invaders in successional series 370
16.4 Invaders along moisture gradients 373
Chapter 17 The Nature and Effects of Disturbance Relative to Invasions
Richard J. Hobbs
17.1 Introduction 389
17.2 Disturbance and patch dynamics 389
17.3 Disturbance, resources and invasibility 390
17.3.1 Background to experiments 390
17.3.2 Communities studied 391
17.3.3 Experimental procedure 392
17.3.4 Results and discussion 393
17.3.5 Other species 396
17.3.6 Interpretation 398
17.4 Comparison with other systems 400
17.5 Summary and conclusions 401

Chapter 18 Chance and Timing in Biological Invasions
Michael J. Crawley
18.1 Introduction 407
18.1.1 Intrinsic rate of increase 407
18.1.2 Exploitation competition 408
18.1.3 Interference competition 408
18.1.4 Natural enemies 408
18.1.5 Mutualisms 408
18.1.6 Refuges 409
18.2 Chance 409
18.2.1 Buffering mechanisms exhibited by plants 412
18.2.2 Buffering mechanisms exhibited by animals 413
18.3 Data on chance in invasions 414
18.3.1 Chance in the weed biocontrol data 414
18.3.2 Number of releases 414
18.3.3 Previous experience 415
18.3.4 Taxonomic mistakes 415
18.3.5 Total effort 416
18.3.6 Spatial distribution of eggs 416
18.3.7 Adult longevity 416
18.3.8 Failure to establish 417
18.4 Timing 417
18.4.1 Seasonal phenology 417
18.4.2 Timing in the Broadbalk experiment 418
18.4.3 Successional timing 419
18.5 Conclusions 420

Chapter 19 Analysis of Risk for Invasions and Control Programs
Simon A. Levin
19.1 Introduction 425
19.2 Risk assessment and risk management 426
Chapter 20 Ecological Control of Invasive Terrestrial Plants
Richard H. Groves

20.1 Introduction 437
20.2 Methods of control 437
20.3 Some examples of ecological control
20.3.1 Control of Hypericum perforatum 442
20.3.2 Control of Eupatorium spp. 447
20.3.3 Control of Acacia longifolia and Chrysanthemoides monilifera 453
20.4 Summary and conclusions 456

Chapter 21 Ecological Effects of Controlling Invasive Terrestrial Vertebrates
Michael B. Usher

21.1 Introduction 463
21.1.1 The perception of the problem 463
21.1.2 The scope of this paper 464
21.1.3 The frequency of control measures 465
21.2 The invasive species
21.2.1 How is the invasive species' ecology affected by control? 467
21.2.2 Are there genetical effects? 467
21.3 The invaded community
21.3.1 Does control affect rare and endangered species? 469
21.3.2 Does the community recover? 472
21.3.3 Are there relationships with other introduced species? 474
21.3.4 Are there undesirable side-effects? 476
21.4 Prognoses for the future
21.4.1 Is control possible? 477
21.4.2 Is modelling helpful? 480
21.4.3 How is success measured? 481
21.4.4 Are control and conservation compatible? 482
21.4.5 Does control increase or decrease genetic diversity? 483
21.5 Conclusion 484
21.6 Summary 484

Chapter 22 Biological Invasions: a SCOPE Program
Overview
H. A. Mooney and J. A. Drake

22.1 Introduction 491
22.2 How many invaders are there?
22.2.1 Invasions into nature reserves 492
22.2.2 Invasions on islands 492
22.3 Who are the invaders?
22.3.1 Functional groups 493
22.3.2 Taxonomic groups 494
Contents

22.4 How do they get there? 494
22.5 Where do they come from? 495
22.6 How do they get established?
   22.6.1 The minimum viable population 496
   22.6.2 Higher-order effects 496
22.7 How fast do they move? 497
22.8 What is the nature of the systems they invade? 498
22.9 How do they impact the systems they invade? 498
22.10 What can we predict at present? 499
22.11 Good intentions are not enough 501
22.12 The costs and benefits of control 502
22.13 The new order 502
22.14 Invasions by genetically designed organisms 503

Topical and Correlative Index 509

Species Index 521