Contents

Contributing Authors

page  xiii

1 Introduction
Richard Law, Ulf Dieckmann, and Johan A.J. Metz

2 A Neighborhood View of Interactions among Individual Plants
Peter Stoll and Jacob Weiner

A Empirical and Statistical Background:
A Plant Ecological Perspective

page  7

2.1 Introduction ............................................. 11
2.2 Competition Mechanisms ............................... 12
2.3 Moving from the Population to the Individual Level .... 18
2.4 What is a Plant’s Neighborhood? .................... 19
2.5 Challenges for a Neighborhood Perspective of
Plant Interactions ............................................ 24
2.6 Suggestions for Modelers .............................. 26

3 Spatial Interactions among Grassland Plant Populations
Jonathan Silvertown and J. Bastow Wilson

28

3.1 Introduction ............................................. 28
3.2 Methods for Measuring Competition in the Field ....... 29
3.3 Results of Field Experiments ........................... 32
3.4 Competition Matrices .................................... 38
3.5 Community Consequences of Spatial Interactions .... 42
3.6 Concluding Comments .................................. 46

4 Spatio-temporal Patterns in Grassland Communities
Tomáš Herben, Heinjo J. During, and Richard Law

48

4.1 Introduction ............................................. 48
4.2 Spatio-temporal Patterns in Plant Communities .......... 48
4.3 Externally versus Internally Generated Spatial Patterns . 52
4.4 Concepts in Spatio-temporal Processes in
Plant Communities ......................................... 54
4.5 Ergodic and Non-ergodic Communities ................... 60
4.6 Concluding Comments .................................. 64
## Table of Contents

### 5 Statistical Modeling and Analysis of Spatial Patterns  
65
David R. Cox, Valerie Isham, and Paul Northrop
- 5.1 Introduction 65
- 5.2 Descriptive Analysis 66
- 5.3 Stochastic Models 70
- 5.4 Model Fitting 80
- 5.5 Concluding Comments 88

### 8 When the Mean-field Approximation Breaks Down  
89

### 6 Grid-based Models as Tools for Ecological Research  
94
Christian Wissel
- 6.1 Introduction 94
- 6.2 Grid-based Simulation Models 95
- 6.3 Spread and Control of Rabies 97
- 6.4 Dynamics of a Dwarf Shrub Community 104
- 6.5 A Generic Forest Fire Model 109
- 6.6 Concluding Comments 114

### 7 Coexistence of Replicators in Prebiotic Evolution  
116
Tamás Czárán and Eörs Szathmáry
- 7.1 Introduction 116
- 7.2 Metabolic Replication: A Cellular Automaton Model 119
- 7.3 The Phenomenology of Coexistence 123
- 7.4 Spatial Pattern and the “Advantage of the Rare” Effect 127
- 7.5 Resistance to Parasites and the Evolution of Community Size 129
- 7.6 Toward a Dynamical Theory of Surface Metabolism 133

### 8 Games on Grids  
135
Martin A. Nowak and Karl Sigmund
- 8.1 Introduction 135
- 8.2 One-round Games 137
- 8.3 Repeated Games 145
- 8.4 Extensions and Related Work 149
- 8.5 Concluding Comments 150
## 9 The Interplay between Reaction and Diffusion

Mikael B. Cronhjort

9.1 Introduction ............................................. 151
9.2 The Models: Cellular Automata versus Partial Differential Equations ............................................. 153
9.3 Spiral and Scroll Ring Patterns ............................................. 159
9.4 Cluster Dynamics ............................................. 163
9.5 Concluding Comments ............................................. 169

## 10 Spirals and Spots: Novel Evolutionary Phenomena through Spatial Self-structuring

Maarten C. Boerlijst

10.1 Introduction ............................................. 171
10.2 A Spatial Hypercycle Model ............................................. 173
10.3 Spirals and Spots ............................................. 174
10.4 Local versus Global Extinction ............................................. 175
10.5 Resistance to Parasites ............................................. 178
10.6 Concluding Comments ............................................. 180

## 11 The Role of Space in Reducing Predator–Prey Cycles

Vincent A.A. Jansen and André M. de Roos

11.1 Introduction ............................................. 183
11.2 Individual-based Predator–Prey Models ............................................. 184
11.3 A Deterministic Model of Two Coupled Local Populations ............................................. 187
11.4 Larger Spatial Domains ............................................. 193
11.5 The Spatial Rosenzweig–MacArthur Model ............................................. 196
11.6 Concluding Comments ............................................. 199
11.7 Stability Analysis of a Multi-patch System ............................................. 200

## C Simplifying Spatial Complexity: Examples

Howard B. Wilson and Matthew J. Keeling

12.1 Introduction ............................................. 209
12.2 Two Models from Evolutionary Ecology ............................................. 210
12.3 Identifying Spatial Scales ............................................. 213
12.4 Dynamics, Determinism, and Dimensionality ............................................. 219
12.5 Concluding Comments ............................................. 225
12.A Singular Value Decomposition ............................................. 225
Table of Contents

13 Lattice Models and Pair Approximation in Ecology 227
  Yoh Iwasa
  13.1 Introduction ............................................ 227
  13.2 Plants Reproducing by Seed and Clonal Growth .. 228
  13.3 Forest Gaps ............................................ 236
  13.4 Colicin-producing and Colicin-sensitive Bacteria .. 243
  13.5 Limitations, Extensions, and Further Applications .. 247

14 Moment Approximations of Individual-based Models 252
  Richard Law and Ulf Dieckmann
  14.1 Introduction ............................................ 252
  14.2 Spatial Patterns and Spatial Moments ................. 253
  14.3 Extracting the Ecological Signal from Stochastic Realizations ............................................ 256
  14.4 Qualitative Dependencies in a Spatial Logistic Equation ............................................ 261
  14.5 Exploration of Parameter Space ......................... 267
  14.6 Concluding Comments .................................... 269

15 Evolutionary Dynamics in Spatial Host–Parasite Systems 271
  Matthew J. Keeling
  15.1 Introduction ............................................ 271
  15.2 Dynamics of the Spatial Host–Parasite Model ....... 272
  15.3 A Difference Equation for the Dynamics of Local Configurations ............................................ 279
  15.4 Evolution to Critical Transmissibility ................. 282
  15.5 Concluding Comments .................................... 288
  15.A Mathematical Specification of the PATCH Model .... 289

16 Foci, Small and Large: A Specific Class of Biological Invasion 292
  Jan-Carel Zadoks
  16.1 Introduction ............................................ 292
  16.2 Epidemic Orders ........................................ 293
  16.3 A Theory of Foci ....................................... 298
  16.4 Generalizations ........................................ 312
  16.5 Concluding Comments .................................... 315
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>Wave Patterns in Spatial Games and the Evolution of Cooperation</td>
<td>318</td>
</tr>
<tr>
<td></td>
<td>Régis Ferrière and Richard E. Michod</td>
<td></td>
</tr>
<tr>
<td>17.1</td>
<td>Introduction</td>
<td>318</td>
</tr>
<tr>
<td>17.2</td>
<td>Invasion in Time- and Space-continuous Games</td>
<td>319</td>
</tr>
<tr>
<td>17.3</td>
<td>Invasion of Tit For Tat in Games with Time-limited Memory</td>
<td>323</td>
</tr>
<tr>
<td>17.4</td>
<td>Invasion of Tit For Tat in Games with Space-limited Memory</td>
<td>329</td>
</tr>
<tr>
<td>17.5</td>
<td>Concluding Comments</td>
<td>332</td>
</tr>
<tr>
<td>D</td>
<td>Simplifying Spatial Complexity: Techniques</td>
<td>337</td>
</tr>
<tr>
<td>18</td>
<td>Pair Approximations for Lattice-based Ecological Models</td>
<td>341</td>
</tr>
<tr>
<td></td>
<td>Kazunori Satō and Yoh Iwasa</td>
<td></td>
</tr>
<tr>
<td>18.1</td>
<td>Introduction</td>
<td>341</td>
</tr>
<tr>
<td>18.2</td>
<td>Pair Approximation</td>
<td>344</td>
</tr>
<tr>
<td>18.3</td>
<td>Improved Pair Approximation</td>
<td>349</td>
</tr>
<tr>
<td>18.4</td>
<td>Improved Pair Approximation with Variable Discounting</td>
<td>355</td>
</tr>
<tr>
<td>18.5</td>
<td>Concluding Comments</td>
<td>357</td>
</tr>
<tr>
<td>19</td>
<td>Pair Approximations for Different Spatial Geometries</td>
<td>359</td>
</tr>
<tr>
<td></td>
<td>Mina van Baalen</td>
<td></td>
</tr>
<tr>
<td>19.1</td>
<td>Introduction</td>
<td>359</td>
</tr>
<tr>
<td>19.2</td>
<td>The Dynamics of Pair Events</td>
<td>364</td>
</tr>
<tr>
<td>19.3</td>
<td>Average Event Rates</td>
<td>368</td>
</tr>
<tr>
<td>19.4</td>
<td>Pair Approximations for Special Geometries</td>
<td>372</td>
</tr>
<tr>
<td>19.5</td>
<td>Pair Approximations versus Explicit Simulations</td>
<td>379</td>
</tr>
<tr>
<td>19.6</td>
<td>Invasion Dynamics</td>
<td>382</td>
</tr>
<tr>
<td>19.7</td>
<td>Concluding Comments</td>
<td>385</td>
</tr>
<tr>
<td>20</td>
<td>Moment Methods for Ecological Processes in Continuous Space</td>
<td>388</td>
</tr>
<tr>
<td></td>
<td>Benjamin M. Bolker, Stephen W. Pacala, and Simon A. Levin</td>
<td></td>
</tr>
<tr>
<td>20.1</td>
<td>Introduction</td>
<td>388</td>
</tr>
<tr>
<td>20.2</td>
<td>Moment Methods</td>
<td>389</td>
</tr>
<tr>
<td>20.3</td>
<td>A Spatial Logistic Model</td>
<td>391</td>
</tr>
<tr>
<td>20.4</td>
<td>A Spatial Competition Model</td>
<td>400</td>
</tr>
<tr>
<td>20.5</td>
<td>Extensions and Related Work</td>
<td>403</td>
</tr>
<tr>
<td>20.6</td>
<td>Concluding Comments</td>
<td>405</td>
</tr>
</tbody>
</table>
20. A Mean Equation  ........................................ 406
20. B Covariance Equation  ................................. 408
20. C Analyzing the One-species System .................. 409
20. D Analyzing the Two-species System .................. 410

21 Relaxation Projections and the Method of Moments 412
Ulf Dieckmann and Richard Law
21.1 Introduction  ............................................. 412
21.2 Individual-based Dynamics in Continuous Space ...... 418
21.3 Dynamics of Correlation Densities ..................... 425
21.4 Moment Closures and their Performance ............... 438
21.5 Further Developments and Extensions ................. 447
21.A Derivation of Pair Dynamics ............................ 452

22 Methods for Reaction–Diffusion Models 456
Vivian Hutson and Glenn T. Vickers
22.1 Introduction  ............................................. 456
22.2 Continuous Models ....................................... 459
22.3 Linearized Stability and the Turing Bifurcation ........ 466
22.4 Comparison Methods ..................................... 471
22.5 Traveling Waves .......................................... 475
22.6 The Evolution of Diffusion ............................... 479
22.7 Concluding Comments ................................... 481

23 The Dynamics of Invasion Waves 482
Johan A. J. Metz, Denis Mollison, and Frank van den Bosch
23.1 Introduction  ............................................. 482
23.2 Relative Scales of the Process Components .............. 483
23.3 Independent Spread in Homogeneous Space:
    A Natural Gauging Point .................................. 485
23.4 Complications ............................................ 497
23.5 The Link with Reaction–Diffusion Models ............... 504
23.6 Dispersal on Reaction–Diffusion Models ............... 507
23.7 Concluding Comments ................................... 512

24 Epilogue  .................................................... 513
Johan A. J. Metz, Ulf Dieckmann, and Richard Law

References  .................................................... 517

Index  ......................................................... 553