

Insect Ecology

Behavior, Populations and Communities

Combining breadth of coverage with detail, this cohesive introduction to insect ecology couples concepts with a broad range of examples and practical applications. It explores cutting-edge topics in the field, drawing on and highlighting the links between theory and the latest empirical studies.

The sections are structured around a series of key topics, including behavioral ecology, species interactions, population ecology, food webs, communities and ecosystems, and broad patterns in nature. Chapters progress logically from the small scale to the large; from individual species through to species interactions, populations and communities.

Application sections at the end of each chapter outline the practicality of ecological concepts and show how ecological information and concepts can be useful in agriculture, horticulture and forestry. Each chapter ends with a summary, providing a brief recap, followed by a set of questions and discussion topics designed to encourage independent and creative thinking.

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CONTENTS

Preface *page* ix Acknowledgments xiii

Part I Introduction 1

- **1** The scope of insect ecology 3
 - 1.1 Fascination with insects 4
 - 1.2 Antiquity of insects 4
 - 1.3 Insect body plan 4
 - 1.4 Richness of the insect fauna 8
 - 1.5 Richness of relationships 9
 - **1.6** Adaptive radiation 14
 - 1.7 Ecosystem processes 17
 - 1.8 Ecological questions and answers 19

Applications: Contributions to many disciplines 20 Summary 22 Questions and discussion topics 23

Further reading 23

Part II Behavioral ecology 25

2 Behavior, mating systems and sexual

- selection 27
- 2.1 The reproductive imperative 28
- 2.2 The life-cycle approach 28
- 2.3 The experimental necessity 28
- 2.4 Survival 29
- 2.5 Foraging behavior 34
- 2.6 A place to live 37
- 2.7 Communication 42
- 2.8 Reproductive behavior 47

Applications: Behavioral approaches to pest regulation 65

Summary 69

Questions and discussion topics 70

Further reading 71

3 Social insects: the evolution and ecological consequences of sociality 72
3.1 What are social insects? 73

- 3.2 Levels of sociality: the other social insects 73
- 3.3 Eusociality: the superorganisms 75
- 3.4 Evolution of sociality: Darwin's dilemma 82
- 3.5 The ecological consequences of sociality 87

Applications: Social insects as saviors and pests 91 Summary 94 Questions and discussion topics 95 Further reading 95

Part III Species interactions 97

4 Plant and herbivore interactions 99

- 4.1 Taxonomic occurrence of phytophagy 100
- 4.2 Diet breadth, feeding strategies and herbivore guilds 100
- 4.3 Plant barriers to herbivore attack 105
- **4.4** Plant defense hypotheses 142
- 4.5 The reciprocal effects of plant–insect interactions on distribution and abundance 150
- **4.6** The evolutionary ecology of plant-insect interactions 159

Applications: Plant-insect interaction theory

in pest management 178

Summary 181

Questions and discussion topics 183

Further reading 183

- 5 Lateral interactions: competition, amensalism and facilitation 184
 - 5.1 Competition and resource limitation 185
 - 5.2 Paradigms of competition theory: evidence for and against 196
 - 5.3 Changing perspectives on competition between insect herbivores 207

vi Contents	
5.4 Competition in omnivores, detritivores, predators and parasitoids 209	Questions and discussion topics 302 Further reading 303
5.5 Comparative overview of competitive	
interactions 214	8 Parasite and host interactions 304
5.6 Facilitation 216	8.1 The parasite and parasitism 305
5.7 Call for broader theory 219	8.2 Kinds of parasites 306
Applications: Humans and insects as competitors 220	8.3 The number of parasitic insect
Summary 222	species 306
Questions and discussion topics 223	8.4 Small body size 308
Further reading 223	8.5 Adaptive radiation of parasites 311
	8.6 Life-history convergence 315
6 Mutualisms 224	8.7 Convergence among parasitoids 317
6.1 Mutualism as a creative evolutionary	8.8 Phylogenetic tracking of host lineages 321
force 225	8.9 Geographic mosaics of variation and patch
6.2 The variety of mutualistic interactions 225	dynamics 326
6.3 Mutualism and the evolution of	8.10 Damage to the host 329
biodiversity 229	8.11 Host defenses against parasites 332
6.4 The origin of mutualisms 234	8.12 Host behavioral modification by parasites 335
6.5 The give and take in mutualism 235	8.13 Modeling host and parasite
6.6 Cheating 245	interactions 336
6.7 Adaptive radiation in mutualistic	Applications: Harmful and beneficial parasites 340
systems 248	Summary 346
6.8 Modeling mutualism 255	Questions and discussion topics 347
6.9 Complexity of interactions 258	Further reading 348
6.10 An historical note 260	
Applications: Beneficial interactions in agriculture 261	Part IV Population ecology 349
Summary 266	
Questions and discussion topics 267	9 Demography, population growth and life
Further reading 267	tables 351
	9.1 Principles of population growth 352
7 Prey and predator interactions 268	9.2 Feedback loops, density dependence and
7.1 What is a predator? 269	population regulation 354
7.2 The generalized feeding habit of	9.3 Life tables 357
predators 269	9.4 Comparison of life tables 361
7.3 Predator effects on prey abundance 270	9.5 Survivorship curves 366
7.4 Predator responses to changes in prey density 270	Applications: Approaching a problem and planning 369 Summary 371
7.5 Prey–predator dynamics 276	Questions and discussion topics 372
7.6 Predation in complex food webs 286	Further reading 372
7.7 Non-consumptive predator impacts on prey 292	-

7.8 Evolutionary response of prey to predation 294Applications: Biological control 297Summary 301

10 Life histories 373

10.1 Scope of studies 374

10.2 Evolutionary strategies and tactics 374

- 10.3 Comparative life-history studies 374
- 10.4 Adaptations, constraints, trade-offs, resource allocation, costs and benefits and alternative strategies 385
- 10.5 Hypotheses on fecundity variation 387
- 10.6 Timing of reproduction 389
- 10.7 Stabilizing selection on life-history traits 394
- 10.8 Life span of adult insects 397
- Applications: Understanding pest species 400 Summary 402 Questions and discussion topics 403
- Further reading 403
- **11 Population dynamics** 404
 - 11.1 Population patterns 405
 - 11.2 The mechanistic understanding of why population density change occurs 415
 - 11.3 Complex interactions 426
 - 11.4 An evolutionary hypothesis 431
 - 11.5 Metapopulation dynamics 432
- Applications: Planning and management 435 Summary 437 Questions and discussion topics 438

Further reading 439

Part V Food webs and communities 441

12 Community structure 443

- 12.1 The community 444
- 12.2 The ecological niches of species 447
- 12.3 Community development 454
- 12.4 Community organization and structure 464
- 12.5 Community genetics 471
- 12.6 The time hypothesis or the area hypothesis? 475
- 12.7 Compound communities 477

Applications: Insects in environmental assessment 482 Summary 486

Questions and discussion topics 487 Further reading 488

13 Multitrophic interactions 489

- 13.1 The trophic level concept 490
- 13.2 Plant traits that affect enemy-prey interactions 491

13.3 Trophic cascades 514 Applications: Choosing plants to encourage trophic cascades 527 Summarv 531 Questions and discussion topics 533 Further reading 534

Part VI Broad patterns in nature 535

14 Biological diversity 537 14.1 Scales of biodiversity 538 14.2 Sampling species density 538 14.3 Importance of pattern detection 541 14.4 Gradients of island size and remoteness 541 14.5 Latitudinal gradients 549 14.6 Altitudinal gradients 563 14.7 Time gradients 567 14.8 Disturbance gradients 573 Applications: Conserving species richness 575 Summarv 580 Questions and discussion topics 582 Further reading 582 **15** Planet Earth: patterns and processes 15.1 The paleobiological record 584

583

15.2 Climate change 590 15.3 Ecosystem dynamics 600 15.4 Invasions 603 15.5 Conservation ecology 609 Applications: Threats and costs 612 Summary 615 Questions and discussion topics 616 Further reading 616

Glossary 617 References 639 Author index 764 Taxonomic index 780 Subject index 791 Color plates are located between pages 306 and 307.



PREFACE

The first edition of *Insect Ecology* was published in 1975, and remained the only textbook in the field for over 20 years, passing through a second edition in 1984, and a third edition in 1997. By the time this book had been in print for 30 years, a change in design and coverage seemed propitious. I (PWP) was fortunate to team up with Dr. Robert Denno, and we engaged in a stimulating, enjoyable and fruitful collaboration designing and writing this new book, *Insect Ecology: Behavior, Populations and Communities.* His tragic death in 2008 left his influence and perspective unrepresented as the book progressed, but some former graduate students of his were eager to see the project completed, and they agreed to write chapters. Hence, we have five authors contributing to the book, giving it a fresh complexion.

We have written this textbook for advanced undergraduates, graduate students, faculty and other kinds of researchers. Our emphasis is on providing an introduction to ecology for entomologists, and an introduction to entomological concerns for ecologists. Providing a conceptual basis for investigating insects to satisfy the empirical and problem-solving motivations broadens the scope of understanding and research from a merely descriptive phase to a hypothesis-testing, theory-building enterprise. Research studies that contribute to entomology and ecology simultaneously can add new dimensions to each field, and ecologists who include entomological studies in their comparative work with other taxa broaden the scope of investigation. Therefore, this book should contribute to the increasing synthesis of science.

We have generally taken the approach of introducing a conceptual area of ecology, with its strengths, weaknesses, hypotheses and debates, and gone on to use published studies to illustrate the relevant research. The reader is introduced to the practical way in which concepts and hypotheses are refined and advanced, through the scientific method.

The book is designed to be covered in a one-semester course of about 15 weeks. The 15 chapters move through behavior and social insect ecology, to communities, biodiversity and large-scale interactions. Major conceptual themes are introduced such that a student will be able to appreciate most of the literature in ecology, and fit it into the various sub-disciplines.

Citations and references

As a professional approach to the field develops we recognize that scientists remember information, discuss it and write about it using three kinds of categorical

Preface

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information, as in the indexes in the book: the subject matter, the organisms studied and the scientists involved. The year of publication is also important as a reference tool. Therefore, citations to published papers in the text are a necessary part of scientific coverage, followed by full details in the reference section of the book. We employ extensive reference to the literature in the book for several important reasons. (1) We give credit to ideas and data where credit is due. (2) The sources provide the reader with original works to which reference can be made for more detail, methodology, conceptual development, and further references. The interested and resourceful reader may enjoy a virtually limitless path of enquiry. (3) References also provide information on the types of journals relevant to the field, particularly for those training for a professional career. (4) The use of citations also illustrates how an argument is developed in the scientific literature; the use of the building blocks in the literature on which we depend to construct new science.

Figures and tables

An integral part of the delivery of information in this book is the figures and tables. They should be studied in detail to gain an appreciation of a concept, a set of results or support for an argument. Figures and tables are not necessarily easy to understand, although we have explained them as best we can. They are a fundamental way of communicating quantitative and qualitative information in science, so students are well advised to familiarize themselves with these illustrative materials, and to even commit to memory some of them. Former students may well remember examination questions which require a relevant figure. Tables also can provide large bodies of information in compact form. They can present the weight of evidence for a particular argument developed in the text.

To the figures we have added small images where appropriate representing the type of organism to which the figure refers. This adds interest and may help some students not well versed in entomology to appreciate the kind of insect involved. However, the illustrations only provide a general picture of the insect type, not necessarily an exact match to the species in question.

Names of species and higher taxa

Our emphasis has been on making the treatment of names as understandable as possible. An introductory course in entomology would help the reader to know the kinds of species we discuss, although this is not a necessary course requirement. Without such a course a helpful text would be *Borror and DeLong's Introduction to the Study of Insects*, by C. A. Triplehorn and N. F. Johnson (2005. 7th edition. Belmont, CA: Thompson Brooks/Cole). We

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Preface
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xi

follow the taxonomy in this book including the common names of insect families and higher taxa, and also the web site *Common Names of Insects and Related Organisms* by the Entomological Society of America. Other introductory texts in entomology would also be worth consulting.

The naming of species and higher taxa changes periodically, posing a challenge for the writer and reader. Our solution has been usually to employ the Latin binomial used in the original paper, or to use an updated name if the species is well known. We have also usually provided a way of knowing the group to which the species belongs, such as the family name or common name, or order.

For plant names and systematics we have referred to *Plant Systematics: A Phylogenetic Approach* by W. S. Judd *et al.* (2002. 2nd edition. Sunderland, MA: Sinauer Associates), which is a helpful reference when the relatedness of plants is of interest.

Remembering the names of species is a challenge for the student, but an essential part of communicating in science.

Important terms in boldface

Throughout the text we have used boldface font to emphasize important terms which the student should remember.

Glossary

Boldface terms in the text are collected into a glossary near the end of the book for speedy reference, and to help the student with reviewing terms and committing them to memory.

Applications

At the end of each chapter we have a section on how ecological information and concepts can be useful in the cultivation of plants for human needs, and the regulation of pest species. We feel compelled to make connections from basic ecology to practical landscape management because this linkage is important, but also intangible to many. We hope that this section will stimulate the reader to conjure up more examples of relevant examples and to read the primary literature with a view to possible applications.

Summaries

Each chapter is provided with a summary statement written to provide a brief recap of the chapter, which should be helpful with preparation for tests and examinations.

xii Preface

Questions and discussion topics

Chapters are concluded with these items designed to encourage independent and creative thinking, and writing skills. The answers will involve essay-type responses or class discussions, in which specific examples should be encouraged where appropriate, and full justification of the position taken is provided.

Further reading

We have included this section in each chapter, with five references which provide a broad perspective for enhanced learning, giving the reader the opportunity to delve more deeply into aspects covered in the chapter.

Debate

A fascinating aspect of the biological sciences, including insect ecology, is the ongoing debate about interactions and processes. Because of the complexity of nature - so many species and environments - little is resolved to the point of becoming solid scientific theory, which is agreed upon by the majority of scientists in the field. So the best we have in ecology is hypotheses, and frequently several alternatives, which form the basis for discourse, and the impetus for research to resolve differences in evidence and opinion, or to broaden perspective, which will encompass and unify formerly disparate views. There is a large opportunity in ecology for synthesis, broad comparative studies and the development of theory. Much of theoretical ecology is more about generating hypotheses than resolving the questions raised, and much of theoretical ecology remains untested with empirical studies. For the empiricist there is much to do, with entomologists well motivated to contribute basic knowledge which will contribute to the resolution of debates in ecology. We have not attempted to resolve debates in all cases in this book because the text should contain heuristic elements of importance in promoting discussion, and further study of the developing literature.

We hope that this fascination for science is stimulated in the student, and enriched in the professional reader. Insect ecology is a rapidly developing field which offers opportunities and challenges to be enjoyed.



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The pleasures and challenges of writing this book have contributed to a rewarding experience which we share with many collaborators. They do not necessarily endorse what is written, but we thank them wholeheartedly for the many reviews of chapters, and contributions of relevant papers: Anurag Agrawal, Joseph Bailey, Randy Bangert, Judith Bronstein, Timothy Craig, Sanford Eigenbrode, Daniel Gruner, Daniel Herms, David Margolies, Nicholas Mills, Yong-Lak Park, Robert Peterson, Jay Rosenheim, John Schneider, Jennifer Schweitzer, Stephen Shuster, Sherilyn Smith, John Spence, Courtney Tobler, Gina Wimp and several anonymous reviewers. Their time, effort and expertise devoted to improving the book are greatly appreciated. Also, Barbara Denno and Courtney Tobler provided invaluable help with figures. Photographs were graciously provided by Thomas and Maria Eisner, David Dussourd, György Csóka and Michael Loeb. These and other photographs and figures are acknowledged in the figure captions, or cited in the reference section of the book. At Cambridge University Press several editors have contributed to this book over the years, most notably Dominic Lewis, Commissioning Editor for Life Sciences, and Sophie Bulbrook, the Textbook Development Editor. We are grateful for their involvement in this project.

Robert Denno was not able to complete this book with us, but he exerted strong impact on its contents, and with the chapters he wrote. We cherish his memory, his friendship, his scholarship and his jovial attitude to life. Bob's passion for insect ecology inspired a new generation of scientists who were fortunate enough to experience the zeal with which he approached his classroom lectures, and the devotion with which he showered his students and post-docs. We (M.D.E., D.L.F. and I.K.) are just a few of the many graduate students who had the privilege of learning the science of insect ecology and the art of life from Bob. We are honored with the opportunity to extend Bob's legacy by taking part in this project, and we hope to reflect his perspective and spirit in our contributions to the work.

> P.W.P. M.D.E. D.L.F. I.K.