

Natural Enemies

An Introduction to Biological Control

This second edition of *Natural Enemies* will give students, professionals, and anyone wishing to learn the basics of biological control a fully updated and thorough introduction. The book discusses the huge diversity of organisms used in the control of pests, weeds, and plant pathogens and compares the many different strategies referred to as “biological control”: the introduction of exotic natural enemies; application of predators, parasitoids, and microorganisms for shorter term control; and manipulation of the environment to enhance natural enemy populations.

The authors present the ecological concepts which form the bases of biological control and discuss recent changes to make biological control safe for the environment. Case studies are included throughout, providing in-depth examples of the use of different organisms and strategies in a variety of ecosystems. A new chapter covers the current challenges, the impact of climate change, the problem of invasive species, and how biological control can aid sustainability.

Ann E. Hajek is a professor in the Department of Entomology at Cornell University, New York, USA. Her career has focused on biological control and insect pathology, with research ranging from developing biopesticides to investigating why epizootics of insect diseases occur. The International Organization for Biological Control, Nearctic Regional Section, presented her with their Distinguished Scientist Award in 2011.

Jørgen Eilenberg is a professor in the Department of Plant and Environmental Sciences at the University of Copenhagen, Denmark, where he leads a research team studying insect pathogens and biological control. He was the president of the Society for Invertebrate Pathology from 2012 to 2014.

Natural Enemies

An Introduction to Biological Control

Second edition

ANN E. HAJEK

Cornell University

JØRGEN EILENBERG

University of Copenhagen



CAMBRIDGE
UNIVERSITY PRESS

Cambridge University Press & Assessment

978-1-107-66824-9 — Natural Enemies

Ann E. Hajek, Jørgen Eilenberg

Frontmatter

[More Information](#)



Shaftesbury Road, Cambridge CB2 8EA, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314–321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi – 110025, India

103 Penang Road, #05–06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of Cambridge University Press & Assessment, a department of the University of Cambridge.

We share the University's mission to contribute to society through the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781107668249

DOI: 10.1017/9781107280267

First edition ©Ann E. Hajek 2004

Second edition © Cambridge University Press & Assessment 2018

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press & Assessment.

First published 2004

Second edition 2018

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

ISBN 978-1-107-66824-9 Paperback

Cambridge University Press & Assessment has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Contents

<i>Preface</i>	<i>page</i> ix
<i>Acknowledgments</i>	xii

Part I Introduction

1	Why Use Natural Enemies?	3
	1.1 Historical Perspective on Chemical Pest Control	4
	1.2 Why Consider Biological Alternatives for Pest Control?	6
	1.3 A Pest or Not?	18
2	Introduction to Biological Control	22
	2.1 Defining Biological Control	22
	2.2 Natural Control	24
	2.3 Diversity in Biological Control	25
	2.4 History of Biological Control	28
	2.5 Studying Biological Control	33

Part II Strategies for Using Natural Enemies

3	Classical Biological Control	41
	3.1 Uses of Classical Biological Control	45
	3.2 Methods for Practicing and Evaluating Classical Biological Control	49
	3.3 Success in Classical Biological Control	55
	3.4 Economics of Classical Biological Control	64
4	Augmentation: Inundative and Inoculative Biological Control	66
	4.1 Inundative Biological Control	66
	4.2 Inoculative Biological Control	68
	4.3 Inundative versus Inoculative Strategies	71
	4.4 Production of Natural Enemies by Industry	72
	4.5 Products for Use	73
	4.6 Natural Enemies Commercially Available for Augmentative Releases	80

vi	Contents	
5	Conservation and Enhancement of Natural Enemies	85
	5.1 Biodiversity Leading to Biological Control	85
	5.2 Conserving Natural Enemies: Reducing Effects of Pesticides on Natural Enemies	87
	5.3 Enhancing Natural Enemy Populations	90
	5.4 Conservation Biological Control Today	104
Part III Biological Control of Invertebrate and Vertebrate Pests		
6	Ecological Basis for Use of Predators, Parasitoids, and Pathogens to Control Pests	109
	6.1 Types of Invertebrate Pests	110
	6.2 Types of Natural Enemies	110
	6.3 Interactions between Natural Enemies and Hosts	111
	6.4 Population Regulation	115
	6.5 Exploring Factors Impacting Pest Regulation and Its Stability	123
	6.6 Microbial Natural Enemies Attacking Invertebrates	127
	6.7 Food Webs and Community Ecology	129
7	Predators	137
	7.1 Vertebrate Predators	137
	7.2 Invertebrate Predators	138
	7.3 Predator Choices and Impacts	152
	7.4 Use of Invertebrate Predators for Pest Control	156
8	Insect Parasitoids: Attack by Aliens	161
	8.1 Taxonomic Diversity in Parasitoids	162
	8.2 Diversity in Parasitoid Life Histories	165
	8.3 Locating and Accepting a Host	174
	8.4 The Battle between Parasitoid and Host	178
	8.5 Use of Parasitoids in Biological Control	182
9	Parasitic Nematodes	189
	9.1 Entomopathogenic Nematodes (EPNs)	190
	9.2 Mermithidae	194
	9.3 Use of Nematodes in Biological Control	195
10	Bacterial Pathogens of Invertebrates	202
	10.1 What is a Pathogen?	202
	10.2 General Biology of Insect-Pathogenic Bacteria	203
	10.3 Use for Pest Control	204

11	Viral Pathogens of Invertebrates and Vertebrates	215
	11.1 General Biology of Viruses	215
	11.2 Diversity of Viruses Infecting Invertebrates	215
	11.3 Use for Pest Control	219
	11.4 Vertebrate Viral Pathogens	224
12	Fungal Pathogens of Invertebrates	229
	12.1 General Biology of Fungal Pathogens of Invertebrates	229
	12.2 Diversity of Fungi and Fungal-Like Protists Infecting Invertebrate Pests	231
	12.3 Use of Fungal Pathogens for Pest Control	233
	12.4 Microsporidia	239
Part IV Biological Control of Weeds		
13	Biology and Ecology of Herbivores Used for Biological Control of Weeds	245
	13.1 Types of Agents	245
	13.2 Weed Characteristics	246
	13.3 Types of Injury to Plants	247
	13.4 Regulation of Weed Density by Herbivores	255
	13.5 Measuring Impact of Weed Biological Control	261
14	Phytophagous Invertebrates and Vertebrates	263
	14.1 Invertebrates	263
	14.2 Successful Attributes of Invertebrate Herbivores	267
	14.3 Strategies for Use of Phytophagous Invertebrates	270
	14.4 Vertebrates	276
15	Plant Pathogens for Controlling Weeds	278
	15.1 Plant Pathogens and Target Weeds for Biological Control	278
	15.2 Augmentation Biological Control	279
	15.3 Classical Biological Control	283
Part V Biological Control of Plant Pathogens and Plant Parasitic Nematodes		
16	Biology and Ecology of Microorganisms for Control of Plant Diseases	291
	16.1 Types of Plant Pathogens and Their Antagonists	291
	16.2 Ecology of Macroorganisms versus Microorganisms	292
	16.3 Ecology of Plant Pathogens and Their Antagonists	293
	16.4 Studying Plant Pathogens and Biological Control Agents	296
	16.5 Modes of Antagonism among Microorganisms	297

viii	Contents	
17	Microbial Antagonists Combating Plant Pathogens and Plant Parasitic Nematodes	308
	17.1 Finding Antagonists	308
	17.2 Types of Antagonists	311
	17.3 Strategies for Using Antagonists to Control Plant Pathogens	313
	17.4 Conservation/Environmental Manipulation	320
	17.5 Biological Control of Plant Parasitic Nematodes	323
	Part VI Biological Control: Concerns, Changes, and Challenges	
18	Making Biological Control Safe	327
	18.1 What are Nontarget Impacts?	327
	18.2 Reasons Nontarget Effects Have Occurred	337
	18.3 Direct versus Indirect Effects	343
	18.4 Predicting Nontarget Effects	344
	18.5 Preventing Nontarget Effects	351
19	Biological Control as Part of Integrated Pest Management	359
	19.1 Using Natural Enemies as “Stand Alone” Strategies	359
	19.2 Integrated Pest Management	359
	19.3 Adding an Ecological Understanding to IPM	368
	19.4 Use of Natural Enemies within IPM Systems	370
20	Our Changing World: Moving Forward	376
	20.1 Major Challenges	377
	20.2 Acceptance by the Public, Scientists, and Governments	385
	20.3 International Cooperation Is Necessary	386
	<i>Glossary</i>	389
	<i>Bibliography</i>	402
	<i>Index</i>	426

Preface

This book provides a new and updated view on what was presented in the 2004 edition by the same name. The first edition was single-authored by Ann Hajek while in this version Jørgen Eilenberg has joined Ann as a coauthor. As in 2004, our goal has been to write an introductory book with broad coverage of the diverse uses of natural enemies for control of invertebrate and vertebrate pests, weeds, and plant pathogens. There are numerous excellent books on biological control that provide more advanced coverage, but our book is intended for people that do not already have extensive knowledge in these subject areas.

The field of biological control has grown and changed in many ways since 2004 and an updated and revised version is needed. Natural enemies are important for pest control in agriculture, in both greenhouses and fields, in forestry, and in managing and protecting natural areas as well as in controlling medical and veterinary pests. One reason for the growth in biological control, especially in agriculture and forestry, is that not as many new chemical pesticides are coming on the market and many older ones can no longer be used. In addition, the public is often more knowledgeable and less tolerant of the uses of pest controls that are potentially harmful to people and the environment. What has changed since 2004 that requires a new book? In particular, in 2004 classical (importation) biological control was considered by many people concerned about the environment and especially biodiversity as being a practice that had great potential for being dangerous to our environment. Since then, the amount that this strategy has been used has decreased significantly, but, with the need to control ever-increasing introductions of invasive species and the development of safer methods for classical biological control, use of this strategy with environmentally safe measures is now beginning to rebound. Another big change is the growth in the diversity and use of natural enemies not released for permanent establishment, a strategy that is generally called augmentation; in addition to arthropod predators and parasitoids applied augmentatively, products based on invertebrate pathogens, insect-pathogenic nematodes, antagonists of plant pathogens, and plant pathogens killing weeds are produced by commercial companies. A prime example of augmentative use of biological control agents today is the greenhouse industry, where natural enemies are often used extensively and very successfully for a variety of reasons including enhanced worker safety. Conservation biological control has also been growing, with practical and theoretical emphases on understanding how we can change environments in order to manipulate the preexisting biodiversity toward controlling pests.

Our book is arranged in the same way as in 2004, beginning with two introductory chapters about why to use biological control and defining biological control. Then we present sections describing the major strategies (classical biological control, augmentation, and conservation), followed by sections on biological control of invertebrates and vertebrates, biological control of weeds, and biological control of plant pathogens, and plant parasitic nematodes. We next discuss safe use of biological control and its integration with other control methods. Finally, we examine the future for this growing and changing field, including discussions on biological control in the context of invasive species, climate change, and the potential for increased use against medically important arthropods, and we discuss how biological control fits into the context of sustainability.

Throughout the book, we have included stories from around the world about how diverse natural enemies have been used successfully in the context of different strategies. As in the 2004 book, we do not provide references throughout the text, with the goal of making this introductory book more easily readable. However, the references that have been used in writing the book are listed at the end of the book in the general references section. We have emphasized examples of biological control that are in practical use, while describing some pest/natural enemy systems that are close to utilization, and only occasionally discussing systems that are simply tantalizing. Those readers interested in biological control agents that hold promise but are not yet being used or who want more in-depth information are referred to the further readings suggested at the end of each chapter, as well as to the large number of reviews and enormous number of primary papers in the scientific literature.

This book is intended as a basic presentation and readers should not need an extensive background in entomology, weed science, or plant pathology. We have attempted to use scientific jargon as little as possible and have provided a glossary at the end to help with specific terms used in the text. We have used English common names for pests and natural enemies when possible, but not all of these organisms have common names (e.g., among insects, actually relatively few have common names). Therefore, we have always provided Latin genus and species names regardless of whether the English common name is given. We assume this will also be helpful for readers who are not familiar with English common names.

Both authors of this book have taught biological control over decades to undergraduate and graduate students at their respective universities and this book grew from their interests in providing more accessible background readings for students taking their classes. The 2004 book has been used for classes around the world and we hope that this version, with many examples from different continents of use of natural enemies in a variety of contexts, finds similar use. In particular, we hope that in reading this book, you will find the interactions between natural enemies and their hosts as fascinating and interesting as we do and will feel that it makes sense to use these relationships to control pests toward increased safety for humans and the environment whenever possible.

Generalization pertaining to biology must always be followed by exceptions. In fact, making generalizations virtually means leaving out at least some of the fascinating variability found in biological systems. There are many tales of amazing interactions and relationships among natural enemies and their hosts or prey and only a small fraction

of these could be included in this book. The diversity of manipulations of biological systems for pest control also made it difficult to decide which examples to include in a book such as this. There are really many good stories to be told. Our emphasis has been on providing a glimpse of the diversity of natural enemies used and the diversity of biological control approaches that have been applied. In summary, with this book we hope that we have shared our personal excitement about the field of biological control and that you will become as fascinated as we are with the practice and potential of using natural enemies to control pests.

Acknowledgments

This book would not have been possible without the help of many knowledgeable, kind, and helpful colleagues. First, special thanks go to Sana Gardescu for her amazing assistance with organizing figures and tables and copyright permissions as well as proofreading. David C. Harris provided help with editing early drafts and Scott Salom helped with proofreading the final version. Edwin Lewis wrote the boxed story about the use of entomopathogenic nematodes in pistachios. All chapters were sent out for external review and we thank external reviewers Raghavan Charudattan, Matthew Cock, Julia Crane, Jodi Gangloff-Kaufmann, Jeff Garnas, Jennifer Grant, Roma Gwynn, Kevin Heinz, Martin Hill, Mark Hoddle, Kim Hoelmer, Judith Hough-Goldstein, Trevor Jackson, Marc Kenis, Douglas Landis, Madoka Nakai, David Shapiro-Ilan, Anthony Shelton, Jennifer Thaler, and Saskya van Nouhuys. We also thank many scientists from different continents for information and opinions, including Arthur Agnello, Renato Bautista, Norbert Becker, Gary Bergstrom, David Biddinger, Eric Brennan, Stephen Danielson, Italo Delalibera Junior, Antonio DiTommaso, Sanford Eigenbrode, Mary Louise Flint, Jeffrey Garnas, Martin Hill, Harriet Hinz, Judith Hough-Goldstein, Tero Klemola, Thomas Kuhar, Lawrence Lacey, Ellen Lake, Edwin Lewis, Pamela Marrone, Russell Messing, Lindsey Milbrath, Michael Milgroom, Madoka Nakai, Steven Naranjo, Louis Nottingham, Katja Poveda, Paul Pratt, Mohsen Ramadan, Neil Reimer, George Roderick, John Sanderson, Mark Schwarzländer, David Shapiro-Ilan, Deborah Sharp, Lene Sigsgaard, Donald Steinkraus, Philip Tipping, Joop van Lenteren, Mark Whalon, Rachel Winston, and Mark Wright.

We thank Michael Raupp for allowing use of his lovely photo of a lacewing for our cover and Catherine Tauber and Oliver Flint for identifying the lacewing. We also thank others who helped with figures including Yuri Baranchikov, Roy Bateman, Charlotte Bering (the drawing of the virus-killed nun moth caterpillars by her late father, Claus Bering), Raghavan Charudattan, Marina Cheyushova, Matthew Cock, Regina Kleespies, Tero Klemola, David Mota-Sanchez, Olga Paschenko, Anthony Shelton, and Tomi Vanek (the painting of the predatory mite by his late father, Gašpar Vanek).

This book has not changed entirely from the 2004 version, although the text has definitely changed quite a lot, and more than we had expected. We are not going to list again the many people who helped in many ways and were acknowledged in the 2004 version, but we thank them again as parts of the 2004 book remain. In particular, many of the figures used in the 2004 book have been used again. We especially want to

acknowledge again Alison Burke, who helped extensively with organizing the excellent figures for the 2004 version and even drew some of the illustrations herself.

We also want to thank our editors, Dominic Lewis and Lindsey Tate, for their steadfast faith and patience that this revised edition could and would be completed. Finally, we thank our spouses, James Liebherr and Betty Østergaard Jacobsen, for their encouragement, patience, and assistance throughout the long process of revising, writing, and putting this book together.