Ecology of Invertebrate Diseases

Edited by Ann E. Hajek and David I. Shapiro-Ilan

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This edition first published 2018

Registered Office(s)
John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA
John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Office
9600 Garsington Road, Oxford, OX4 2DQ, UK

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Library of Congress Cataloging-in-Publication Data
Names: Hajek, Ann E., editor. | Shapiro-Ilan, David I., editor.
Title: Ecology of invertebrate diseases / Edited by Ann E. Hajek, David I. Shapiro-Ilan.
Description: Hoboken, NJ : John Wiley & Sons, 2017. | Includes bibliographical references and index. |
Identifiers: LCCN 2017023661 (print) | LCCN 2017035570 (ebook) | ISBN 9781119256014 (pdf) | ISBN 9781119256069 (epub) | ISBN 9781119256076 (cloth)
Subjects: LCSH: Invertebrates--Ecology. | Invertebrates--Diseases.
Classification: LCC QL364.4 (ebook) | LCC QL364.4 .E26 2017 (print) | DDC 592.17/82--dc23
LC record available at https://lccn.loc.gov/2017023661

Cover Design: Wiley
Cover Image: Top photo by Ann E. Hajek; bottom photo by Ivan Hiltpold

Set in 10/12pt WarnockPro by SPi Global, Chennai, India

10 9 8 7 6 5 4 3 2 1

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Preface

All have their worth and each contributes to the worth of the others.
J.R.R. Tolkien, *The Silmarillion*

When you try to study something in isolation, you find it hooked to everything else.
John Muir

It becomes necessary in any active scientific discipline to sit back every few years and take stock of the "state of the art." The time arrives to review recent progress, inspire new ideas, and propose critical and novel lines of research.

In 1963, Yoshinori ("Joe") Tanada laid the foundation for the current book with his chapter "Epizootiology of Infectious Diseases" in E.A. Steinhaus' *Insect Pathology: An Advanced Treatise*, a two-volume reference that defined the scope of invertebrate pathology. By 1987, after almost a quarter-century, the time had come for more than just a review of the "state of the art." Fuxa and Tanada formalized the new scientific discipline in their edited monograph, *Epizootiology of Insect Diseases*, organizing an emerging field of study by establishing its components, definitions, types of studies, and research methods.

Another 30 years have passed, and that time has come again. Much has happened since 1987 – science never stands still. New methods have opened doors unheard of in the 1980s, most notably in molecular biology. Detection and characterization of strands of DNA, RNA, and transposable genetic elements create almost unlimited research opportunities in ecology. New diseases have emerged, such as the mysterious colony collapse disorder of the honeybee, which has raised concern throughout much of the world. Previously characterized diseases have erupted again in devastating epizootics, notably MSX disease (*Haplosporidium nelsoni*) and dermo disease (*Perkinsus marinus*) in populations of oysters. New relationships have opened eyes – who would have thought that microsporidia are highly evolved fungi, not primitive protozoans that evolved before the advent of mitochondria? New concepts have arisen for invertebrate pathogens, contributing to theory in general ecology and host–pathogen coevolution.

Thus, we arrive at this new book. The reader, however, might ask, why *Ecology of Invertebrate Diseases* rather than *Epizootiology of Insect Diseases*? A definition of epizootiology borrowed from the 1987 volume, "the science of causes and forms of the mass phenomena of disease at all levels of intensity in a host population," allows for study of the total environment, including the host and pathogen populations, even a pathogen's environment inside its host. Epizootiology in turn is a subset of ecology, which was defined by H.G. Andrewartha as "the scientific study of the distribution and abundance of organisms," a definition that has evolved to embrace concepts of "population" and "ecosystem."

Simpler may be better. Epizootiology is the study of animal disease at the population level. It fits well into a broader mold of ecology, as outlined by Tolkien and Muir, if they may be paraphrased, that everything is "connected to everything else" and "contributes to the worth of the others." Perhaps these two authors were not trying to define ecology, but they might just as well have been.

The editors of this book realized that the "state of the science" has exceeded the scope of the 1987 monograph, thereby creating a multitude of opportunities to discuss new concepts and types of studies, not to mention the myriad of non-insect hosts of infectious disease. Even in a new volume, however, old questions arise, especially, why study ecology of pathogens and their hosts?

First and foremost, parasites are not just dirty little things living a disgusting lifestyle. They are highly evolved organisms – or near-organisms – as intricate and unique as any creature on the planet. They contribute to all, whether by culling the weak or by transporting bits of DNA, in relationships with their hosts ranging from near-benign to something out of a horror film. The reader who delves into this book will see the "worth" in these fascinating little creatures, whether prokaryotic, eukaryotic, or viral.

And, of course, invertebrate pathogens certainly are "hooked to everything" abiotic and biotic, even to humans, a web of life and environment and planet earth. Many such interactions almost defy belief, for that is life.

Science also is called upon to provide tangible benefit. The historical advantages of studying invertebrate diseases remain as important as ever – enhancing disease in pestiferous organisms and preventing disease in invertebrates useful to humans. Pathogens, even viruses, function as parasites with population-level and ecological characteristics, parasites that must be suppressed in populations of beneficial organisms or conserved or enhanced if they are to succeed in pest management. Critics, however, might say that such "germ warfare" against pests is passé, that we now have genetically modified crops, recombinant mosquitoes, and on and on. Perhaps. However, the biopesticide market, which is based on mass production of invertebrate pathogens, continues to grow. Moreover, nothing works in isolation. For example, understanding the dynamics of insect population resistance to disease facilitated management of resistance in widespread use of crops incorporating toxin genes and environmental risk assessment contributed to a safe, first release of a recombinant baculovirus.

Diseases of invertebrate hosts, many of them easy to culture, with their tiny sizes and short generation times, also serve as model systems giving insight into disease ecology in higher organisms – for example, contributions of pathogen reproductive rate, transmission, and virulence to epizootics.

So much for the "What?" and the "Why?" of this book – how about the "Who?" Many decisions were made in compiling this monograph, not the least of which is, where does one stop if everything is "hooked to everything else"? Researchers will find themselves fortunate in this volume's scientific writers, fortunate because they will recognize the names of the editors and authors, all outstanding pathologists, ecologists, or epizootiologists. Readers will appreciate as they peruse this book that, much like Tolkien's world, every author has indeed "contributed to the worth of the others."

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Section I

Introduction

1

General Concepts in the Ecology of Invertebrate Diseases

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1.1 Introduction

With the advent of molecular methods, new species of pathogens and parasites are constantly being described, and as these new species are found, we are learning more about the ecology of new invertebrate diseases, as well as diseases known for many years. Parasitism is a specific and common life-history strategy, and understanding the activity of parasites is central to community and population ecology (Bonsall, 2004). Parasitism of invertebrate hosts also has practical sides, because diseases can help to control insects in an environmentally friendly manner, but we also need to understand the ecology of diseases killing beneficial invertebrates, ranging from pollinators to clams and shrimp, in order to protect managed populations.

The ecology of invertebrate diseases is often referred to as the epizootiology of invertebrate diseases; the word **epizootiology** is similar to the term epidemiology but refers specifically to "the science of causes and forms of the mass phenomenon of disease at all levels of intensity in an animal population" (Fuxa and Tanada, 1987). The ecology of animal diseases, with emphasis on vertebrates, has been treated in an edited book on disease ecology (Hudson et al., 2002), followed by books emphasizing community and ecosystem ecology (Collinge and Ray, 2006; Hatcher and Dunn, 2011; Ostfeld et al., 2014).

Disease ecology with an emphasis on invertebrates was first addressed by Steinhaus (1949), specifically in relation to insects, and the treatment of this subject developed depth and breadth with the publication of an edited volume by Fuxa and Tanada (1987). Around this time, Anderson and May (1981, 1982) created models to investigate factors driving the development of disease epizootics, with at least one system involving epizootics caused by a granulovirus in a forest-defoliating lepidopteran (Anderson and May, 1980). Today, studies of the ecology of invertebrate diseases are commonly conducted, often to understand the ecology underpinning control of invertebrate pests by pathogens, or to understand protection from pathogens for invertebrates valued by humans. In addition, ecological studies of invertebrate diseases are used to build theoretical insights into the causes and dynamics of all diseases. With the wealth of knowledge that

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has accumulated since the last synthesis on the ecology of invertebrate diseases in 1987, it is high time to pull together information on this subject. We are also broadening the focus of this book to include the ecology of diseases of all invertebrates and not only insects. Therefore, the hosts included in this book range from pest insects like grasshoppers and caterpillars to valued insects like bees, along with marine and soil invertebrates that are important to humans or ecosystems.

In this chapter, we will present and define the basic concepts on which this field of study is built. Concepts that will be defined will be consistent with definitions in the online glossary published by the Society for Invertebrate Pathology (Onstad et al., 2006).

1.1.1 What Is Disease?

There are numerous definitions for disease, but we consider **disease** to be a departure from the state of health or normality. Of course, this creates a very broad characterization, including multitudes of causes. However, this book will focus on **infectious** diseases, which are those diseases caused by living organisms. Invertebrates are also hosts to many **noninfectious diseases**, of which physical and chemical injuries, genetic diseases, and cancers are a few examples. An example of noninfectious disease impacting insects can occur due to exposure to pesticides. Noninfectious diseases are, however, outside of the material being covered in this book. Descriptive treatments of noninfectious diseases of a diversity of invertebrates can be found in Lewbart (2012) and Sparks (1972).

Returning to disease being a departure from health, this can be much more difficult to determine for invertebrates than for higher vertebrates. Diseases of invertebrates that cause subacute effects and which do not kill hosts could very well be regularly occurring at low prevalence but going undetected. Perhaps recent studies demonstrating the diversity of previously undetected and unrecognized pathogens occurring in honey bee (*Apis mellifera*) colonies that do not die (see Chapter 14) indicate that departures from health being caused by a diversity of parasites acting together can be quite common. The most frequent way that invertebrate diseases are recognized is due to the death of hosts, so emphasis in this field has been on acute diseases. However, in recent years, investigations have included the impact of disease on host fitness, both for pathogens causing chronic diseases and for acute pathogens, after infection and before host death.

The living organisms causing infectious diseases are **parasites**, which are organisms that live at a host's expense. This is a very successful life-history strategy as it has been estimated that the majority of species on earth have parasitic lifestyles (Price, 1980; Zimmer, 2000). **Pathogens** are defined as microorganisms capable of producing disease under normal conditions of host resistance and rarely living in close association with a host without producing some level of disease. Simply put, pathogens can be thought of as microscopic parasites. In this book, the main groups of pathogens that will be covered are viruses, bacteria, fungi, nematodes, and protists. Although many nematodes are not microscopic, the genera that constitute a special group – entomopathogenic nematodes – kill their hosts with the aid of symbiotic bacteria; these nematodes have traditionally been included and studied within the discipline of invertebrate pathology, and thus we include them as well. With the great diversity of pathogens and hosts being covered, of course examples will be missed. In addition, this is presently an expanding field of study, as new species of pathogens are constantly being found. One good example of this is the number of different pathogens that infect honey bees, with numerous examples discovered in recent years. We will focus on representatives from the diversity of pathogens and hosts for which we know the most about disease ecology.

Diseases may be **chronic** or **acute** (or somewhere in between). Chronic diseases are of a long duration, and thus the host is expected to survive a relatively long time before expiring, or to die of other causes before the disease can become fatal. Acute diseases of invertebrates are often of a short duration; host mortality or maximum severity is expected to occur within a relatively short time after infection. Certain pathogen groups, such as entomopathogenic nematodes (Heterorhabditidae and Steinernematidae) and their symbiotic bacteria tend to cause acute disease, whereas others, such as most Microsporidia, tend to cause chronic diseases. Within other pathogen groups, chronic versus acute diseases vary among combinations of pathogens and hosts.

1.1.2 Terminology and Measurements

Accurate use of terminology is critical to effective communication in science. In pathology, a number of terms have been used with variable meanings in the literature (Shapiro-Ilan et al., 2005). The terminology used in this book is supported by a widely accepted glossary by Onstad et al. (2006), which is based on an earlier glossary by Steinhaus and Martignoni (1970). Thus, we refer the reader to Onstad et al. (2006) as a reference for definitions that may not be spelled out in this chapter or other chapters within this book. Nonetheless, some of the more common terms in invertebrate pathology are defined and discussed in this section.

1.1.2.1 Prevalence/Incidence

Prevalence and incidence are examples of terms that have been variably defined in the literature. **Prevalence** refers to the total number or proportion of disease cases in a population at a given time. For example, if a survey of 10 000 pecan weevil (*Curculio caryae*) larvae in a population indicates that 4000 of the individuals are infected with the fungus *Beauveria bassiana*, then the prevalence rate is 40%. In contrast, **incidence** is the number or proportion of new cases of a disease within a population during a specific period of time. For example, in a given week, if 200 *C. caryae* larvae were found to be infected with *B. bassiana* within a population of 10 000 larvae, then the incidence rate would 2% for that week. Both terms are important for quantifying infection and disease levels over space and time. The difference lies in incidence emphasizing only new cases versus prevalence including both new and old cases. Therefore, incidence may be more useful in predicting risk or spread of disease within a certain timeframe, while prevalence provides an assessment of the full impact of a disease on a population at a given time.

1.1.2.2 Pathogenicity/Virulence

The terminology of pathogenicity and virulence has also been variably defined in the literature. However, definitions of pathogenicity and virulence in the field of invertebrate pathology have been largely consistent over time, and are in agreement with definitions found in the fields of human pathology and microbiology (Shapiro-Ilan et al., 2005). **Pathogenicity** is the quality or state of being pathogenic: the potential ability to produce disease. **Virulence** is the disease-producing power of an organism: the degree of pathogenicity within a population or species. Generally, the term pathogenicity is applied to entire populations or species, whereas virulence is usually intended for within-group or within-species comparisons. Yet, both terms can conceivably be applied across any taxonomic level (strain, species, genus, family, etc.), provided that pathogenicity is a qualitative and virulence a comparative measure.

Indeed, for a given pathogen and host, pathogenicity is absolute whereas virulence is variable (e.g., due to strain or environmental effects). Pathogenicity is an all-or-none phenomenon. An organism is either pathogenic to a host or it is not. Pathogenicity can be established based on Koch's postulates (Shapiro-Ilan et al., 2005; Lacey and Solter, 2012). Virulence can be measured using various approaches, such as LD_{50} or LC_{50} (dosage or concentration required to cause 50% mortality in the test organisms), LT_{50} (time required to cause 50% mortality in the test organisms), or comparative mortality or infection rates at a given dosage or concentration (Shapiro-Ilan et al., 2005).

1.1.2.3 Infection/Infectivity

An **infection** is the entry of a microorganism into a susceptible host. The presence of the organism may or may not cause overt disease (obvious pathological effects) in the host. If the infection is not immediately followed by overt disease then it is termed an attenuated infection. There are three types of attenuated infections: latent, carrier state, and microbial persistence. A latent infection is an asymptomatic infection that is in a dormant or stationary phase and is capable of being activated at a later time. In the case of viruses, a latent phase is also called an occult phase (and the virus is an occult virus at that stage). In a carrier state, the infection remains as an inapparent infection (no overt sign of its presence) in the current host but is capable of being transferred to other hosts. Microbial persistence is characterized by the continued presence of a pathogenic microorganism within the host in the absence of overt disease but following a period of overt disease.

Infectivity is the ability to produce infection. Thus, infectivity is a measurable characteristic. Infectivity can be measured by assessing the number of pathogenic units (e.g., spores, virus particles, infective juvenile nematodes, or other propagules) that have entered a host following exposure to a known quantity. Infectivity can be positively affected by the number of infection routes; infection routes include per os (through the mouth), through the cuticle or natural openings in the host, and vertical transmission (see later).

1.1.2.4 Immunity

Immunity is innate or induced resistance to a disease agent. It tends to be species-specific but can also vary within species. Invertebrates have immune systems, although predominantly without memories; they are not known to recover from infections and become resistant to further infections of the same pathogens, as vertebrates often can. Immune responses can be cellular (via hemocytes) or humoral (e.g., via antimicrobial peptides), or they may involve both humoral and cellular reactions (e.g., melanization) (Chapter 4). The effectiveness of immune responses may depend on strain or population variation, age and fitness, and stress factors such as environmental conditions or diet. For example, feeding an improper diet resulted in higher percentages of *Drosophila* being killed by a bacterium in their hemolymph (Galac and Lazzaro, 2011; Howick and Lazzaro, 2014). See Chapter 4 for a more in-depth discussion of immunity.