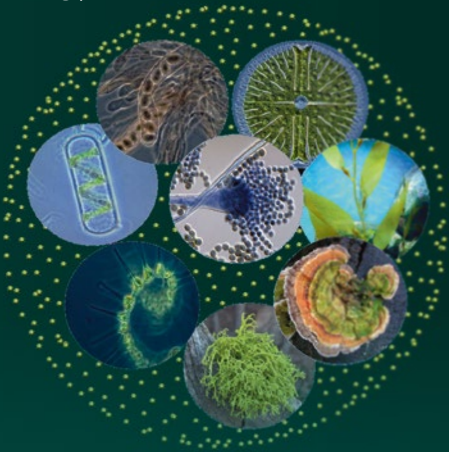
Advances in Environmental Microbiology 5



Christon J. Hurst *Editor*

The Connections Between Ecology and Infectious Disease

Springer

Advances in Environmental Microbiology

Volume 5

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The Connections Between Ecology and Infectious Disease

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I am very fortunate by having been allowed two set of parents in this lifetime. My parents by birth were Hubert and Joy Hurst. They met when my father, Hubert, was a college student and would eat his noontime meal at the luncheon counter of a pharmacy in Cincinnati, Ohio near where he was studying. My mother, Joy, worked there at the pharmacy and perhaps the best part of my father's day was a smile that she served to him along with that daily lunch as the two of them fell into romance. He graduated, they married, and then they had three children which were in order of birth my brother Preston, myself, and our sister Embeth. Hubert and Joy loved their children and they generally tolerated our childhood misdeeds. That tolerance required patience because some of my misdeeds must have seemed nearly intolerable! But, most importantly for me, my parents encouraged my efforts to understand science and lovingly they showed pride of my achievements.

Joy and Hubert Hurst on vacation in 1975

When I still was a young child, my family moved into a large housing complex in Cincinnati, Ohio where I soon met Rebecca Wadlin and also met Becky's older sister Caroline, plus their parents Herbert and Renko. It often must have seemed as though Renko and Herbert had five children instead of just their two, Carrie and Becky, because my brother, sister, and I spent a great many hours in their apartment and Herb invited us along on numerous local adventures. Herb was from New York state and fortunately met Renko in Tokyo, Japan while he was on assignment there with the United States Air Force after the Second World War had ended. When they met, Renko was studying English *and her instructor had invited Herb to speak with their class. Herb and Renko corresponded when he was assigned to Okinawa. Eventually, they reunited in Tokyo, where they married and had two children. Herbert then brought their family to Cincinnati so that he could study here for a Master's Degree which he succcessfully earned. It was a sad day for me when their family moved onward to California. Decades later, Herb and Renko's family informally adopted me and that has brought me great pleasure. I happily have considered their family as also being my mother, father, and sisters.*

Renko and Herbert Wadlin with Christon Hurst in 2003

My personal beliefs being what they are, I also wish to thank Johann Meyer and

Eleonora Diebold Meyer who were the parents of Guilelmina Eleonora "Mina" Meyer. John and Ellen, as they came to be known, were immigrants to the United States from the Kingdom of Württemberg. Mina was born in Sedamsville, which was then just slightly west of Cincinnati's city boundary in Hamilton County, Ohio. She was baptized on November 7th, 1868 in Saint Michael the Archangel church, located in the neighboring Lower Price Hill section of Cincinnati. Unfortunately, Mina passed away in Lower Price Hill on May 28th, 1882 and she was laid to rest at a pretty location on top of the hill, at Saint Joseph Cemetery in the Price Hill neighborhood of Cincinnati. I do as well thank Dr. Max Cohn and Anna Weiland Cohn who were the parents of Herbert Max Cohn. Herbert Cohn was born in Berlin, Germany on August 23rd, 1900. Eventually Herbert lived as a family with his parents, along with his wife Ursula Sara Gerling Cohn and their own son Charlie Max Cohn, in Bad Harzburg, Germany where his family operated their home as a pension called Haus Frohsinn and Villa Frohsinn.

Postcard image of Haus Frohsinn in Bad Harzburg

Sadly, Herbert Cohn was arrested from their Bad Harzburg home in November, 1938 as part of the Reichspogromnacht raids and taken to Buchenwald Concentration Camp, Germany where he became ill. Herbert Cohn died in Buchenwald Camp on November 30th, 1938 and the historical records suggest that he was shot, listing even the minute of his death. Herbert's father Max was attacked by a mob in Bad Harzburg and he thus died on December 26th, 1938. Despite the tragedy of those two months, things ended better for the rest of Herbert's family. Herbert's wife Ursula and their son Charles fortunately were sponsored into England as refugees during April, 1939 where they survived the Second World War and remained living near London. Ursula eventually had a second chance at romance and in September, 1945 remarried *which gave Herbert’s son a new father. Herbert’s son remains alive and in good health. Anna eventually returned to living in the familys Bad Harzburg home in 1940 and there she survived the war. Their home in Bad Harzburg still stands and has been well kept. Bad Harzburg thoughtfully memorialized both Herbert and his father with their names on a plaque in the local cemetery. I can attest that Bad Harzburg again is a cheerful place and that the people now residing there are very kind.*

Christon Hurst at memorial in Bad Harzburg Cemetary July 25th 2013

Series Preface

The light of natural philosophy illuminates many subject areas including an understanding that microorganisms represent the foundation stone of our biosphere by having been the origin of life on Earth. Microbes therefore comprise the basis of our biological legacy. Comprehending the role of microbes in this world which together all species must share, studying not only the survival of microorganisms but as well their involvement in environmental processes, and defining their role in the ecology of other species, does represent for many of us the Mount Everest of science. Research in this area of biology dates to the original discovery of microorganisms by Antonie van Leeuwenhoek, when in 1675 and 1676 he used a microscope of his own creation to view what he termed "animalcula," or the "little animals" which lived and replicated in environmental samples of rainwater, well water, seawater, and water from snow melt. Van Leeuwenhoek maintained those environmental samples in his house and observed that the types and relative concentrations of organisms present in his samples changed and fluctuated with respect to time. During the intervening centuries we have expanded our collective knowledge of these subjects which we now term to be environmental microbiology, but easily still recognize that many of the individual topics we have come to better understand and characterize initially were described by van Leeuwenhoek. van Leeuwenhoek was a draper by profession and fortunately for us his academic interests as a hobbyist went far beyond his professional challenges.

It is the goal of this series to present a broadly encompassing perspective regarding the principles of environmental microbiology and general microbial ecology. I am not sure whether Antonie van Leeuwenhoek could have foreseen where his discoveries have led, to the diversity of environmental microbiology subjects that we now study and the wealth of knowledge that we have accumulated. However, just as I always have enjoyed reading his account of environmental microorganisms, I feel that he would enjoy our efforts through this series to summarize what we have learned. I wonder, too, what the microbiologists of still future centuries would think of our efforts in comparison with those now unimaginable discoveries which they will have achieved. While we study the many wonders of microbiology, we also further our recognition that the microbes are our biological critics, and in the end they undoubtedly will have the final word regarding life on this planet.

Christon J. Hurst in Heidelberg

Indebted with gratitude, I wish to thank the numerous scientists whose collaborative efforts will be creating this series and those giants in microbiology upon whose shoulders we have stood, for we could not accomplish this goal without the advantage that those giants have afforded us. The confidence and very positive encouragement of the editorial staff at Springer DE has been appreciated tremendously and it is through their help that my colleagues and I are able to present this book series to you, our audience.

Cincinnati, OH Christon J. Hurst

Volume Preface

Infectious disease is part of an interconnected ecology that involves a pathogenic microorganism and the host species in which that microbe causes illness. The ecology of that microorganism may include a more extended set of connections which could involve a natural environmental presence, its possible carriage by vehicles such as air, water, and food, and interactions with other host species including vectors for which the microbe either may or may not be pathogenic. This book explains these connections. The contents of this volume are divided into three sections, the first of which presents an introduction to the field of science currently titled disease ecology and explains both the role of biological community interactions plus the impact of biodiversity. The second section considers diseases directly affecting humans with a focus on waterborne and foodborne illnesses and importantly examines the critical aspect of microbial biofilms. The third section presents ecology of infectious diseases from the perspective of their impact upon mammalian livestock and wildlife plus includes understanding of the fact that those same diseases often affect humans.

Decades ago I presented two specialty courses on disease ecology at Universidad del Valle in Cali, Colombia for their graduate students in the School of Public Health and professional members of the community. The first of those courses was titled "La Ecología de la Transmisión de Infecciones y la Aplicación de Modelos en Salud Pública" [The Ecology of Infection Transmission and the Application of Models in Public Health] during August and September of 1998, which was sponsored by the Fulbright program. The second course was titled "La Ecología de Enfermedades Infecciosas Transmitidas por el Agua" [The Ecology of Infectious Diseases Transmitted by Water] during March of 2000, for which I served as an International Professor for Latin America and was sponsored by the American Society for Microbiology. Including those courses among my previous experience, I presumed that I would be qualified to write the introductory chapter for this book. However, while reading the chapters written by this books other contributing authors, the realization came to me that those others have a level of expertise which now outweighs mine and so the banner representing his subject area clearly has been passed onward. Many of these authors and also our readers for this book represent the next generation of scientists to be exploring this field of endeavor and I feel reassurance from knowing how well they and you will proudly carry the banner forward.

I am tremendously grateful to Hanna Hensler-Fritton, Andrea Schlitzberger, and Isabel Ullmann at Springer DE, for their help and constant encouragement which has enabled myself and the other authors to achieve publication of this collaborative project.

Cincinnati, OH Christon J. Hurst

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Part I
Introduction to Disease Ecology

Chapter 1
Interkingdom Community Interactions in Disease Ecology

M. Eric Benbow, Jennifer L. Pechal, Jeffery K. Tomberlin, and Heather R. Jordan

Abstract A key tenet of community ecology is the interactions of individual organisms contribute to the ecological structure and function of ecosystems. Within these networks of interacting organisms are those taxa important for human and animal health: disease systems defined by combinations of host, pathogen, reservoir, and vector or a subset of these components. While the simplest disease system is that of the host and pathogen, more complex systems include the direct interactions of a pathogen with other hosts and the microbial communities of those hosts, reservoirs, and sometimes vectors. Each of these disease system components is made up of species that directly and indirectly interact with other species in ways that affect their individual fitness, population biology, and role in communities of the ecosystem. This chapter recognizes the direct interactions of those species that make up the primary components of disease systems; however, the focus and examples provided relate to the more indirect interkingdom (or domain) interactions that impact disease system components. The examples provided include how microbial communities mediate invertebrate and vertebrate fitness and behavior, often in systems where the

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hosts play important roles in pathogen transmission and disease emergence. The potential mechanisms of these interkingdom interactions are also developed in detail, as the mechanisms of such interactions are likely the target of future studies that could directly inform disease management strategies. Based on these examples and mechanisms, the existing literature suggests there are likely undiscovered and complex interactions of species within communities that affect disease systems.

1.1 Introduction

A key tenet of community ecology is the interactions of individual organisms contribute to the biological structure and function of ecosystems. Within ecosystems, infectious disease systems (i.e., the network of species involved in the existence and emergence of disease caused by pathogenic microorganisms) are defined by at least two species interacting in a way that leads to a pathogenic outcome affecting at least one of those species. This minimum system is composed of the pathogenic microorganism species (e.g., bacteria, virus, fungi, or eukaryotic parasite; hereafter referred to as pathogen) and a host species, and inherently implies a minimal interaction between the two with the host negatively affected by the pathogen (Fig. 1.1). This minimum infectious disease system is the simplest scenario in disease ecology defined as an interkingdom interaction or, as we define here, the ecological relationship where two or more species from different domains or kingdoms of life interact in a way that has a demonstrated or hypothesized biological, ecological, or evolutionary importance to one or all of the species in the disease system.

Disease ecology involves at least two different species that define a disease system within a larger community of organisms in nature. However, many disease systems of humans, other animals, and plants involve multiple intermediate species with the pathogen transmitted to one or more host or reservoir species (Fig. 1.1). These multi-species pathogen transmission pathways are also interkingdom interactions that lead to the movement of the pathogen in the environment, and ultimately to the host, resulting in pathogenesis and disease symptoms. Therefore, in its simplest form, understanding the ecology of a disease rests on defining the components, constraints, and dynamics of interacting organisms from different domains and kingdoms. The discipline of disease ecology also includes asking questions about coevolutionary relationships and the broader impact of species interactions on the community that are not a direct component of the disease system but might indeed be influential (Burdon and Thrall 2008; Ricklefs 2010). The more traditional interkingdom interactions defining many infectious disease systems will be covered in this chapter; however, this will be done with a focus on how the interactions mediate transmission and pathogenesis. This chapter will also cover how interkingdom interactions may influence infectious disease systems without the interacting organisms being any of the disease system component species (i.e., pathogen, host, reservoir, vector; Fig. 1.1). Further, because an entire book could

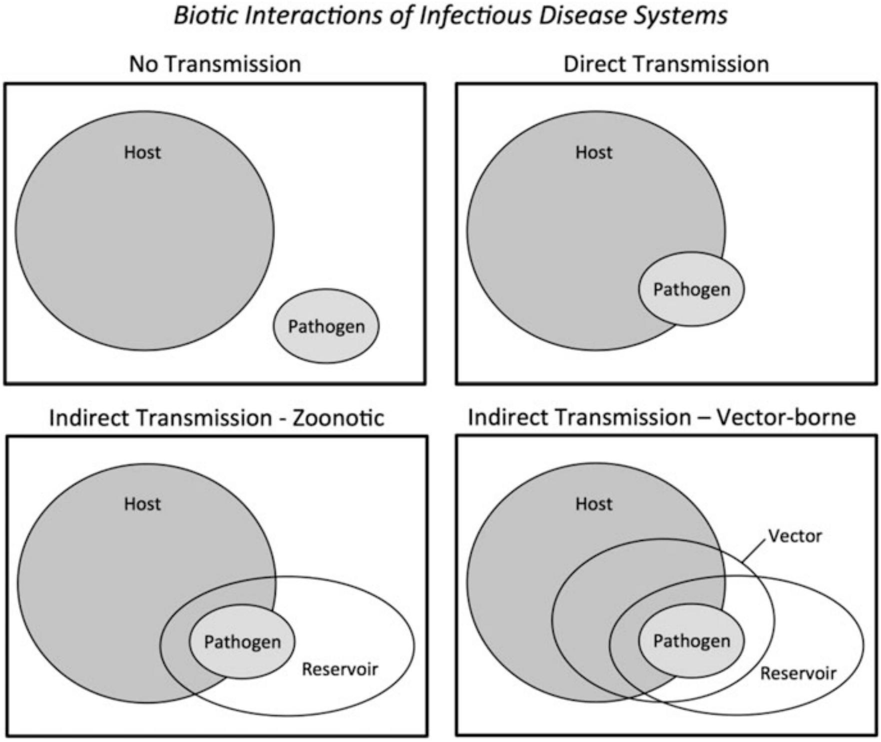

Fig. 1.1 Conceptual depiction of the interkingdom interactions involved in an infectious disease system. When there is no transmission (top left), there are no interactions among organisms involved in the disease system. When there is direct transmission (top right), the only interaction is with the host and pathogen—the minimal disease system. Indirect zoonotic transmission involves the interaction of the host, a reservoir (often animal), and pathogen (bottom left), whereas indirect, vector-borne transmission includes these interactions but also a fourth, vector species (bottom right)

be written on all interkingdom interactions important to disease ecology, this chapter will highlight recent advancements in understanding how microbial taxa influence species of other domains and kingdoms. By introducing aspects and examples of interkingdom interactions that have been investigated in the primary ecological literature, the chapter will synthesize how this understanding can influence the scientific approach to studying disease ecology.

Lastly, disease ecology is a discipline involving the study of how hosts, reservoirs, vectors, and pathogens interact within and among populations and communities in a way that ultimately defines ecosystem structure. Since populations are inherent components of communities, we focus here on the interactions among different species within larger communities of organisms where disease systems are nested. While it is acknowledged that specific examples of interkingdom interactions occur within a broader and more complex ecological network, we focus on examples and provide discussion of interactions that often involve two or three species with biological or ecological function, which may have relevance to the broader understanding of infectious disease ecology and evolution.

1.2 Background of Microbial Interkingdom Interactions

Microbes, particularly bacteria, historically were viewed as recyclers of nutrients; however, as pointed out by Janzen (1977), this role is truly limiting as they actually fill many niches in an ecosystem ranging from competitor to predator. For decades microbes have been explored for their interactions with higher life specifically from an interkingdom perspective. The idiom, "Beauty is in the eye of the beholder," rings true in the interkingdom interactions' world but with a slight twist. The idiom would be more applicable with "Relationship is in the eye of the beholder." Point being, defining the role of bacteria in a given environment truly depends on the scale one is using as well as the players identified in the process. This nuance can be a tedious road to explore and requires strict guidelines and definitions for the system being explored. One misstep and the message could be lost or confused by the researcher.

Janzen (1977) masterfully articulated in his view a world where microbes are more than simple by-standards in a realm of multicellular "giants" serving as the cogs responsible for ecosystem operations. As a great example demonstrating how bacteria are in fact competitors with animals for similar resources, consider the case of spoiling milk. Milk that spoils smells "bad" to us and thus we do not drink it. Janzen's presumed interpretation would be bacteria modified the resource in a manner resulting in reduced competition from vertebrates that would otherwise drink this resource that is common to the bacteria. While this example is anecdotal, others have tested his hypothesis and empirically demonstrated this competition does occur in nature. Burkepile et al. (2006) demonstrated reducing microbes associated with carrion in shoreline estuaries allows for crustacean scavengers to feed for longer periods of time on the decaying fish resource; however, like with the red queen (Van Valen 1973), such an arms race opens opportunities for other organisms to take advantage of these resources. Thus, as the resource decomposes and the interest of consumers of fresh carrion decreases, other animals are attracted to and consume the degraded resource.

This interaction is prominent in the vertebrate carrion literature, specifically when one considers vultures and their affinity for decomposing vertebrate remains (Kruuk 1967). These species have developed an ability to tolerate bacteria-laden resources. Even brown tree snakes are known to use volatile organic compounds (VOCs) resulting from microbial activity in mouse carcasses as a means to locate these resources (Shivik and Clark 1997).

While insects, such as blow fly (Diptera: Calliphoridae) larvae, competing for these resources can release antimicrobial products that kill competing or pathogenic bacteria (Greenberg 1968) on the resource, the bacteria may also affect the behavior (Ma et al. 2012) and ecology (e.g., oviposition) (Tomberlin et al. 2012) of flies on a resource. For a comprehensive review of these interkingdom interactions involving bacteria and insects, see Tomberlin et al. (2017a). Briefly, bacterial communities are known to go through community succession on decomposing vertebrate remains (Pechal et al. 2013). During this process, blow fly attraction to carrion can be related to the sex and physiological state-specific aspects of the blow flies (gravid vs non-gravid) (Mohr and Tomberlin 2014, 2015). Subsequent research has determined that the potential mechanisms regulating these blow fly behavioral responses (e.g., attraction and colonization) are in part regulated by VOCs associated with microbial degradation of essential amino acids associated with the resource (Liu et al. 2016). Further, Flores et al. (2017) demonstrated that bacteria associated with blow fly larvae impact the development of larvae of a competing species. These data by Flores et al. (2017), as well as several other studies of similar interkingdom interactions (Tomberlin et al. 2012; Pechal et al. 2013; Mohr and Tomberlin 2014, 2015; Liu et al. 2016), provide new data suggesting that microbes could be serving a mechanism regulating arthropod succession patterns during colonization of vertebrate carrion. These interactions could result in pathogenic bacteria associated with a decomposing resource to either proliferate or be suppressed. Thus, complex interkingdom interaction may mediate pathogen emergence and dispersal in natural environments.

Additional studies have demonstrated that interkingdom interactions may manifest within trophic networks as well. Previous research has shown that insects, such as blow fly (Greenberg 1971a; Greenberg and Klowden 1972) and house fly [*Musca domestica* L. (Diptera: Muscidae)] (Zurek et al. 2001) larvae, consume microbes associated with decomposing organic matter. Some microbes are thought to be digested and assimilated, while others are thought to pass through the alimentary canal (Mumcuoglu et al. 2001), thus being potentially dispersed to resources in other habitats, as reviewed in Nayduch (2017). Microbial pathogen dispersal in the environment via flies is a key aspect of the transmission of some foodborne illnesses (Greenberg 1971b). For instance, Weatherbee et al. (2017) described interkingdom interactions of microbial communities with blow fly larvae on swine carcasses where taxa from the carcass became integrated into the internal microbiome of feeding and developing larvae, with distinct shifts in microbial phyla composition that showed convergence of the carcass and larval microbiomes later in decomposition.

Further Pechal and Benbow (2016) demonstrated that the internal microbial communities of aquatic insects in streams with decomposing salmon were structurally different from the same insect taxa from streams without carcasses or historic salmon spawning. Similar to Weatherbee et al. (2017), they also reported the internal microbial communities of larvae collected from masses of the salmon carcasses were similar to the carcass microbial communities. These field studies confirmed previous findings from culture-based laboratory research of bacteria that showed differential acquisition of microbial taxa from decomposing organic matter by blow flies and other filth flies (see review of Nayduch 2017). Lastly, Pechal and Benbow (2016) showed in the same field studies that the internal microbial communities of adult blow flies captured above salmon carcasses varied in time, and adults captured nearer the time of larval collections had microbiomes more similar to the larvae than adults captured 10 days later. These results suggest the microbial ecology of carcass microbial communities in an ecosystem plays important roles in determining the internal microbial communities of both larvae that colonize and consume the resource but likely also influence adults that emerge from those larvae and then disperse into the landscape.

While descriptive, the previous examples provide evidence that the dispersal of microbes into surrounding communities and ecosystems may involve aspects of trophic ecology that provided the foundation for more deeply rooted evolutionary relationships, an area of inquiry that requires additional investigation. The current mechanisms of these potentially evolved interactions are only recently being uncovered, with recent findings showing a future for exciting avenues of research. This new area of research is especially true for those interkingdom interactions among prokaryotic microbes and eukaryotes.

1.3 Mechanisms of Interkingdom Interactions in Disease Ecology

Eukaryotes have variable relationships with prokaryotes, and these interactions can range from beneficial to detrimental. These associations are clearly facilitated by complex bidirectional communication taking place between them and that information exchange, physical interactions, and chemical signaling likely resulted from coevolutionary processes. Furthermore, though bacterial growth and virulence are influenced by local environmental parameters such as temperature, pH, and nutrient availability, the influence of host chemical stimuli on bacterial behavior has only recently become apparent (Rumbaugh 2007; Hughes and Sperandio 2008). Microbial receptors are able to recognize that the particular microbe is within the locality of a suitable host and, for commensals, that it is the appropriate time to initiate expression of genes involved in host colonization. Pathogens can then hijack these signals, leading to activation of their virulence genes (Rumbaugh 2007; Hughes and Sperandio 2008). Moreover, hosts and microbes have developed multiple mechanisms to protect themselves from each other and have, in some cases, also evolved mechanisms that allow a mutualistic coexistence. In this section, we discuss several mechanisms that are used for communication interaction and exchange between bacteria and their hosts. We focus particularly on methods of information transfer, as well as mechanisms for detection of and response to host signals. Deciphering such communication is needed for understanding the evolutionary biology of signal development and information exchange. Also, in terms of practical applications, greater understanding of the mechanisms mediating these processes could lead to strategies which disrupt the more damaging aspects of the information exchange and exploitation of the more beneficial and efficient segments within each process (Fig. 1.2).

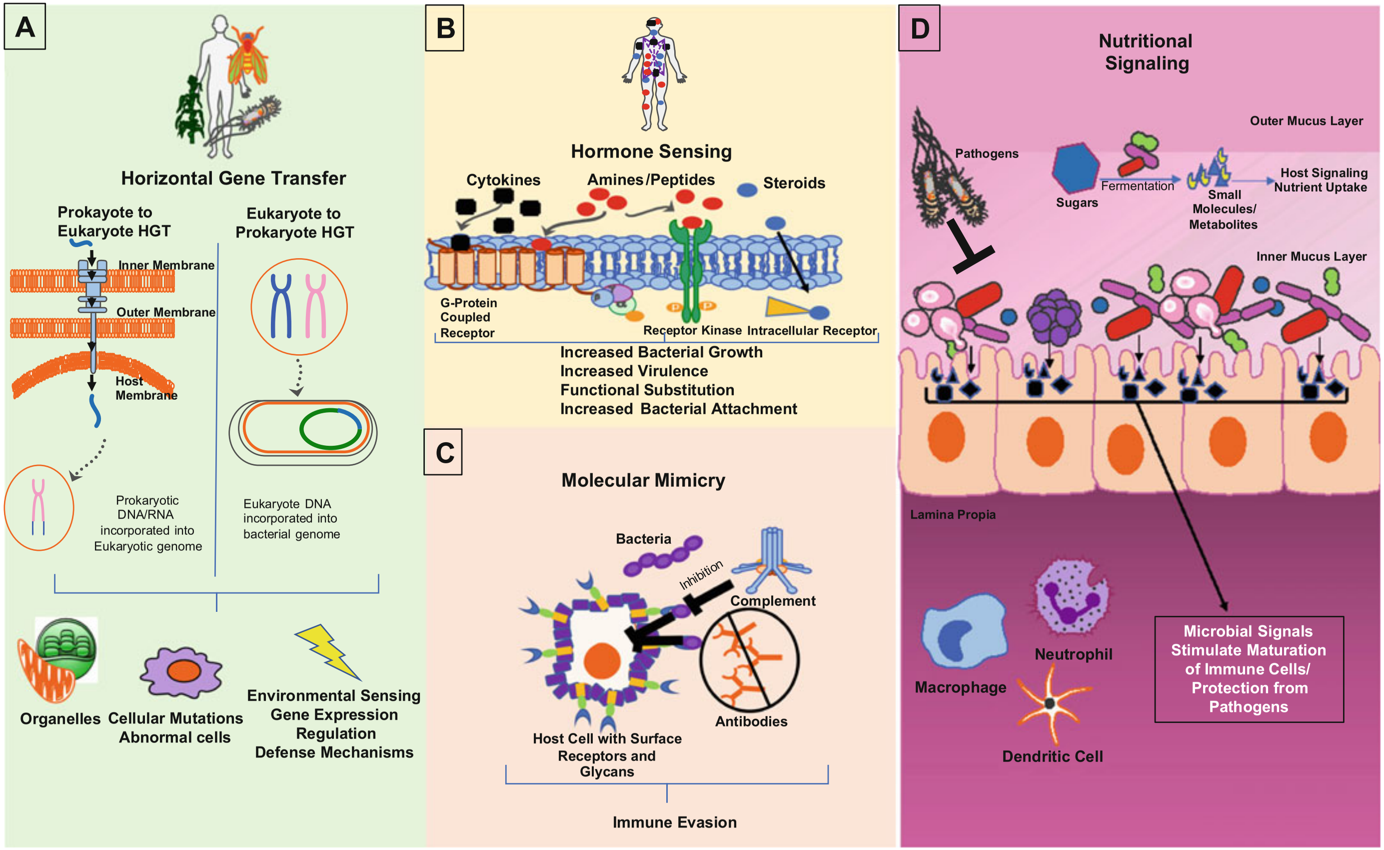

Fig. 1.2 Conceptual mechanisms and consequences of interkingdom communication between hosts and microbes through (**a**) horizontal gene transfer, (**b**) hormone signaling, (**c**) molecular mimicry, and (**d**) nutritional signaling