

# Chapter 2

## Communication Among Phages, Bacteria, and Soil Environments

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### 2.1 Introduction

Bacteriophages (phages) are viruses that infect members of domain *Bacteria*, contrasting the *viruses* of domains *Archaea* or *Eukarya*. Ecology is the interaction of organisms with environments, and those interactions, broadly speaking, may be depicted as forms of communication – the movement of information between or among entities, or at least the presentation of potentially detectable signals. Reception of these signals can result in organism modification, including in terms of their behavior. Alternatively, signals can impact the survival and reproduction of genes, giving rise to natural selection, a consequence of environment-to-organism communication.

Organism modification, in turn, can create detectable signals that may be received by the originally emanating entity, resulting, for instance, in environmental feedback loops. For example, the presence of lactose provides a signal that can result in alteration of gene expression by *Escherichia coli*, as in Jacob and Monod's classic operon model. This change can be viewed as an environment-induced reconfiguration of the bacterium's "behavior," one that results in lactose being used as a carbon and energy source. With this use the environment's lactose signal may become modified, and *E. coli* in response might again revise its behavior. "Communication," though, does not strictly require such direct, two-way aspects.

Within body tissues, communication occurs as a consequence of the expression of genes that are genetically linked and which therefore are less free to evolve toward antagonistic (fitness-reducing) interactions. Contrast microbiomes, communities of microorganisms found within specific environments such as soils. There, genes are much less likely to be genetically linked so have much greater potentials

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to evolve independently, such as toward reducing the fitness of other components. Thus, while our body's homeostasis can be viewed as predominantly a consequence of cooperative actions between clonally related entities (cells), the relative stasis seen within microbiomes is a consequence, to a much larger extent, of exploitative interactions. The latter includes both competition and direct, physical antagonism, such as phage lytic infection of bacterial cells.

Here I consider the many ways in which phages communicate with biotic as well as abiotic components of their environments, and *vice versa*. The results are environments that differ from what would exist given an absence of phage action. By and large I concentrate more on behavioral, ecological, or evolutionary ecological (i.e., adaptive) aspects of communication rather than genomic, metagenomic, or phylogenetic attributes (see contributions of Srividhya and S. Krishnaswamy, Riley in this volume). Where possible, I supply data or insights which pertain especially to soil environments.

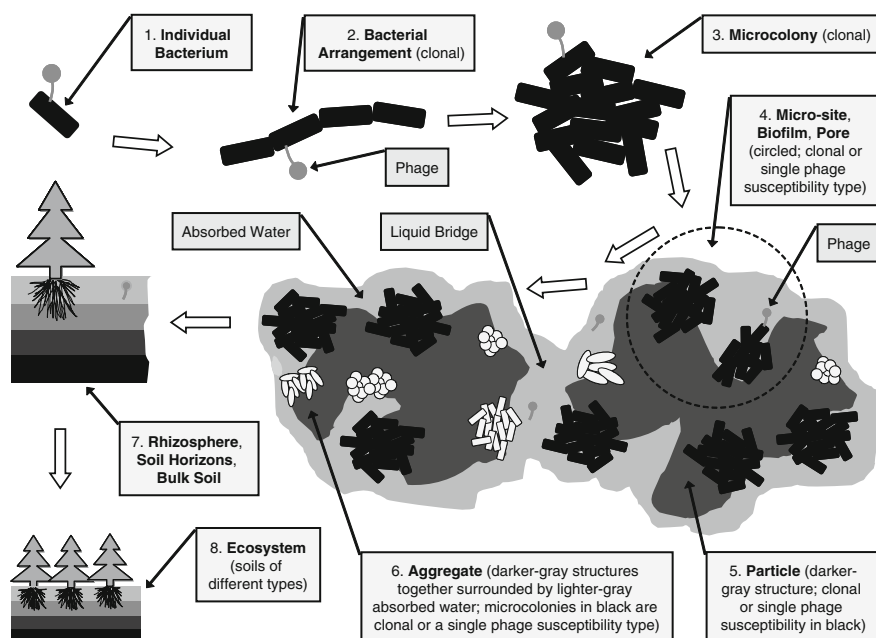
Phage–soil reviews include those of Williams et al. (1987) and Day and Miller (2008). Reviews of phage–bacterial interactions within an artificial, spatially structured environment, i.e., phage plaques, are also available (Krone and Abedon 2008; Abedon and Yin 2008, 2009; Abedon 2010). Note the potential commonalities between phage population growth within soils, within biofilms, and as plaques: In each case, the predominant phage-exploitable units presumably are immobilized bacterial microcolonies (Fig. 2.1) rather than the planktonic, individual cells more typically envisioned as phage targets (O'Donnell et al. 2007; Abedon 2010; Abedon and Thomas-Abedon 2010).

## 2.2 General Concepts

In this section I review basic principles of environments and communication, especially as viewed from the perspective of microflora and particularly from the standpoint of phages.

### 2.2.1 *Microbe-Containing Environments*

One can categorize microorganism-containing environments or microenvironments in terms of levels of water saturation, degrees of spatial structure (i.e., tendencies to inhibit free movement of materials, especially as via mixing), porosity, permeability, and the extent to which the materials making up an environment are organic vs. inorganic. From this point of view we can envisage at least ten variations: (1) aqueous solutions; (2) sediments found within aqueous environments; (3) flocculations; (4) soils; (5) surfaces of nonparticulate solids such as rocks but also, e.g., of medical devices; (6) porous interior surfaces of otherwise nonparticulate solids, e.g., fluid-filled microfractures (Gomez and Laubach 2006) within rocks, or both micropores and macropores found within or between aggregates of materials



**Fig. 2.1** Hierarchy of soil targets of phage attack. Spatially clumped, related groups of bacteria can serve as targets for phage attack in the sense that the infection of one bacterium within a group results in an increase in the likelihood of infection of other members. Groups, as shown, form a nested hierarchy that begins with individual cells and then includes arrangements of not-yet separated bacteria (not necessarily biofilm associated) through microcolonies and collections of microcolonies forming biofilms. Biofilm adherence is to particles which collectively form aggregates of such particles, collections of which represent soils, etc. Phage infection of a single bacterium found on, for example, an aggregate, thus increases the odds that other bacteria found on the same aggregate will also become phage infected, particularly to the degree that aggregates hold absorbed water through which phage movement via diffusion might occur. Phage movement likely is enhanced with increasing soil saturation such as occurs due to rain

(Ranjard and Richaume 2001); (7) living organisms; (8) decaying (no longer living) organisms; (9) organismal excreta; and (10) air.

Soils can be viewed as intermittently aqueous, colloidal suspensions that possess substantial spatial structure and which consist, in their dried form, of particulate mixtures of components that are either inorganic (i.e., sand, silt, or clay) or organic (living as well as decaying organisms). Aqueous sediments, by contrast, are continuously and fully saturated with water while the overlying planktonic world displays much less spatial structure than either sediments or soils. Many rocks are less particulate as well as less readily water saturated or porous within their interiors, though rocks such as sandstone are quite permeable, allowing large amounts of water transmission to occur. Living organisms tend to remain fully water saturated, like sediments and planktonic aqueous environments, but at the same time are only selectively permeable, plus display extensive spatially structured habitats (e.g., our skin and mucous membranes).

Rocks typically also have lower ratios of organic to inorganic materials, those consisting of organic materials, i.e., coal, being an exception. Living organisms, in contrast to rocks, consist of much higher ratios of organic to inorganic materials than many of these other environments. As a consequence, the addition of organisms, either alive or decaying, can increase the organic content of soils considerably. The presence of rocks and their breakdown products instead usually will directly *decrease* the organic content of soils, though at the same time can impact organism prevalence by supplying inorganic nutrients.

The overall nutrient content of soils is dependent, thus, on both biotic and abiotic components. Biotic components provide nutrients, especially organic carbon, that contribute particularly to soil secondary productivity (which involves animal, fungal, protist, and bacterial growth). Abiotic components, especially dissolved minerals such as phosphorous as well as inorganic nitrogen, contribute to soil or soil-associated primary productivity (which is dominated by plant growth). The living, biotic component of soils also contributes substantially to mineralization, i.e., the freeing up of especially inorganic nutrients, which then are available to both autotrophs (particularly photosynthetic organisms) and heterotrophs (which constitute everything else).

Soils also may be viewed as complex combinations of the other environment types listed at the beginning of this section (e.g., air, rocks, etc.). However, it is not possible for all of these environment types to exist simultaneously. Instead, soils can be temporarily fully saturated (and therefore aqueous like), can overlie permanently wet sediment-like environments, can contain flocculations of organic material, and can certainly contain or overlie large, solid, inorganic materials (porous or otherwise). Unless sterilized, soils will contain living organisms, and sterile or not will contain dead organisms and excretions. In addition, when dehydrated, either partially or fully, soils will become impregnated with air, plus, through the action of wind and other forces, can become suspended in air. Soils thus are organic and inorganic, biotic and abiotic, nutrient poor or more nutrient rich, solid as well as liquid and gaseous, etc. Soils also contain numerous interfaces between their various environmental and microenvironmental aspects.

Soils can be aerobic or anaerobic, with levels of molecular oxygen ranging from atmospheric concentrations to effectively nonexistent. Deeper, water-saturated soils, or water-filled microsites, for example, can tend toward the anaerobic end of the spectrum. Soils also can be differentiated in terms of texture (sand vs. silt vs. clay content), structure (aggregation properties along with porosity between aggregates, which together can greatly influence movement of water), and in terms of horizons. The latter term is a description of a soil's horizontal layering, which often varies predictably starting from the surface and going downward, e.g., organic matter, surface soil, subsoil, substratum, and then underlying bedrock. One can also differentiate soils, *vis-à-vis* plants, into the rhizosphere (soil immediately surrounding plant roots) and those soils which are not associated with plant roots (known as bulk soil).

Soils thus may be too complex to yield to general principles regarding phage-to-bacteria-to-environment, etc., communication. One can simplify things, however,

by assuming a perspective of soils as alternatingly somewhat water soaked, during which biological processes such as movement, reproduction, and decay occur, and more air-like environments, during which desiccation survival is emphasized. Soil heterogeneity furthermore results in different microsites experiencing different degrees of desiccation within the same soil sample. From this vantage, the biology of soils perhaps can be viewed as analogous to that of sediments, though typically much more complex and heterogeneous (O'Donnell et al. 2007), and with the important property that often they are less than fully water saturated. Alternatively, from the perspective of individual phages, soils may be envisaged as heterogeneous mazes within which susceptible bacteria may be periodically encountered (Fig. 2.1).

### 2.2.2 *Communication and Microorganisms*

Communication is an important concept with many facets, depending upon both one's discipline of study as well as personal proclivity. A lay definition, anchoring one end of a spectrum, might entail two-way, abstract exchanges involving verbal or written language. That is, for example, where one individual speaks, a second (or more) listens, ponders, responds, and so on, with perhaps various verbal and nonverbal interactions occurring simultaneously. At its basis, though, communication involves simply signals emanating from one or more entity that are received by other entities. These other entities then can respond in some manner by modifying their physical, chemical, or behavioral state.

In addition to visual as well as vocal interactions between animals, communication can involve touch, plus extensive forms of communication exist that occur via chemical signals, whether airborne (e.g., pheromones, the sweet smell of a flower, etc.), fluid-based, or found in soils, such as secondary metabolites associated with soil bacteria (Karlovsy 2008). The latter also includes the chemically mediated cell-to-cell signaling that coordinates the growth and behavior of multicellular organisms. Indeed, extensive communication continuously takes place within our own bodies, maintaining, in a process collectively described as homeostasis, a perturbation away from an otherwise inevitable decay.

The coordination seen with homeostasis is the product of an evolution that is possible only because the genes involved are genetically linked, that is, they are found within the same genomes and the survival (and reproductive success) of one such gene is not independent of nor necessarily even possible without the success of others. Such coevolution of genes is much less likely without genetic linkage (e.g., see Hyman and Abedon 2008 for discussion), and the default state among most of the genes found within individual ecosystems, except those found within the genomes of individual organisms, is one of competition, and even antagonism, rather than coordination (or cooperation). An ecosystem thus may be viewed as consisting of partially isolated islands of active perturbation away from an otherwise inevitable decay toward chemical equilibrium, that is, islands consisting of

individual organisms. These islands are connected by regions that either are at chemical equilibrium or are in the process of moving toward that equilibrium. Collectively, these ecosystems do not display homeostasis so much as attract or retain organisms that are able to exploit existing conditions, all toward their own, individual gain. Their interactions, absent environmental perturbation, give rise approximately to steady states.

Though interactions within ecosystems, or microbiomes if we are focusing predominantly on the microorganisms present, are not necessarily coordinated or cooperative, they nevertheless are communicative. Whether through soluble chemicals, intentionally or inadvertently released, or entities physically touching, signals of various sorts can emanate from one individual and be received by others. The result can be either a passive response by the signal's recipients, such as is the case at least initially when damaging agents are conveyed from one individual to another, or a more active response by the recipient, e.g., as seen with quorum sensing (Bonfante and Anca 2009; Dessaux and Faure in this volume). One can view the generation of signals also as passive vs. active, such as the passive release of chemicals upon decay versus the active exporting of signal molecules to the extracellular environment. Situations also can occur where both signals and responses are intentional and occur expressly for the sake of conveyance of information, phenomena that can be more easily appreciated as a form communication from a human-centered perspective. Irrespective of such details, natural selection favors those organisms whose survival and reproduction tends to *not* decline in response to environmentally common signals. Thus, we can envisage microbiomes as consisting not just of myriad organisms, but also of myriad communicative pathways, which to recipients can be beneficial, benign, or detrimental. Here I consider especially those pathways involving phages.

### **2.2.3 *Bacteriophages, Bacteria, and Environments***

Originally, bacteriophages were macroscopically observed as consumers of bacterial cultures, either the clearing of broth cultures or as plaques on solid media (Abedon 2008). Thus, while the word virus, once meaning poison, fittingly describes the macroscopic consequences of viral infection of plants and animals, the term phage – from Greek meaning to eat or devour – apparently seemed more appropriate for the viral infection of bacteria. Consistently, this potential for phages to clear pure bacterial cultures, that is, their “phage”-like lytic ability, provides us with clues as to the phage potential to impact bacterial communities (Abedon 2009c). Similarly, impediments on this lytic ability are indicative of the negative impact of bacteria, or environments in general, on phages. All of these negative impacts, as well as interactions between entities that are positive, i.e., that are fitness enhancing, result from communicative processes.

Phages are often described as the most numerous organisms on Earth, though all estimations of phage prevalence are just that: estimations. For instance, there are

many who note that viruses tend to be present in ratios of about ten-to-one to cellular organisms. Since prokaryotic organisms, a combination of both *Bacteria* and *Archaea*, are prevalent with a total of about  $10^{30}$  individual cells (Whitman et al. 1998), then the global phage total count logically would be about  $10^{31}$ . This estimation is similar to the product of the volume of the world's oceans and estimations of  $10^7$  virus-like-particles per ml of sea water, which is not too excessive a possibility as an average density (Abedon 2008). Such virus total-count determinations typically involve electron or epifluorescence microscopy (Abedon et al. 2009), but generally are easier to obtain from water vs. within soil. This is because, with soils, the presence of debris and potential for virion absorption to particles (and debris) seems to obscure direct counts. Nevertheless, phage density estimations range up to and over  $10^8 \text{ g}^{-1}$  in soil, as extrapolated from transmission electron microscopy total counts (Ashelford et al. 2003) or as determined via epifluorescence microscopy (Williamson et al. 2003). Interestingly, though ratios of viruses to bacteria in forested soils can also be in the range of ten-to-one ( $>10^9$  virus-like particles to  $>10^8$  bacteria), agricultural soils containing a measured bacterial prevalence of  $>10^5 \text{ g}^{-1}$  can still have densities of virus-like particles of  $\sim 10^9 \text{ g}^{-1}$  (Williamson et al. 2005). Numerous additional studies have characterized temperate phages isolated from soil or lysogeny in soil-associated bacterial species (e.g., Fink and Zahler 2006; Williamson et al. 2007, 2008; Ghosh et al. 2008; see contributions of Kimura and Srividhya/S. Krishnaswamy in this volume).

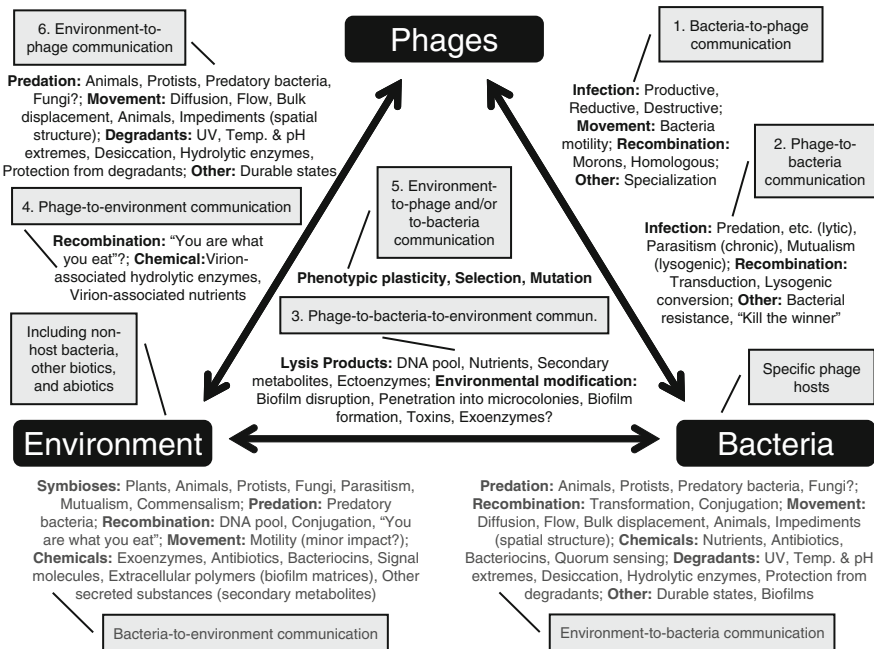
Another bulk means of viewing phages within environments is in terms of their diversity, which in modern times has been analyzed especially via metagenomic techniques. Metagenomics takes a snapshot of a portion of the genetic diversity found within a given environment, e.g., such as that associated (seemingly) with the viral fraction (Casas and Rohwer 2007), or of the entire soil metagenome itself (Vogel et al. 2009). Alternatively, it is possible to be more directed in one's analysis by employing specific PCR primers, particularly in conjunction with sequencing (Jia et al. 2007). From such analyses, in light of the high number of sequences found that fail to match any currently present within databases, some have argued that phages are the most diverse organisms on Earth, which is in addition to being the most numerous (Pedulla et al. 2003; Weinbauer et al. 2007). A good take-home message from these musings is simply that phages can do many things within environments (i.e., they possess many different genes) and, based on analysis of measurements of phage turnover rates (in aquatic environments), must do those things fairly often (Hendrix 2008).

Bacteria in soil environments may be similarly considered. For instance, both bacterial diversity and density in soils can be high, with numbers of bacterial phylotypes – a species-like taxonomic designation applied to microorganisms – varying between locations especially as a function of pH (Fierer and Jackson 2006), with species number per 10 g of soil reportedly well in excess of  $10^4$  (Gans et al. 2005; Burmølle et al. 2007), and with prokaryote counts often in the range of  $10^9 \text{ g}^{-1}$  (Gans et al. 2005; Burmølle et al. 2007; O'Donnell et al. 2007). An additional consideration is that many bacteria within soils grow within biofilms (Burmølle et al. 2007; O'Donnell et al. 2007) and their arrangement within those

biofilms likely impacts the phage potential to penetrate to and otherwise affect bacteria. Bacteria which phages can use as hosts thus will have certain densities, certain properties, and will be dispersed in certain ways, all of which will affect phages and, in turn, the phage impact, that is, phage communication with both bacteria and the larger environment.

### 2.3 Pathways of Communication in Soil

In this section I distinguish among phage-associated communication processes in terms of directions of communication, i.e., from specific categories of originators of signals (such as phages) to specific categories of recipients (such as bacteria). These various lines of communication are summarized in Fig. 2.2. An additional category, not presented in that figure, nor otherwise discussed, is that since bacteria can serve as prey for soil-dwelling animals, protists, predatory bacteria, and phages, then communication in the form of interorganismal competition will occur among these disparate organism types.



**Fig. 2.2** Mechanisms of communication between phages, their hosts ("Bacteria"), and the non-host environment. Numbers refer to the order of discussion in the text. Text in gray (bottom) does not involve phages and is not otherwise discussed in the chapter



### **2.3.1 *Bacteria-to-Phage Communication***

Communication that can be viewed as coming from bacteria and being received by phages may be differentiated into a number of distinct facets. These include (1) transfer of DNA sequences (i.e., so-called moron acquisition by phages, as discussed in Sect. 2.3.1.2), (2) physical and chemical interactions between phage- and bacteria-sourced molecules (e.g., protein–protein or protein–DNA interactions), or (3) more general bacteria-mediated modifications of phage phenotype. The latter may be differentiated into modifications that impact the replication, survival, or movement of individual phages (their ecology), on the one hand, or, on the other hand, may be the product of bacteria-mediated natural selection on phage populations (their evolution). Except for phage interaction with bacteria-sourced, decay-mediating molecules such as extracellular proteases (Nasser et al. 2002), these mechanisms of bacteria-to-phage communication are, by and large, associated with phage infection of bacteria. I consider them in terms of bacterial impact on phage phenotype, genotype, and movement.

#### **2.3.1.1 Bacterial Impact on Phage Phenotype**

Phage infection can occur in a number of distinguishable modes: productive, reductive, and destructive (Abedon et al. 2009). Which mode is displayed during a given infection is determined in the course of communication between molecules produced by phages and bacteria. Productive infections are ones which produce and release phage virions. Reductive infections, such as lysogeny, are ones in which the phage survives but the infection does not immediately gear up to produce phage virions. Destructive means that the phage does not survive. It seems reasonable to suppose that all nondefective phages must be capable of productive infections and likely that all can also be subjected to phage-destructive infections.

#### **Destructive Infection: Antagonism, Deception, and Primitive Immunity**

There are a number of obvious situations in which bacteria noticeably impact phage phenotype. These include when bacteria effect phage restrictive or abortive infections, which are phage-destructive infections that may be distinguished in terms of whether bacteria survive or don't survive, respectively (Abedon 2008; Abedon et al. 2009; Hyman and Abedon 2010). These are clear examples of bacteria-to-phage communication, particularly ones with negative consequences for the phage.

In addition to destroying phages, restriction-modification systems can also modify phage genomes in a manner that alters their susceptibility to cutting by the same restriction-modification system. Notably, the latter is a rare occurrence in terms of its ability to forestall phage restriction, though important in that it imparts on the progeny of so-modified phages the ability to display bacteria-killing infections (Korona and Levin 1993). These inadvertent modifications confer to phages

the power to communicate a *lie*; that is, to mislead bacteria into treating a phage genome as self.

There also exists a type of destructive infection that may be viewed as a form of phage-mediated bacterium-to-bacterium communication (Sumbly and Smith 2002). In this instance phages are modified during productive infection such that subsequent infection of a clonally related bacterium, here the soil bacterium, *Streptomyces coelicolor*, results in phage restriction. The previously infected bacterium thus seems to be communicating, through the released phages, that those phage genomes represent foreign DNA that therefore should be eliminated. This “Phage growth limitation system” may be viewed as analogous to animal immune system functions in which the molecules of parasites are tagged, as foreign, and subsequently eradicated. Also analogous to animals, it is the passage of parasites among clumped, clonally related tissues, in this case bacterial tissue, which fosters the utility of this mechanism.

### Reductive Infection: Sleeping with the Enemy

Phages may be packaged into bacterial endospores, increasing phage survival within soils (Pantastica-Caldas et al. 1992; Sonenshein 2006). Since bacterial genes are responsible for the sporulation phenotype (Errington 2003), phages may be viewed as modifying their infection outcome in response to bacterial signals, from obligately productive to at least temporarily reductive (Abedon 2009b). Similarly, phage survival may be extended via lysogenic infection (Stewart and Levin 1984). Continuing this theme, arguably any bacterial mutation that affects phage infection characteristics or any differences in phage phenotype when infecting different bacterial strains – such as display or lack of display of lysogenic infections – can be described as examples of bacterial gene impact on phage phenotype, and which therefore is illustrative of bacteria-to-phage communication. Furthermore, it seems logical that these interactions between phage- and bacteria-encoded molecules, interactions which are potentially disruptable by bacterial mutation, are products of phage evolution rather than of bacterial evolution, unless those interactions are antagonistic to phages or, alternatively, enhance the overall fitness of a lysogen.

#### 2.3.1.2 Bacterial Impact on Phage Genotype (Evolution)

The ability of bacterial genes to modify phage phenotype underscores the obvious potential of bacteria to impact phage evolution. A large fraction of this impact can be described as resulting from bacterial mechanisms of resistance to phages, e.g., restriction-modification systems as well as evolved abortive infection mechanisms (Hyman and Abedon 2010). These and other phenomena collectively make up the “bacteriophage ‘resistome’” (Hoskisson and Smith 2007), which has been explored by Coberly et al. (2009) in terms of its impact on phage evolution within spatially

structured environments. However, to the extent that phages can form mutualisms with bacteria, then phage–bacterial coevolution presumably can occur other than as a consequence of antagonistic interactions (Sect. 2.3.2.2).

Another general mechanism of phage evolution involves their specialization on specific bacteria, which can be viewed as a form of bacteria–communicated phage adaptation. Biological adaptation, however, often involves tradeoffs where improvement in one character gives rise to reduced function in another, a process described as antagonistic pleiotropy (Duffy et al. 2006; Heineman et al. 2008). An extreme of such antagonistic pleiotropy is seen with host-range switching, where phage interaction with one bacterial moiety (e.g., the phage receptor molecule) is lost upon acquisition of phage affinity for a different bacterial molecule (the new phage receptor molecule). Alternatively, some phages have been found which display fairly wide host ranges, spanning multiple bacterial genera (Hyman and Abedon 2010). These broader host ranges presumably would facilitate access to greater host numbers but perhaps at the expense of more effective infection of any one host type.

Phage evolution also occurs as a consequence of acquisition of bacterial genetic material. The “Moron-accretion hypothesis” in fact posits that all phage genetic material had its ultimate origin from bacterial DNA (Hendrix et al. 2000). That DNA which increases phage fitness, or at least does not decrease phage fitness too greatly, is retained and subject to subsequent mutational modification, which again is subject to natural selection (Hendrix 2008). A more specific form of recombination between phages and bacterial chromosomes is the homologous recombination that can occur between phages and prophages found in the infected bacterium; see Abedon (2009a) for discussion and references. Here phage-evolved genes can be transferred intact to a second phage, though it’s a matter of semantics whether this represents bacteria-to-phage communication vs. phage-to-phage communication.

### 2.3.1.3 Bacterial Impact on Phage Location

Bacteria can impact phage movement. If bacteria are immobile, such as are bacteria found in association with biofilms, then phage infection can have the consequence of temporarily halting phage movement. This temporary immobility presumably is equivalent to that which occurs upon bacterial infection during phage plaque formation (Abedon and Yin 2008, 2009; Abedon and Thomas-Abedon 2010). Bacteria also may obstruct phage movement by being tightly packed, perhaps even if those bacteria are not a phage’s host (Yin and McCaskill 1992), plus can secrete substances, such as extracellular polymers, which bind together bacterial biofilms but which also may inhibit or at least slow the movement of phage particles (Abedon 2010; Abedon and Thomas-Abedon 2010). On the other hand, if bacteria are filamentous, then phage adsorption to one end presumably could result in virion release at the other. Another means by which phage movement can occur during infection is when bacteria themselves are motile, which may move infecting phages along faster than can diffusion alone, though only so long as the infected bacterium has not yet lysed.

In soils, we thus can expect a number of ways by which bacteria can impact phage movement, ranging from substantial inhibitors to highly effective enhancers. One can even speculate that environmental conditions, such as degree of water saturation, may modify the relative impact of these various mechanisms. I now turn from bacteria-to-phage communication to the seeming reverse, i.e., phage-to-bacteria communication.

### ***2.3.2 Phage-to-Bacteria Communication***

Phage-to-bacteria communication varies in terms of the costs, and benefits, experienced by recipient bacteria. These impacts range from depletion of bacterial fitness to zero, i.e., bacteria are killed by phage action, or worse (Sect. 2.3.2.1), to where bacterial fitness is enhanced in the course of lysogenic conversion (Sect. 2.3.2.2).

#### **2.3.2.1 The Many Costs of Phage**

The worst thing that could happen to a bacterium as effected by a phage is a noninduced lytic infection, that is, a productive infection terminating in lysis that does not follow lysogeny. This is because not only does the infected bacterium die but so too, upon subsequent infection, may the bacterium's fellow clone mates. With lysogeny, by contrast, clone mates generally do not also die, following induction and subsequent phage release, because of the expression of superinfection immunity by these fellow lysogens (Sect. 2.3.2.2). An abortive infection, which is bactericidal but nonetheless does not produce phages, should in these terms also be preferable to a productive, lytic infection.

Chronic infections, too, would be preferable to lytic ones. However, though not necessarily lethal, chronic infections still have the potential to slow bacterial growth and therefore reduce bacterial fitness, plus can increase a bacterium's susceptibility to environmental toxins such as antibiotics (Hagens et al. 2006). In each case, the negative effects are consequences of phage infection, though with abortive infections the actual effector of bacterial death can be the bacterium (Hyman and Abedon 2010). That bacteria would encode such a mechanism, however, makes sense so long as productive lytic infections are more costly than abortive ones, to clonal bacterial populations. With restrictive infections, by contrast, the phage dies but the bacterium survives, so, on that basis, phage restriction should be preferable to the bacterium than either abortive or chronic phage infections.

#### **2.3.2.2 Phage Infection as Symbiosis**

In reductive infections neither phage nor bacterium is killed, plus phages do not produce virions. The more familiar reductive infections are lysogenic, where infecting phages exist as intracellular prophages (Miller and Day 2008; Abedon 2009b). Lysogeny can be viewed as a symbiosis, as too can phage chronic infections, since in

both cases the phage and bacterium are independent organisms that nonetheless are intimately associated over multiple generations. Myriad intraspecific communication can occur within symbiotic relationships, some protective while others are antagonistic to the relationship's existence. Prophage induction as well as nonlethal metabolic demands, for example, can be detrimental to host bacteria, and bacteria possibly possess antiprophage mechanisms (Lawrence et al. 2001).

Prophage–bacterial interactions can also be mutualistic, especially within the context of so-called lysogenic conversion, where bacterial phenotype is modified by phage gene expression (Miller and Day 2008; Hyman and Abedon 2008; Paul 2008). The most common such benefit is superinfection immunity (a.k.a. homoimmunity), which protects bacteria from exploitation by additional phages, ones of the same immunity type. In another example, though not necessarily mutualistic, prophages can down-regulate the metabolic activities of bacteria, which possibly provides lysogens with increased survival potential (Chen et al. 2005). As perhaps an extreme example of such tendencies, infection by various phages of soil bacteria has been shown to have positive impacts on host sporulation rates (Silver-Mysliwiec and Bramucci 1990).

Prophage induction itself can lead to the destruction of neighboring, potentially lysogen-competing bacteria, thereby providing a benefit to unlysed lysogen clones. A phage of *Bacillus aneurinolyticus*,  $\phi$ BA1, in fact, displays bacteriocin-like activity on some hosts (an apparently phage-DNA-independent bacterial death that occurs also without phage survival) but normal phage infection on other hosts (Ito et al. 1986). This process of temperate-phage induction and subsequent killing of nonlysogenic bacterial neighbors has been dubbed as a form of allelopathy by Stewart and Levin (1984) and more recently has been described as “kill the relatives” (Paul 2008). See Abedon and LeJeune (2005) and Brown et al. (2006) for additional discussion of “lysogen allelopathy” along with possible consequences. Temperate phages also have been implicated as contributors to bacterial biofilm formation (Rice et al. 2009; Abedon 2010), plus lysogenic conversion can provide metabolic functions that can be useful to bacteria only under certain circumstances, as considered in Abedon and LeJeune (2005).

Contrasting prophages, chronically infecting phages may be described as classically parasitic organisms since they display ongoing, detrimental, but typically sublethal infections. Lytic phages are viewed as parasites as well, as in “obligately intracellular parasites,” but due to their propensity to kill their host bacteria they often are described as predators instead. In ecology, however, predators typically represent a higher trophic level, i.e., a feeding position one level above that of prey, while phages fail to achieve the molecular assimilation of bacteria that “feeding” would imply, since most of the consumed bacterium is discarded as waste (Thingstad et al. 2008). Phagotrophic protists, by contrast, clearly can be viewed as predators that feed on bacteria. It has been argued, alternatively, that lytic phages may be described as parasitoids (Forde et al. 2004), parasites that consume their hosts, often from the inside out. The analogy is that phages similarly consume their bacterial hosts from the inside out. However, the same lack of molecular assimilation that can be used to criticize the labeling of phages as predators similarly could be

applied to the labeling of phages as parasitoids. It is important, though, to not lose sight of the fact that lytic phage infections are equivalently detrimental to their bacterial hosts regardless of how we choose to label those interactions.

### 2.3.2.3 Phage-Mediated Horizontal Gene Transfer (Transduction)

The above considerations are ecological in terms of the consequences of phage-to-bacterium communication. Alternatively, one can view these communications from an evolutionary perspective, that is, in terms of mutation, sampling error (i.e., genetic drift), and migration, as well as, of course, natural selection (Duffy and Turner 2008; Abedon 2009a). In this section I emphasize the phage impact especially on the migration of genetic material between bacteria.

Migration can be viewed as the physical movement of organisms or, more pertinently with regard to evolutionary biology, the movement of individuals into or out of populations. While bacteria are capable of migrating into and out of populations, it is important to realize that bacterial genes, independent of bacteria themselves, also are capable of such movement. In microbiology, one typically describes this migration of genes between populations as horizontal gene transfer or lateral gene flow, though another term which seems equally applicable is introgression (Cohan et al. 1991; Campbell 1994; Lawrence and Ochman 1997; Brown et al. 2001; Colegrave 2002; Johnson et al. 2004; Abedon 2009a); that is, the low-level gene flow between otherwise minimally genetically interacting populations. Such gene flow is readily mediated by phages, including among soil bacteria, in a process termed transduction: the packaging of bacterial DNA within phage capsids and subsequent delivery of that DNA to a second bacterium. The recipient bacterium both survives and integrates the DNA into its genome via various forms of recombination (see contribution of Armon in this volume). A pertinent recent study is that of Ghosh et al. (2008) who showed that transducing particles could be induced, via treatment with mitomycin C, from soil-isolated lysogens.

Bacteria additionally may be recipients of what are better described as phage genes, i.e., genes that normally are found within a phage's genome rather than ones which are accidentally packaged into phage capsids. Lysogenic conversion is the most familiar context within which such genes are observed (Sect. 2.3.2.2). More generally, phages might serve as "the proving ground of choice for evolutionary innovation" for potential bacterial genes, "the critical motive force for the evolution of the entire biosphere" (Krisch 2003). Phages also can inactivate bacterial genes, most prominently via prophage insertion into bacterial chromosomes, e.g., as by phage Mu (Paolozzi and Ghelardini 2006).

### 2.3.2.4 Kill the Winner

In terms of natural selection, as mediated by phages upon bacteria, one can clearly differentiate between positive and negative impacts (above). In this section, I consider two interesting negative impacts. The first is the tendency for *tradeoffs*,

where phage-resistant bacteria, in the absence of phages, tend to be less fit than otherwise isogenic, phage-sensitive bacteria (Gill and Abedon 2003; Kerr et al. 2008). The consequence of this effect is that in a world lacking in phages, the dominating bacteria will be inclined to be those that display the least tendency toward phage resistance.

The second impact is a frequency-dependent selection (Abedon 2009a), typically described in the phage literature as “Kill the winner” (Thingstad et al. 2008). That is, bacterial winners, i.e., phage-susceptibility types displaying the greatest densities, will be more susceptible to phage attack simply due to those higher bacterial densities. The result is a potential for greater fitness for lower-density phage-susceptibility types along with a resulting selection for greater overall bacterial diversity. So goes the concept of kill the winner as it was formulated to explain phage–bacterial community dynamics within aquatic environments (Thingstad 2000), but it is a valid question whether kill the winner is similarly applicable to soil environments (Day and Miller 2008).

While one should always expect higher bacterial densities to support greater phage densities and therefore greater bacteria killing potential, all other factors held constant, in fact a shortcoming of the idea of kill the winner, in terms of validation, is that dramatic bacterial killing will only occur if dramatic phage densities can be achieved, such as in the range of  $10^7$  or more phages of a single type per ml (Appunu and Dhar 2008; Abedon and Thomas-Abedon 2010). Alternatively, we can view kill the winner from the perspective of bacterial microcolonies as a phage target (Fig. 2.1). For two bacterial types, otherwise identical, the microcolony that is larger overall – in a sense, a winner among microcolonies – will be more likely to encounter a phage and therefore more likely to be reduced or eliminated by phage infection. Of course, the more microcolonies of a given type, too, the more prevalent will be those would-be microcolony-encountering phages.

The less water that is present in soil, the greater the effective phage density. Indeed, when calculating phage densities within soils, often conveniently determined on a per gram basis, it is highly relevant just what volume of free water for phage diffusion is available within that gram, and how that water is arranged with regard to the potential for phage diffusion between bacteria (Fig. 2.1) (see contribution of Armon in this volume). In particular, while water saturation of soils should allow greater potential for phage diffusion between bacteria, it also may have the effect of reducing phage densities such that phage–bacterial encounter and therefore kill the winner is less likely. In addition, regardless of the level of water saturation, the rate of impact of phages on bacteria in soils will be expected to be slower than that observed within well-mixed broth (Tan and Reanney 1976; Pantastica-Caldas et al. 1992), presumably also reducing the efficiency of kill the winner. A few experiments exist, however, which provide results that are at least consistent with the possibility that kill the winner could function at least in some soils, at some scales, against some bacteria.

Keel et al. (2002), in what represents essentially an augmented kill the winner scenario, added phages to target bacteria in soil at a ratio of 1.6:1.0 and observed a one-thousandfold drop in bacterial densities. The added phage-to-bacterium ratio,



though, is insufficient to explain the resulting decline in bacterial densities, which at best would provide a reduction of 80%, i.e.,  $e^{-1.6} = 0.2$  (20%) = the expected number of surviving bacteria following phage attack (Carlson 2005). Instead, the phage-to-bacterium ratio must have reached at least  $\sim 7$  fold (Abedon 2009d; Abedon and Thomas-Abedon 2010), which is about what was experimentally observed in terms of *in situ* increase in phage density. Such results are very much consistent with a kill the winner effect: the ability of high bacterial densities (there  $10^8 \text{ g}^{-1}$  soil) to support phage population growth to sufficient densities to substantially reduce bacterial numbers. It must be stressed, however, that phages were applied to soils at their initially high densities,  $>10^8 \text{ g}^{-1}$ , rather than amplified to those levels while *in situ*. In addition, phages were added soon after target bacteria were mixed into soils, suggesting more or less uniform bacterial dispersion within soils along with a lack of biofilm formation prior to phage addition. Conditions thus were likely ideal, and artificially so, for both phage amplification and subsequent bacterial killing. Importantly, the phage densities involved approached or even exceeded total phage densities that have been reported for soils in general (Sect. 2.2.3).

Zeph and Casida (1986) provide additional, arguably less artificial evidence that kill the winner might potentially take place, at least upon soil manipulation. They added bacteria to soil as prey for indigenous bacterial predators. As a means of monitoring for enrichment of these predator bacteria, they assayed for increases in the prevalence of indigenous phages active against the predator bacteria. The soil, however, appears to have been well mixed prior to the start of experiments, implying some loss of spatial structure. In addition, typically no more than about  $10^6$  phages  $\text{ml}^{-1}$  of “percolate” were produced (except for one experiment in which peak phage densities instead were  $10^7 \text{ ml}^{-1}$ ). It is uncertain, though, how these titers translate into within-soil bacteria killing potential, and therefore whether kill the winner could have been effected. Importantly, less artificial studies of phage–bacterial dynamics in soil have yielded even lower phage densities, i.e., at best little more than about  $10^4 \text{ g}^{-1}$  (Campbell et al. 1995; Ashelford et al. 1999, 2000). In other studies, however, counts well in excess of  $10^6$  phages  $\text{g}^{-1}$  have been observed in which soil had been amended with nutrients and/or host-bacteria (Reanney and Marsh 1973; Tan and Reanney 1976; Germida 1986; Pantastica-Caldas et al. 1992; Hussein et al. 1994; Burroughs et al. 2000).

In short, there is no evidence that kill the winner cannot, in principle, function in soil ecosystems, but there also is little evidence that it in fact does. My opinion is that it probably does operate on microscales, at least to the extent that soil phages are able to effectively reach, penetrate into, and otherwise fully lyse bacterial microcolonies. However, even on gram scales a modest proportion of local bacteria (one-third or two-fifths) appear to be sensitive to local phages while phages can be slightly more infective of more-local bacteria than of less-local bacteria (Vos et al. 2009). These observations suggest a failure of at least some local phages to drive at least some local bacteria to extinction. Two key questions therefore remain vis-à-vis our understanding of the degree to which phages can negatively impact bacterial soil communities: (1) Is phage exploitation of soil microcolonies efficiently



accomplished, i.e., are phages highly virulent on a per-microcolony basis? (2) Do phages possess the means to effectively move from microcolony to microcolony, also within soils? Principally, if phages cannot destroy microcolonies, then they cannot eliminate microcolony-forming bacterial winners even on microscale. Furthermore, if phages cannot efficiently locate new microcolonies, then even if they are highly virulent against individual microcolonies, they will not succeed in effecting kill the winner on macroscale. See Williams et al. (1987) for additional complications on our potential to comprehend phage–bacterial population dynamics in soil.

### ***2.3.3 Phage-to-Bacteria-to-Environment Communication***

In addition to phage-to-bacteria communication, phages can impact aspects of environments other than hosts, but nonetheless as mediated through their impact on bacteria. This can be accomplished via phage-induced bacterial lysis but also can be effected through prophage gene expression. Among lysis-related effects is the likely phage impact on the quantity and quality of free DNA found within environments.

#### **2.3.3.1 Lysis-Mediated Phage-Environment Communication**

Other than in terms of their own existence as virions found in the extra-bacterial environment, phages can influence environments specifically through bacterial lysis and do so in at least four basic ways. First, by effecting lysis, phages convert bacteria-associated insoluble nutrients into soluble ones that are then available primarily to heterotrophic bacteria, i.e., as described within aquatic environments (Weinbauer 2004; Suttle 2007). Within soils, though, these nutrients may also be available to eukaryotic heterotrophic absorbers, such as fungi, whose soil presence can be vast (O'Donnell et al. 2007). Another interesting break from the experience of aquatic environments is that in soils the primary ecological process carried out by microorganisms is decay, rather than the photosynthesis of many aquatic bacteria. Since bacterial lysis too represents a form of decay, of bacteria, we can describe phage lytic action not just as interfering with ecosystem productivity but also as contributing to it. Indeed, phages, by lysing bacteria, could very well play a key role in the mineralization process that decay ultimately represents. In addition, phages could play a role in the release of secondary metabolites from bacteria, adding to those released into soils through bacterial secretion (Karlovsy 2008).

A second means by which phages affect ecosystems, in the course of lysing bacteria, is by releasing internal bacterial enzymes which can hydrolyze otherwise nutritiously unavailable substrate. While I find it compelling that these so-called ectoenzymes probably play relevant and even important roles within relatively simple ecosystems (Abedon and LeJeune 2005), I am less sanguine toward accepting that possibility within soils, especially more complex, less disturbed soils

containing large diversities of decay-mediating microorganisms. Nonetheless, there remains at least a possibility that phage-released enzymes could play relevant roles in soil ecosystem ecology (see, e.g., Sect. 2.3.3.2).

The third mechanism of phage-to-environment communication, as mediated through bacterial lysis, involves the release of DNA. While this DNA can be viewed as another solubilized nutrient, released DNA if not too fragmented also can serve as a source of genetic material for bacterial transformation (Pietramellara et al. 2009). That is, certain bacteria are able to pick up environmental (naked) DNA into their cytoplasm and subsequently incorporate these “snippets” into their genomes (Day 2004). It is conceivable that the DNA pool available for this transformation is larger than it would be absent phage-mediated bacterial lysis (Abedon 2009a). To the extent that the winner operates, the DNA available upon phage-mediated lysis may either be more diverse owing to a greater assortment of bacteria which are available for lysis over time or less diverse owing to a bias toward lysis of particular (winner) populations. In addition, not only is bacterial DNA potentially released upon phage-mediated lysis, but so too is unencapsidated phage DNA, which also may be available to bacteria for transformation. In a study on DNA extraction from soils, however, *HindIII*-digested phage  $\lambda$  DNA was found to be difficult to recover, which at least in part was a consequence of DNA absorption to soil colloids such as clay (Frostegård et al. 1999).

Yet another potential consequence of phage-mediated bacterial lysis is the disruption of bacterial biofilms, microcolonies, or arrangements. Though such disruption is readily demonstrated in the laboratory (Abedon 2010; Abedon and Thomas-Abedon 2010), and there may even be augmented, i.e., as reviewed by Azeredo and Sutherland (2008), it is an open question how significant a role phages play in these processes in natural environments, such as soil. Furthermore, I am uncertain what might be the consequence of such disruption other than in terms of reduction in the competitive ability of these phage-susceptible bacteria vs. those which instead are phage resistant.

### 2.3.3.2 Prophage-Mediated Environmental Modification

Phages might also modify soil environments toward their own ends. This consideration is based on speculative analogies to phage encoding of bacterial virulence factors. These virulence factors, and encoding phages, are associated with many bacterial pathogens of animals (Abedon and LeJeune 2005; Hyman and Abedon 2008). Some phage-associated virulence factors, particularly exotoxins such as Shiga, diphtheria, or cholera toxins, can be viewed as environment-modifying enzymes. That is, the disease symptoms that these toxins effect are a consequence of their disruptive modifications of the body environment. In addition, the resulting environmental modifications might serve to enhance a phage’s replication or dissemination (Abedon and LeJeune 2005).

It is conceivable that similar factors are encoded by soil phages and expressed perhaps chiefly during lysogenic infection. These factors might modify soil

environments and do so in some manner that benefits the producing phage. For example, phages might encode enzymes whose release from bacteria can lead to the digestion of local substrate either for the sake of providing nutrients to host bacteria or to enhance the potential for phage diffusion, such as away from the lysed parental bacterium and toward not yet phage-infected bacteria. Indeed, phage-encoded depolymerases perhaps could be viewed as such enzymes (Barnet and Humphrey 1975; Abedon 2010). Phage DNA extracted from soil samples has been shown to carry exotoxins *sensu stricto*, such as Shiga toxin (Casas et al. 2006). Whether additional factors exist among soil phages, acting within soils, is however an open question.

### 2.3.4 *Phage-to-Environment Communication*

Bell (1992) discusses five general properties of environments, which roughly can be translated to that they are (1) highly variable and (2) complex, (3) that organisms respond to them inconsistently, (4) that they self regulate, and (5) that they “tend continually to deteriorate” (p. 34). The impact of phages on environments corresponds to at least the last three of these properties. That is, infections vary and have unexpected outcomes (e.g., transduction), bacterial density can be limited also by phage infection (i.e., environment self regulation), and, by lysing bacteria, phages contribute directly to environmental deterioration, in this case decay of what otherwise would be living entities (bacteria). Each of these mechanisms acts via phage infection of bacteria.

Can phage-to-environment communication also occur *without* a bacterium intermediary other than the bacteria needed to produce the phages themselves? I posit three mechanisms. First, phages can be consumed by certain eukaryotes, at least in lakes (González and Suttle 1993; Bettarel et al. 2005), and perhaps under some rare circumstances contribute to the genetic material of those organisms, i.e., the “you are what you eat” hypothesis (Doolittle 1998). Second, there exist certain virion-associated hydrolytic enzymes which, for example, can disrupt bacteria-secreted extracellular polysaccharides (Sutherland et al. 2004). Finally, phages themselves can serve as nutrients. This latter role can follow their decay and thereby solubilization, follow their consumption by eukaryotes, or, indeed, follow their adsorption to and restriction by otherwise phage-susceptible bacterial hosts (Fuhrman 1999).

### 2.3.5 *Environment-to-Phage and/or to-Bacteria Communication*

For phage biologists with an interest in phenotype, perhaps the most fascinating aspect of communication, as it occurs between phages, bacteria, and environments,

is how modifying environmental parameters can result in modification of phage phenotype. This concept we can loosely describe as a phenotypic plasticity. Basically, it represents a physiological modification of a phage infection that may or may not be adaptative. Perhaps the most familiar phage response to environmental stimulus is the induction of prophages following lysogen exposure to DNA damaging agents, such as UV or mitomycin C (Campbell 2006). This response happens to be one that is both stimulated and mediated while a phage is associated with its bacterial host. Another and similar phenomenon is the resolution of the otherwise reductive pseudolysogenic type state (Miller and Day 2008; Abedon 2009b) in which increasing host metabolic activity results in increased phage metabolic activity, producing a productive, lysogenic, or perhaps even phage-destructive infection.

With both induction of prophages and activation of pseudolysogens, the phage is potentially displaying an adaptive response to changes in environmental conditions, in both cases increasing infection activity. Alternatively, the response to a worsening of environmental conditions can be a reduction in the activity of a phage infection, or even an avoidance of adsorption altogether (Kutter et al. 1994). At an extreme, the phage could display the above-noted pseudolysogeny, a nonlysogenic, nonproductive, nondestructive, *and* nonreproductive delay in initiation of a more active infection (Abedon 2009b). Less extreme responses can involve decreases in phage burst sizes, lengthening in phage infection periods, or both. This has been observed in laboratory culture following nutrient limitation (Hadas et al. 1997) including with soil phages (Webb et al. 1982). These responses may be relevant especially to the extent that soils are oligotrophic or alternate between eutrophic and oligotrophic (feast-famine; Williams et al. 1987). Also with soil phages, Williams et al. (1987) review similar results associated with changes in temperature. Environments also can supply mutagens, some of which interact with phages while they are free, that is, not yet infecting, with mutations then observed only upon bacterial infection (Drake and Ripley 1994). Day and Miller (2008) provide a more general discussion of virion perturbability.

Another phage infection response to environmental stimulus involves detection of the presence of free phages, which make their presence known by adsorbing infected bacteria. The phage's response, when it occurs, can be an extension in the phage latent period and an associated *increase* in phage burst size (Abedon 1990). Perhaps more commonly, the response involves instead an increase in phage burst number, i.e., as can be subsequently mediated by multiple inductions of populations of clonally related phage lysogens (Abedon 2009a; Abedon et al. 2009). That is, higher phage multiplicities of infection can give rise to higher likelihoods of temperate phage reduction to lysogeny (Weitz et al. 2008) which, via binary fission, can produce a population of clonally related, potentially productive phage infections. In terms of the study of phages in soil, or any environment for that matter, the key take-home message is that phage characteristics can change in response to changes in environmental conditions, whether *in situ* or in comparing *in situ* conditions to those in the laboratory. In addition, even when held in constant, well-defined environments, phages and bacterial hosts can be expected to evolve, and often not independently of each other (Brockhurst et al. 2007).

### 2.3.6 *Environment-to-Phage Communication*

Soil components, in communicating their presence, can impact phage movement, survival, and reproduction. For this final discussion, however, I ignore two environmental aspects: First is the impact on phages of their bacterial hosts, which I specifically considered in Sect. 2.3.1. Second is phage–phage communication, e.g., such as via genetic recombination, which I mostly avoid here as genomic or phylogenetic concerns, or, as involving various sorts of antagonistic interactions which are reviewed elsewhere (Abedon 1994; Turner and Duffy 2008; Abedon et al. 2009). I instead concentrate on phenomena originating from nonhost and nonphage environmental aspects. That is, predation of phages along with mechanisms giving rise to phage virion movement, degradation, and durability.

#### 2.3.6.1 **Predation of Phages**

Soil or soil-contaminated materials ingested by animals likely will contain phages, given phage ubiquity. The ingested phages may be digested along with other organic matter, except to the extent that they are resistant to digestive processes. One can envisage, for example, phage loss as a consequence of earthworm action, as well as from protist engulfment (Sect. 2.3.4). It seems unlikely, though, that phages would contribute greatly to either's nutrient needs. Predatory bacteria, such as *Myxococcus*, secrete hydrolytic enzymes as groups to obtain nutrients from soil-associated organisms, materials, and, potentially, even phages (Berleman et al. 2006; Evans et al. 2007); of course, as *Myxococcus* spp. are bacteria, there also exist phages which are capable of infecting them (e.g., Azuaga et al. 1990), and see also Zeph and Casida (1986). Other, more sedentary organisms, such as fungi, though not necessarily a major contributor of soil proteases (Watanabe and Hayano 1994), nonetheless could potentially affect phages.

#### 2.3.6.2 **Phage Movement**

Many things can contribute to phage movement, though in soils mixing is limited or, at least, extremely slow. Diffusion and fluid flow, by contrast, should be major contributors to phage movement in soil. Nonetheless, as soil colloids, phage movement from location to location within soil, or in terms of penetration into partially closed off volumes, should be expected to be *limited* in comparison with dissolved materials or even soluble enzymes (McKay et al. 2002). These limitations are especially as compared with the potential for phage movement given less spatially structured environments, or if a phage should happen to infect a motile bacterium.

Given sufficient water, then fluid flow also can take place through soils, such as through “cracks” (Choi et al. 2004), “fractures,” or “root holes” (Blanc and Nasser

1996), i.e., so-called bypass flow and finger flow (McLeod et al. 2001). The consequence can be phage transport from place to place without substantial interaction between phages and the soil matrix. At an extreme, groundwater, like surface water (Ferguson et al. 2007), may allow phage movement over meters, at least (Bales et al. 1995; McKay et al. 2002). Both diffusion and flow, however, may be inhibited by various obstructions (e.g., Davis et al. 2006; Van Cuyk and Siegrist 2007; Wong et al. 2008). These obstructions include especially colloidal substances to which phages can be absorbed, particularly clays (Duboise et al. 1979; Williams et al. 1987; Chattopadhyay and Puls 2000; Hassen et al. 2003; Day and Miller 2008; but also see Bixby and O'Brien 1979, and Armon chapter in this volume).

Animals also can play a role in the movement of phages, in part if phages can survive ingestion, but perhaps more likely with phages nonspecifically adhering to animals which are moving through soils, or through specific or nonspecific adherence between phage-infected bacteria and animals (Dennehy et al. 2006). Bulk movement of soils also occurs, such as a consequence of mechanical action, e.g., due to trees falling, the surface locomotion of relatively large animals, burrowing by animals in general, growth of plant roots, freeze-thaw cycles, gravity (mediating, for example, landslides), anthropogenic disturbances, etc. Soil-borne phages probably also spread from location to location through the air (Weinbauer 2004) and a number of papers consider such movement especially from the perspective of sewage aerosolization, e.g., Brooks et al. (2004) who point out (p. 8), "It is known that a bioaerosol is subject to intense physical pressures from the environment (specifically low humidity, ultraviolet and temperature extremes), which tend to inactivate microbes during transport of bioaerosols over long distances." See also (Clark 2005).

### 2.3.6.3 Phage Survival

Soils can be protective of phages such as from UV irradiation or otherwise as a function of phage absorption onto soil particles (Vettori et al. 2000 along with references cited). In addition, temperature and pH extremes can be buffered in soils, such as in comparison to water (pH; Tan and Reaney 1976) or air (temperature). That phages must display at least some virion durability in soil environments is speculated by Williams et al. (1987) who suggest (p. 162), "There is evidence that most soil bacteria have only spasmodic periods of activity in micro-sites dispersed within the soil mass... Therefore, it is likely that virulent phage in the absence of an active susceptible host must exist for considerable periods as free virions in the soil and be subjected to environmental factors and fluctuations." They then go on to provide a review of the evidence from which this position is derived. Phage durability also may be enhanced through lysogenic or pseudolysogenic infection (Stewart and Levin 1984; Williams et al. 1987; Miller and Day 2008; Abedon 2009b).

In many cases, by contrast, the impact of soil residence on phages can be negative (Williams et al. 1987; Day and Miller 2008). The latter can be a consequence of temperature or pH extremes and can vary with soil type, organic matter prevalence, electrolyte concentrations, and what organisms are present; see Williams and Lanning (1984), Song et al. (2005), and Davies et al. (2006) for data and references. Notwithstanding tendencies toward phage instability at higher temperatures, phages have been detected in surface sands of the Sahara Desert, though survival characteristics there were not determined (Prigent et al. 2005). Desiccation, of course, can also be a concern, especially for those phages which are less desiccation resistant, though there is evidence that for phage PRD1, a coliphage, there may exist an optimal soil-moisture content that confers extended survival (Song et al. 2005). Hydrolytic enzymes excreted by soil microorganisms, as noted (Sect. 2.3.6.1), also may degrade soil phages. McKay et al. (2002) suggests lodging of phage particles within tight pores or fractures as another possible phage loss mechanisms (so-called “straining”) plus lists various other blocks on phage movement.

## 2.4 Conclusion

In this chapter, I strive to educe an expansive view of phages, bacteria, and soil, and how these entities communicate, especially as pathways of communication involve phages. I have attempted to identify broad principles rather than narrowing in on mechanisms that are specific to particular soil types, horizons within soils, biomes, phage–bacterial systems, etc. This has been done in part because those specifics, as derived from a very soil-centered point of view, as opposed to bulk phage or bacteria-centered perspectives, are somewhat lacking in the phage literature. However, I have also taken this broader perspective for the sake of presenting a guide to the range of questions that may be addressed for phages and communication within soils, or indeed any environment. That is, to achieve anything close to a comprehensive understanding of the phage role in soil environments there needs to be an understanding of phage biology, as it occurs within soils, at microscales, and in terms of the spatial and temporal complexity as well as heterogeneity which are the hallmarks of soil ecosystems.

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