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Bacterial Biodiversity in Natural Environments

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1. Introduction

Increased accessibility to the technologies for high-throughput sequencing has revealed the diversity and dynamism of bacterial genomes. It is now known that variation in gene content between bacterial strains may encompass 30–35% of the genes in the genome. Because this genetic diversity and genome variability triggers the emergence of pathogens as well as novel metabolic capabilities in the newly originated strains, there are implicit consequences to human health and the economy. Equally, genomic flexibility is understandably an impacting factor for bacterial populations because of the important role in their evolution and speciation. Conversely, in natural environments, bacteria species are constantly exposed to chemical, physical, and trophic gradients, as well as intra- and inter-specific interactions that may play an additional role in shaping bacterial biodiversity.

More specifically in interactions between bacteria and hosts, it is well accepted that the bacterial counterpart are highly susceptible to genetic changes. They usually have increased generation times when compared to eukaryotic organisms, and are genetically more diverse (Steinert et al., 2000). These aspects, in addition to the production of extremely large populations, allow bacterial species to be efficient at acquiring novel metabolic traits that facilitate their success in colonizing new environments.

Highly controlled processes of genetic regulation and genetic diversity are responsible for the ability of bacteria to live and survive under environmental conditions that are continuously changing. Processes that give rise to the genetic variability in bacteria are ultimately responsible for bacterial adaptation. Such processes are represented by point mutations, homologous recombination, and horizontal gene transfer events. Genetic and phenotypic variation is more frequently observed among bacteria since they are haploid organisms and are more susceptible to such changes that are not masked by recombination.

2. Horizontal/lateral gene transfer and biodiversity

Horizontal or lateral gene transfer (HGT or LGT) is one factor, if not the most important mechanism, influencing genomic variability and diversity in bacteria. New research efforts have recognized the importance of this process and aim to understand the rates of genetic exchange in bacterial species in natural settings. Whole genome analysis has corroborated that bacterial evolution may occur by horizontal gene flow between a range of species and genera. The current section briefly describes the role of gene transfer processes between

various bacterial species, and whether this influences microbial biodiversity in a variety of ecological niches in natural environments.

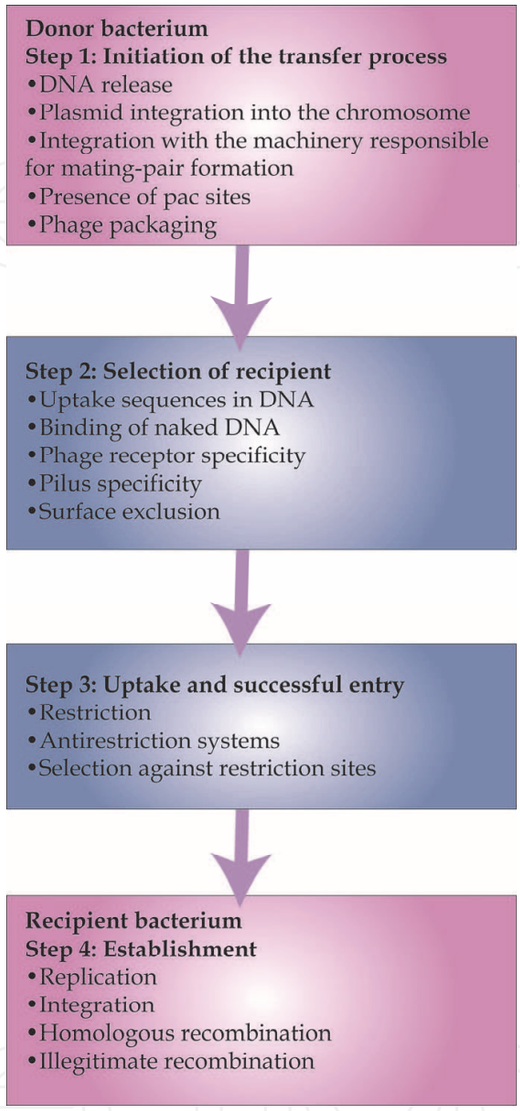

Fig. 1. Modified from Thomas & Nielsen (2005). This figure outlines the steps that take place during transfer of DNA from a donor to a recipient bacterium. The process starts with the availability of DNA from the donor cell and ends with DNA being acquired permanently by the recipient bacterium.

HGT has been observed in a wide variety of species, both in the Archaea and Bacteria domains (Smets & Barkay 2005). A number of mechanisms have accounted for the amount of transfer in specific groups, namely gene acquisition, homologous recombination, and orthologous replacement (Boucher & Stokes 2006). These processes are particularly important for changing the ability of an organism that is "clonal" and never changing, to one that has newly acquired traits that allow adaptation, speciation, and evolution to a new ecological niche. Numerous studies have documented the similarity between species of

bacteria based on phylogenetic analysis of specific genes. For example, the HMG-coenzyme A reductase gene (*mvaA*), responsible for lipid metabolism, is found in a number of *Vibrio* species and was likely transferred from an archaeal donor, since mevalonate biosynthesis/degradation is an archaeal trait (Boucher & Doolittle 2000). Likewise, studies analyzing metabolic networks in *Escherichia coli* have demonstrated that particular changes are due to HGT, with very little contribution from gene duplication events (Pal et al., 2005). These changes can be linked to bacterial response to the environment, particularly when the change requires some specific metabolic capability allowing the organism to adapt more quickly to the selection imposed by the surrounding habitat. Such HGT events are usually driven by newly acquired genes that are coupled by their enzymatic pathways (*i.e.*, operons), which allow processes such as transport and degradation of external nutrients, or accommodation of an abiotic pressure (temperature, salinity). Interestingly, most HGT loci that are environment-specific are not expressed under normal laboratory conditions, demonstrating that selection of HGT loci is in part driven by adaptation to novel environments (Pal et al., 2005). This supports that HGT is a mechanism that is probably more common in natural environments than previously thought; indeed, when analyzing genes that are physiologically coupled, their functions are specific for certain environmental conditions (*i.e.,* arabinose or mannitol uptake; (Pal et al., 2005; Thomas & Nielsen 2005).

HGT has also been examined via phylogenetic reconstruction, where similar suites of genes that group together do not have a common ancestor (Gogarten & Townsend 2005). Unexpected phylogenetic distributions can therefore be explained as either HGT or an ancient gene duplication followed by differential gene loss. Oftentimes, deep-branching lineages with commonly used loci (rRNA) may also contain artifacts that are exhibited during phylogenetic reconstruction, and may provide discordance when compared to less conserved (faster adapting) molecules. This can be observed in genes that experience little or no purifying selection and are oftentimes saturated with substitutions, resulting in little phylogenetic information (Gogarten & Townsend 2005). Interestingly, examining the ratio of non-synonymous to synonymous substitutions (K_a/K_s) between *E. coli* and *Salmonella enterica* demonstrated that most horizontally acquired genes were under purifying selection, despite the K_a/K_s ratio being higher than other *E. coli* genes (0.19 vs. 0.05; (Daubin & Ochman 2004). Another example of this "neutral" selection is found in *Vibrio splendidus* (Thompson et al., 2005), where diversity at the genome level is huge compared to the sequence divergence at the 16S rRNA locus. Genome size differed between 4.5 and 5.6 Mb, eluding that there are multiple subpopulations that have unique ecological niches, despite that most of the HGT events are neutral to the recipient. If HGT events are rare, they have the probability of becoming fixed (due to selective sweeps), and are not detected under modern molecular analysis (Gogarten & Townsend 2005). Thus, in contrast to network modeling predictions, HGT may be selectively filtered against in order to deter any novel deleterious functions that may override adaptive advantages to a novel environment.

Clearly, the acquisition of genes through HGT is a much quicker and effective way for an organism to adapt to changing environments rather than their evolution via natural selection (Smets & Barkay 2005). This can be supported by observations of beneficial gene acquisition, such as antibiotic resistance, degradation pathways for xenobiotics, and bioremediation. But such observations may not be driven by environmental change alone; specific gene cassettes or mobile genetic elements may be augmented due to the increased

presence of substrates that are useable by such organisms. Recently, there have been *in vitro* experiments on microbial communities to determine whether HGT events are induced by changes in environmental conditions through plasmid transfer (Sorensen et al., 2005). Such studies have allowed the detection of environmental hotspots that influence the rate of transfer via conjugation. Combining this experimental information with mathematical models (Sorensen et al., 2005) that utilize variables such as the rate of transfer, formation of new conjugants, density of donors and recipients, cell growth, and plasmid loss in homogeneous and mixed communities will be helpful in determining whether HGT is an important mechanism for driving ecological adaptations. This is particularly important in epidemics where pathogenic bacteria are more increasingly virulent. Since HGT events basically drive the evolution of bacterial "chimeras", categorizing whether a particular strain or species is genetically similar is becoming more and more difficult with modern technology (Gevers et al., 2005). The combination of both genetic background and ecological specificity will undoubtedly be the future criteria used for understanding how HGT drives microbial evolution in natural populations.

3. The role of bacterial viruses in bacterial biodiversity

In addition to the inter-specific relations that occurs within bacterial populations in nature, the association between bacteria and their viruses (bacteriophages or phages) is, quantitatively speaking, the dominant host-pathogen relationship in nature (Calendar 2006). Interactions between bacteria and phages are also expected to be particularly important, owing to the considerably fast rates of evolution of the two counterparts, the essential role bacterial communities play in ecosystem dynamics, and the emerging interest on phages as an alternative to antibiotics in the control and treatment of bacterial infections in agricultural and clinical settings (Levin & Bull 2004). More importantly, recent studies on soil bacteria and their phages have demonstrated that ecological interactions alone are not sufficient to explain the structure, population dynamics, and function of microbial communities in nature, but that rapid coevolution of bacteria and bacteriophages is also indispensable (Gómez & Buckling 2011).

Bacteriophages (also known as phages) are viruses that infect bacteria. They are widespread, with many known groups existing and found in abundance in open and coastal waters, sediments, soils, and animal tissues (Ackermann 2003). Their general life cycle (Fig. 2) varies between phage families, but generally involves adsorption, infection, and release from the host (Calendar 2006). During this cycle of phage production, the cell's metabolic machinery is reprogrammed to continually produce new phage particles with the components of the biosynthetic apparatus rerouted from basal tasks necessary for bacterial growth (Campbell 2003).

Among bacteriophage groups, infection by temperate bacteriophages often results in modification of existing properties or the acquisition of new capabilities in the bacterial host (Waldor 1998). Bacteriophages are able to integrate within the host genome during infection (a process known as lysogenic conversion), making them accountable for bacterial adaptation to new niches (Canchaya et al., 2003) and known contributors to host virulence (Rajadhyaksha & Rao 1965; Takeda & Murphy 1978; Waldor & Mekalanos 1996; Lee et al., 1999; Oakey & Owens 2000). In actuality, the process of lysogenic conversion is a key player in the evolution of Gram-positive and Gram-negative pathogens.

By definition, lysogeny is the process by which bacteriophage genome is stored in a quiescent state within the genome of a host bacterium (lysogen) (Canchaya et al., 2003). During this harboring period, transcription of the phage (temperate) genome does not take place, allowing the bacterial host to remain functional. Activation of phage transcription at this time would result in cell death (Campbell 2001). Exchange of genetic material from the virus to the bacteria can be so all-encompassing that bacteriophages have become recognized as considerable, if not the most important drivers of bacterial evolution (Krisch 2003). Temperate phages are thought of as important players in bacterial evolution because of their ability to establish long-term genetic symbioses with their host bacterium (Abedon & Lejeune 2005).

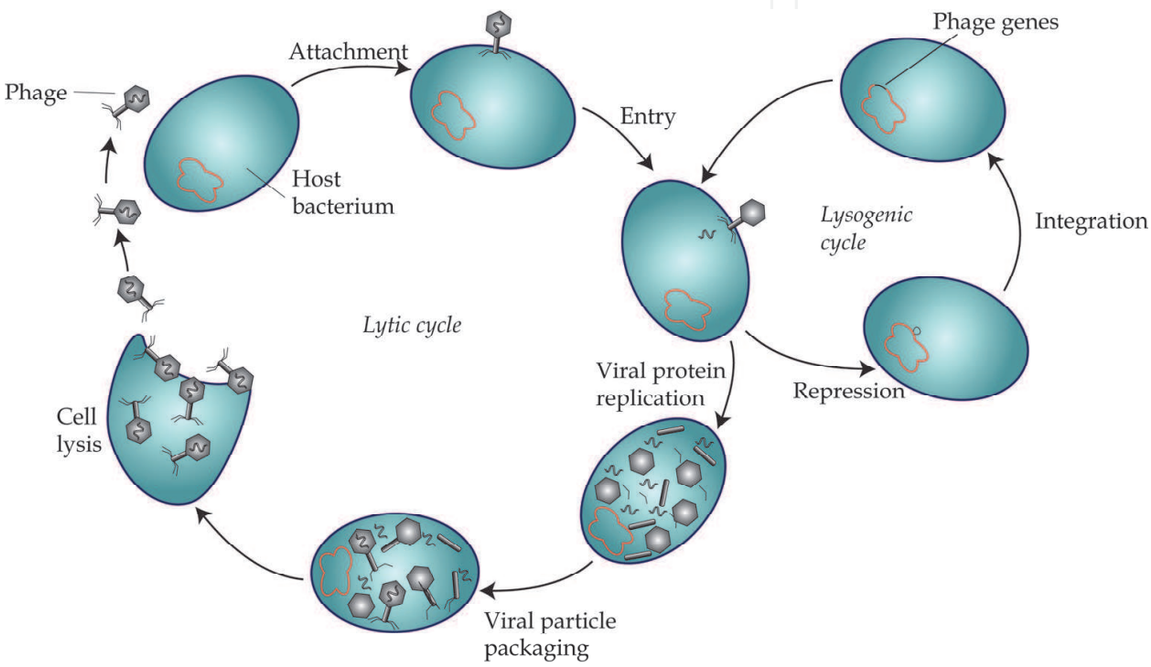

Fig. 2. Basic Phage life cycle, modified from Campbell (2003). Adsorption includes extracellular search (diffusion-mediated), random encounter between phage and host bacterium, attachment of phage to bacterium via a specific receptor, and injection of nucleic acids into the bacterial cytoplasm. This figure represents infection by a temperate phage. Phage development is temporarily repressed and phage DNA integrates into the bacterial chromosome (lysogenic cycle). Virulent phages, as well as temperate phages during their lytic cycles assemble by means of the bacterial metabolic machinery. Lastly, the cell lyses for phage progeny release.

These types of genetic associations have severe consequences in human populations owing to the variety of bacterial virulence factors that are known to be of prophage origin (Brussow et al., 2004). Among others, human diseases such as botulism, diphtheria, cholera, and *E. coli* associated conditions are virus mediated. For a more comprehensive review of prophage associated diseases please refer to (Boyd et al., 2001; Boyd & Brüssow 2002; Brussow et al., 2004).

In a recent work by Canchaya et al. (2004) it was determined that prophages are particularly abundant in the genomes of bacterial pathogens. As expected, the authors confirmed that

the presence of these prophages was in most cases responsible for encoding virulence genes and that the phenotypic characteristics that allow a strain its "uniqueness" within a bacterial consortia were contributed by the viral genome. However, this observation is not unique to pathogenic bacteria since other types of symbioses may require the bacterium to acquire particular functions to successfully colonize a host. For instance, in the gut commensal *Lactobacillus johnsonii*, it has been demonstrated that prophage derived genetic material contributes to approximately 50% of strain-specific DNA (Ventura et al., 2003).

Mechanistically, it would not be beneficial for a bacterium to fix an entire prophage genome. On the other hand, phage-derived functions that have been co-opted by the host bacterium would very likely be subjected to fixation (Casjens 2003). This makes sense considering that new ecological niches can be exploited by a bacterial species more rapidly with the acquirement of genetic material in the form of mobile DNA of phage origin. Genes of viral origin that are of no intrinsic evolutionary value to the bacterium are consequently expected to be deleted (Casjens 2003; Brussow et al., 2004). Considering that a very small amount of prophage DNA is found in the bacterial chromosome, this raises the question of why phages do not accumulate in large numbers in most cases. Campbell (2001) suggested that some genes may remain phage-borne instead of being incorporated into the bacterial genome when the host does not benefit constantly, but rather intermittently, from the product of these genes.

Prophages from bacterial pathogens that encode virulence factors have two situations that are observed (Brussow et al., 2004). Firstly, a phage-encoded toxin could be directly responsible for causing the specific disease. This is the case of *Vibrio cholerae*, Shiga toxin-producing *Escherichia coli*, *Corynebacterium diphtheriae*, and *Clostridium botulinum* (Abedon & Lejeune 2005). Conversely, the bacterial host may carry more than just the prophage material, and each phage-encoded factor contributes incrementally to the fitness of the host (either by direct contribution to fitness or by causing disease).

4. The role of biofilms in bacterial biodiversity

It is widely understood that most bacteria found in natural environments, as well as clinical and industrial settings, exist in biofilms. These are complex communities of microorganisms attached to surfaces or to the tissues of specific hosts, or any substrate with the adequate supply of nutrients and water (Costerton et al., 1987). These surface-associated communities are often composed of more than one species that interact with one another and their environment, and are distinct from bacteria growing in a free-living, planktonic state (Stewart & Franklin 2008).

Biofilm formation has evolved as a strategy of bacteria to establish themselves as a substrate-associated community in the environment or to become more persistent and less invasive to a host, while simultaneously taking advantage of the availability of nutrients found in those settings. The biofilm state is considered the stable period in a biological cycle that is comprised of several steps, namely initiation, maturation, maintenance, and dissolution (Fig. 3). Cells initially attach to a surface, which in most cases requires swimming motion generated by rotating flagella, and is initiated in response to specific environmental stimuli, such as nutrient availability. In most cases, the organisms undertake a series of physiological and morphological changes, transitioning from free-living, planktonic cells to non-motile, surface-attached cells. Biofilms continue to persist and grow for as long as the nutrient requirements are met. Once they are nutrient deprived, the cells separate from the surface and initiate to a free-living state (O'Toole et al., 2000).

Due to the variations in environmental conditions within the biofilm, represented by both chemical and biological heterogeneity, members of a biofilm community are subject to different selective pressures according to their location within the biofilm matrix. Therefore, bacterial cells not only express phenotypic traits that allow adaptation for growth in these surface-associated communities (as opposed to planktonic growth), but they also display phenotypic variability that allows them to thrive within a chemically heterogeneous environment.

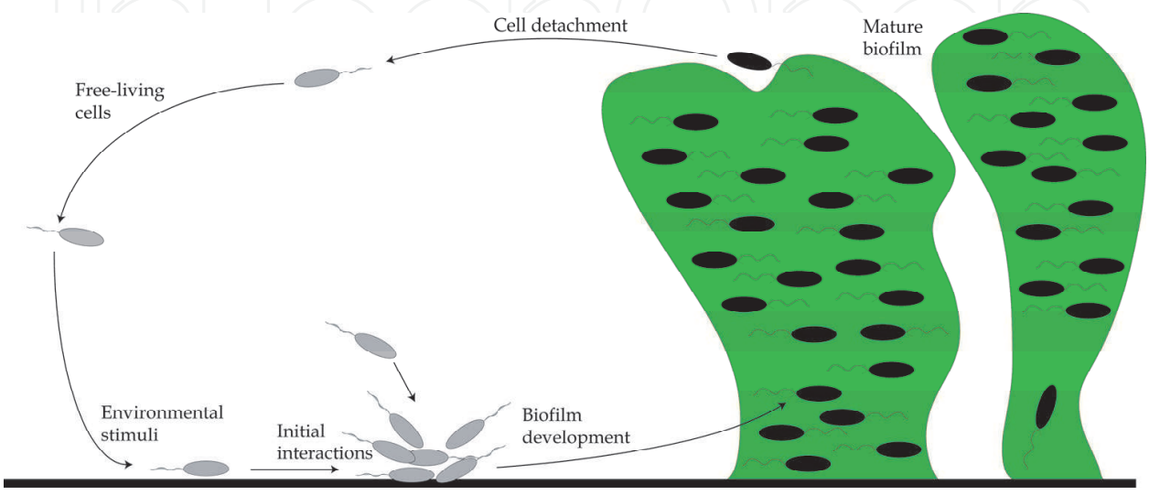

Fig. 3. Model of biofilm development. Modified from O'Toole et al. (2000). Free-living cells establish contact with other cells or with surfaces, which results in the formation of microcolonies and further maturation of the biofilm matrix. Cells from a mature biofilm can go back to a planktonic lifestyle to complete the cycle of biofilm formation.

It is expected that the chemical variability within a biofilm matrix would lead to considerable variability in the physiology of the cells that occupy the various areas within the community (de Beer et al., 1994; Xu et al., 1998). As observed in liquid cultures *in vitro,* where varying growth conditions such as temperature, aeration, and nutrient availability may impair the ability of the bacteria to grow, it is not surprising that limiting conditions within specific regions of a mature biofilm may slow or even completely stop bacterial growth and activity (Chavez-Dozal & Nishiguchi 2011). Also, metabolic waste accumulation would have an effect on the physiological state of the bacteria, mostly by changes in pH within the matrix (Stewart & Franklin 2008).

One important aspect affecting the success of a multi-species biofilm community is the ability of each member of the consortium to adapt to the presence of a second species. In a two-species community (*Acinetobacter* sp. (strain C6) and *Pseudomonas putida* (strain KT2440)), Hansen et al. (2007) demonstrated that selection in an environment such as a biofilm leads to the evolution of unequal interactions. Specific mutations in the genome of one species lead to adaptation to the presence of the other. The resulting community proved to be more successful in stability and productivity, than the ancestral community. This indicates that simple mutations due to the interactions in the biofilm generated a more intimate and specialized association.

Biofilms are ideal for the exchange of genetic material of various origins (bacterial or viral). Several studies have also demonstrated that bacterial conjugation (horizontal transfer of

genetic material between two cells by physical contact) occurs within biofilms (Christensen et al., 1998; Hausner & Wuertz 1999) and this process is known to have a high impact in the evolution of bacterial lineages (Ochman et al., 2000). In a study of *E. coli* K12 biofilms, Ghigo (2001) studied how conjugative plasmids directly contribute to the ability of a bacterial cell to establish a biofilm. In this study, the author demonstrated that natural conjugative plasmids expressed factors that promote the transition of the bacteria to a biofilm forming state from a free-living state, and argued that this process supports the infectious transfer of the plasmid. Considering that antibiotic resistance is carried by bacteria through conjugative plasmids, the use of antibiotics and biocides in clinical and agricultural settings may have promoted the selection for resistant strains (bearing specific plasmids) that are more likely to form a biofilm.

It is clear that in order to be successful in the environment, a bacterial community needs to be efficient in growth and reproduction. However, it is equally important to be able to avoid, tolerate, and defend themselves against natural predators. Most studies on bacterial predation have looked at the strategies they use to increase their survival under grazing pressure by protozoans (Matz & Kjelleberg 2005). Among these adaptive traits, cell surface properties (Wildschutte et al., 2004), motility (Matz & Jurgens 2005), microcolony establishment, and quorum sensing (Matz et al., 2004) are the most studied and their results suggest that grazing by protozoans is an important contributor to bacterial diversification and to the selection of specific adaptations to defend themselves against predators. Biofilm formation has therefore emerged as an adaptive response to flagellate predation. Previous results (Matz et al., 2004) have demonstrated that *Pseudomonas aeruginosa* cells transition into a microcolony forming state upon encounter with a predator. These cell conglomerates reach a size that is beyond the prey size of the protozoan. In addition, mature biofilms build up acute toxicity to the flagellate predator via quorum sensing-mediated up-regulation of lethal compounds.

Bacterial-host interactions during mutualistic symbiosis are another, well studied example of associations in which bacteria utilize adaptive strategies of survival and reproduction in order to fight the normal defense mechanisms of the host (McFall-Ngai 1994; McFall-Ngai 1998). Similar to virulence determinants in bacteria which are regulated in their expression by both environmental and host factors (Heithoff et al., 1997; Soto et al., 2009), many novel genes are selectively expressed during the establishment and persistence of a mutualistic association (Jones & Nishiguchi 2006; Guerrero-Ferreira & Nishiguchi 2010). An example of this type of association is the mutualistic interaction between *Vibrio fischeri* and the bobtail squid *Euprymna scolopes.* It is understood that the bacterial symbionts are able to establish themselves within the host tissue by forming biofilm in the epithelium-lined crypts of the squid light organ. This was demonstrated by Ariyakumar & Nishiguchi (2009), where *V. fischeri* mutants with a reduced ability to form biofilm in vitro were unable to successfully colonize squid light organs and were not detected in any section of the crypt region.

Biofilms are the leading cause of contamination of medical devices and in industrial and agricultural settings. The initial adhesion and further colonization of bacteria onto solid surfaces is essential for biofilm formation, and therefore is the cause of infections of material of biological or medical use (Shemesh et al., 2010). Formation of microcolonies within a biofilm facilitates genetic exchange, favors genetic diversity, and promotes phenotypic variability within bacterial communities. Further understanding of these phenomena is necessary to understand the mechanisms bacterial communities utilize to infect and persist

in humans and other organisms and surfaces. Deciphering the factors that control bacterial diversity will not only permit a more vigorous model of bacterial evolution and speciation but also a more comprehensive analysis of the likelihood of emergence of new biofilm-forming infectious agents.

5. Conclusion

Bacterial diversity in natural populations is continually being revitalized and revisited due to the availability of whole genomes, *in situ* measurements of HGT, and manipulation of regulatory genes that are influenced by changes in the natural environment. It is especially important to consider the diversity of bacteria, and what selection pressures have driven the evolution of species or strains that can accommodate such a wide ecological breadth. Combining phylogenetics, metabolic networks, models of HGT, and phenotypic characterization of ecotypes, will help provide meaningful explanations of how bacteria can adapt so quickly to specific abiotic and biotic factors, and what forces are important to create the diversity of microbes we observe today.

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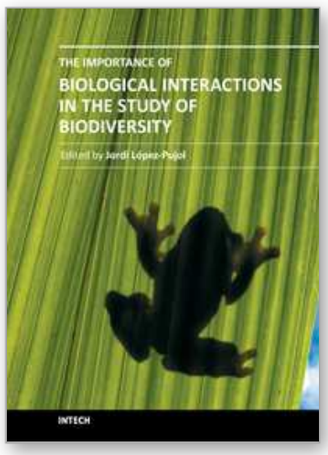

The Importance of Biological Interactions in the Study of Biodiversity

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The term biodiversity defines not only all the variety of life in the Earth but also their complex interactions. Under the current scenario of biodiversity loss, and in order to preserve it, it is essential to achieve a deep understanding on all the aspects related to the biological interactions, including their functioning and significance. This volume contains several contributions (nineteen in total) that illustrate the state of the art of the academic research in the field of biological interactions in its widest sense; that is, not only the interactions between living organisms are considered, but also those between living organisms and abiotic elements of the environment as well as those between living organisms and the humans.

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