Review

The pig gut microbial diversity: Understanding the pig gut microbial ecology through the next generation high throughput sequencing

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ABSTRACT

The importance of the gut microbiota of animals is widely acknowledged because of its pivotal roles in the health and well being of animals. The genetic diversity of the gut microbiota contributes to the overall development and metabolic needs of the animal, and provides the host with many beneficial functions including production of volatile fatty acids, re-cycling of bile salts, production of vitamin K, cellulose digestion, and development of immune system. Thus the intestinal microbiota of animals has been the subject of study for many decades. Although most of the older studies have used culture dependent methods, the recent advent of high throughput sequencing of 16S rRNA genes has facilitated in depth studies exploring microbial populations and their dynamics in the animal gut. These culture independent DNA based studies generate large amounts of data and as a result contribute to a more detailed understanding of the microbiota dynamics in the gut and the ecology of the microbial populations. Of equal importance, is being able to identify and quantify microbes that are difficult to grow or that have not been grown in the laboratory. Interpreting the data obtained from this type of study requires using basic principles of microbial diversity to understand importance of the composition of microbial populations.

In this review, we summarize the literature on culture independent studies of the pig gut microbiota with an emphasis on its succession and alterations caused by diverse factors.

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1. Introduction

The mammalian gastrointestinal tract (GIT) has been estimated to contain 500–1000 bacterial species that constantly interact with the host and other members of the microbial community. The microbiota of GIT, the collection of microbe living inside the gut, is estimated to be composed of approximately 10^{14} bacteria (Savage, 1977; Xu and Gordon, 2003). The term "microbiome" is used to describe the totality of the microbes, their genetic elements (genomes including extrachromosomal elements), and the environmental interactions in a particular environment (Dubos et al., 1965). Frequently the term "microbiome" has been restricted to bacteria (Holmes et al., 2008; Isaacson and Kim, 2012). The genetic diversity of the microbiota in the mammalian GIT is very large. The gut microbiota may contain more than 100 times the number of genes in mammalian genome and has the potential to add numerous biological activities that the host lacks (Backhed et al., 2005).

The interactions between the microbiota and the host were postulated by Dubos et al. (1965) who suggested that the host and its microbes coevolved. The intimate interactions that occurred between host and microbes resulted in a give and take that drove anatomical and functional evolution of the GIT. As such, the indigenous microbiota within the GIT is known to provide important benefits to its mammalian host (Berg, 1996). For instance, the mammalian distal intestine is a bioreactor containing anaerobic bacteria that are capable of degrading a variety of otherwise indigestible polysaccharides (Backhed et al., 2005). The gut microbiota is known to provide other beneficial functions for the host including the re-cycling of bile salts, production of vitamin K, and the production of exogenous alkaline phosphatases (Yolton and Savage, 1976; Gilliland and Speck, 1977; Ramotar et al., 1984). The gut microbiota is also an essential stimulus that results in the maturation of the animal's gut immune system (Berg, 1996; Bik, 2009).

Because most of the bacterial species that comprise the animal intestinal microbiota have not been cultured, it has been difficult to extensively explore microbial diversity in the healthy gut using the culture-dependent methods. Even though culture based systems to explore gut bacterial diversity have been important in determining the major groups of bacteria in the gut, the vast majority of the gut bacteria have never been grown outside the gut. It has been estimated that at least 50% of microbiota of GIT cannot be grown outside the gut (Shanahan, 2002; Sears, 2005). Therefore, using culture dependent methods, the composition and roles of gut bacteria have not been comprehensively defined. Using high throughput DNA sequencing the composition and distribution of the microbiota are only now being extensively described.

In-depth descriptions of the gut microbiota are being facilitated by using high throughput DNA sequencing of 16S r RNA genes. The use of the 16S rRNA gene has become the de facto tool to determine taxonomic identities of bacterial populations and the sequence data provides a means to extensively describe the gut bacteria when coupled with a variety of bioinformatics tools (Woese and Fox, 1977; Schuster, 2008; van Dijk et al., 2014). Thus, these technical developments have provided the tools to comprehensively study the composition of microbial populations in the gut. The diversity of the gut microbiota and its related functions can be described in-silico using diverse tools and observations used in the study of microbial population ecology. Deciphering the sequences of 16S rRNA genes and its aggregate genetic information requires base line knowledge of sequencing techniques, normal bacterial composition in a certain niche, and basic principles of microbial ecology.

The objective of this review is to provide details of the pig gut microbial community. Important questions concerning the pig gut microbial diversities will be discussed.

2. 16S rRNA genes to determine taxonomic identity

The pioneering work of Carl Woese, who studied the sequences of bacterial 16S rRNA genes, led to the understanding that the 16S rRNA gene could be used to infer taxonomic designations for bacteria (Woese and Fox, 1977; Fox et al., 1980). Woese et al. showed that prokaryotes could be classified into two distinct groups: Bacteria and Archaea, based on differences in their 16S rRNA genes (Woese and Fox, 1977). Using constructed recombinant clone libraries, Olsen et al. showed that the sequences of the 16S rRNA gene could be used to describe complex microbial structures (Pace et al., 1986; Olsen et al., 1986). The 16S rRNA gene is unique in that it is present in all prokaryotes and is structurally composed of multiple conserved sequences that are maintained in all species and that flank unique hyper variable regions. The hypervariable regions correlate with species (Van de Peer et al., 1996; McCabe et al., 1999). In its simplest implementation, physical methods such as denaturing gradient gel electrophoresis coupled with the subsequent cloning and sequencing of the 16S rRNA gene can be used to differentiate between different bacterial species (Nocker et al., 2007). Recently, next generation sequencing has provided 16S rRNA gene sequence reads that can be further analyzed to provide in depth bacterial taxonomic assignments (Claesson et al., 2010; Liu et al., 2012; van Dijk et al., 2014).