

# Diversity, distribution and sources of bacteria in residential kitchens

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## Summary

**Bacteria readily colonize kitchen surfaces, and the exchange of microbes between humans and the kitchen environment can impact human health. However, we have a limited understanding of the overall diversity of these communities, how they differ across surfaces and sources of bacteria to kitchen surfaces. Here we used high-throughput sequencing of the 16S rRNA gene to explore biogeographical patterns of bacteria across > 80 surfaces within the kitchens of each of four households. In total, 34 bacterial and two archaeal phyla were identified, with most sequences belonging to the *Actinobacteria*, *Bacteroidetes*, *Firmicutes* and *Proteobacteria*. Genera known to contain common food-borne pathogens were low in abundance but broadly distributed throughout the kitchens, with different taxa exhibiting distinct distribution patterns. The most diverse communities were associated with infrequently cleaned surfaces such as fans above stoves, refrigerator/freezer door seals and floors. In contrast, the least diverse communities were observed in and around sinks, which were dominated by biofilm-**

**forming Gram-negative lineages. Community composition was influenced by conditions on individual surfaces, usage patterns and dispersal from source environments. Human skin was the primary source of bacteria across all kitchen surfaces, with contributions from food and faucet water dominating in a few specific locations. This study demonstrates that diverse bacterial communities are widely distributed in residential kitchens and that the composition of these communities is often predictable. These results also illustrate the ease with which human- and food-associated bacteria can be transferred in residential settings to kitchen surfaces.**

## Introduction

Of all locations in our homes, kitchens are among the most heavily colonized by bacteria, and are likely where we are exposed to the broadest diversity of microbes (Scott *et al.*, 1982; Ojima *et al.*, 2002a,b; Sinclair and Gerba, 2011). Microbial exposures arise both directly, from handling, preparing and eating food, and indirectly, from contact with surfaces that harbour microbes derived from a range of potential sources, including humans, food and aerosolized water (Scott, 2000; Mattick *et al.*, 2003; Medrano-Felix *et al.*, 2011). Although it is well known that food items can harbour pathogenic bacteria (e.g. *Campylobacter*, *Salmonella*, *Listeria*) (Heaton and Jones, 2008; Luber, 2009; Berger *et al.*, 2010), and that proper kitchen hygiene is critical for minimizing the spread of such disease-causing organisms (Rusin *et al.*, 1998; Cogan *et al.*, 1999; 2002; Scott, 2000), the vast majority of bacteria on kitchen surfaces are likely harmless. However, the full extent of bacterial diversity in kitchens remains largely unknown as most previous studies of kitchen microbes focused on pathogen detection and relied upon cultivation-dependent techniques that preclude in-depth community characterization (Scott *et al.*, 1982; Ojima *et al.*, 2002a,b; Sinclair and Gerba, 2011). Nevertheless, from these studies it is apparent that both Gram-negative and Gram-positive bacteria can readily be cultivated from a variety of kitchen surfaces, with moist surfaces typically yielding the greatest number of colony-forming units.

Recently, high-throughput sequencing of the 16S rRNA gene has been used to study the bacterial communities of other indoor environments including public restrooms

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(Flores *et al.*, 2011), hospitals (Kembel *et al.*, 2012) and office buildings (Hewitt *et al.*, 2012). In addition to revealing an enormous and unexpected amount of bacterial diversity in indoor settings, these studies have begun to identify important sources of bacteria in the built environment. For example, human skin was found to be the primary source of bacteria in each of these locations, whereas other environmental sources such as soil and outdoor air were much less important. In the kitchen environment, both humans and raw foods brought into the kitchen are likely major contributors of bacteria, although their relative importance as sources has not previously been studied.

To gain a deeper understanding of the biogeography of kitchen surface communities and to examine how bacterial communities vary across the wide range of surface types and environments present within kitchens, we characterized the bacterial communities of > 80 surfaces in each of four residential kitchens using high-throughput sequencing of the 16S rRNA gene. Communities associated with surfaces from different households were expected to be dissimilar because of both behavioural (e.g. diet, disinfection frequency, cleaning products used, usage patterns) and intrinsic factors (e.g. surface material, differences in skin communities of residents, location of residence, kitchen design). Therefore, our intent here was not to control for these differences or investigate any individual factor in detail, but rather to determine bacterial community composition of 'typical' kitchens, and whether these communities exhibited distribution patterns that were predictable across the wide array of surface types present within kitchens. We also sought to determine the relative importance of different sources of bacteria to the kitchen environment, because kitchen bacterial communities are likely composed of bacteria drawn from a range of potential sources including raw foods, faucet water and the humans that inhabit the home.

## Results and discussion

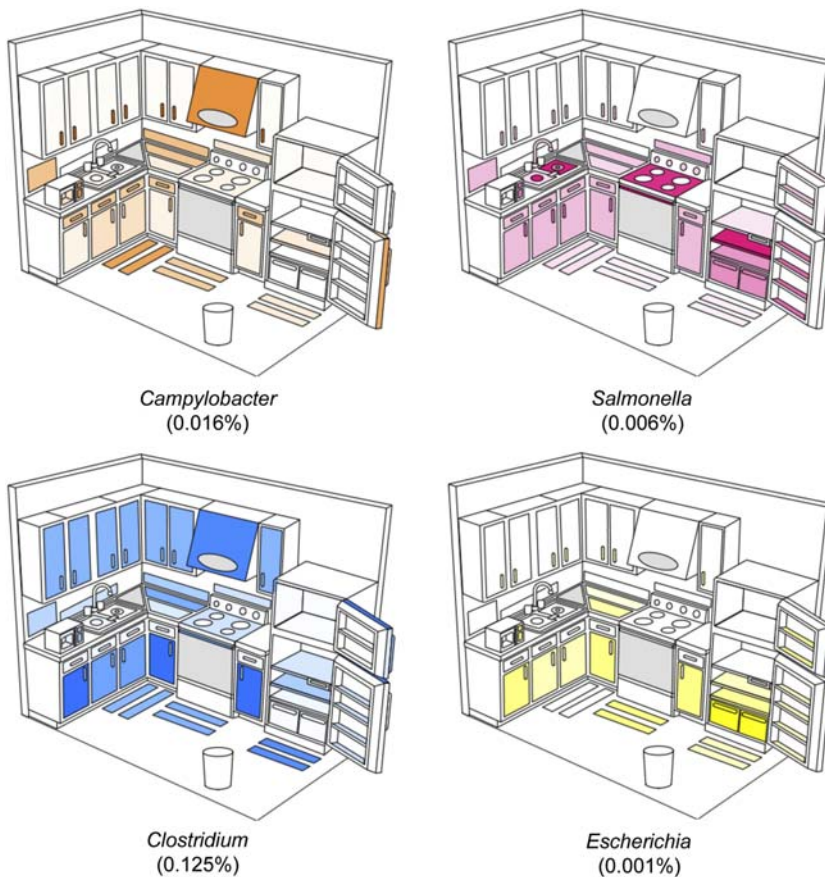
To explore the biogeographical patterns of bacteria in residential kitchens, we sampled over 80 surfaces per kitchen (Table S1) in the homes of four families living in Boulder, Colorado. We characterized the bacterial and archaeal communities using high-throughput sequencing of the 16S rRNA gene on the Illumina HiSeq platform and, after removal of sequences of poor quality and rarefying each sample to 10 000 reads, analysed the communities of 248 of the 332 original samples. From this unique data set, we identified 34 bacterial and two archaeal phyla, with the overwhelming majority of sequences (~ 98% of all sequences) belonging to only four bacterial phyla: *Actinobacteria*, *Bacteroidetes*, *Firmicutes* and *Proteobacteria* (Fig. 1). Previous studies have also identified these as the

dominant bacterial phyla in indoor environments (McManus and Kelley, 2005; Lee *et al.*, 2007; Rintala *et al.*, 2008; Aydogdu *et al.*, 2010; Flores *et al.*, 2011; Kembel *et al.*, 2012). Within these dominant phyla, the most abundant families were the *Micrococcaceae* (~ 6%), *Flavobacteriaceae* (~ 4%), *Streptococcaceae* (~ 10%) and *Moraxellaceae* (~ 14%). Organisms from these families are found in a wide range of environments, including the human body (Wilson, 2008; Costello *et al.*, 2009; Grice and Segre, 2011) and foods (Eribo and Jay, 1985; Jooste and Hugo, 1999; Rodriguez-Alonso *et al.*, 2009). In addition, these families contain genera that are known to survive on surfaces for extended periods of time (Kramer *et al.*, 2006; Santo *et al.*, 2010). For example, several *Acinetobacter* spp. (*Moraxellaceae*) have been successfully cultivated from a variety of dry and wet surfaces (e.g. stainless steel, ceramic, rubber, copper coins) up to 2 weeks after inoculation (Getchell-White *et al.*, 1989; Wendt *et al.*, 1997; Santo *et al.*, 2010). Our results thus show that the major bacterial taxa found on kitchen surfaces are qualitatively similar to those found in other indoor environments, and many of the dominant taxa appear to be able to persist on surfaces for extended periods of time.

A major concern in kitchen microbiology is the potential transmission of pathogens from raw food items brought into the kitchen. The most common culprits of bacterial food-borne illnesses in industrialized nations are *Campylobacter* spp., *Salmonella* spp., *Clostridium perfringens* and various strains of *Escherichia coli* (Mead *et al.*, 1999). Although our techniques lack the phylogenetic resolution to detect pathogens, and not all members of these genera are pathogenic, these genera were not dominant members of the communities in any kitchen, suggesting that pathogens in the average kitchen are relatively rare (Fig. 2). These genera were, however, widely distributed in the four kitchens examined, even in areas where direct contact with raw food is unlikely. The relative abundance of *Campylobacter*, for example, was greatest on surfaces above counter tops, including upper cabinet handles and the microwave panel (Fig. 2). Because *Campylobacter* contamination in kitchens is typically attributed to raw poultry (Cogan *et al.*, 1999; Luber, 2009), one possible explanation for these patterns is that contamination occurred from the hands of an individual who had handled raw poultry. Although the relative abundance of *Campylobacter* and other potentially pathogenic genera is low, these distribution patterns illustrate the ease with which food-associated bacteria are dispersed throughout residential kitchens. It is important to note, however, that the relative abundance data do not tell us if the distribution patterns are a product of differences in survivability, growth or frequency of transmission of certain bacteria on particular surface types.





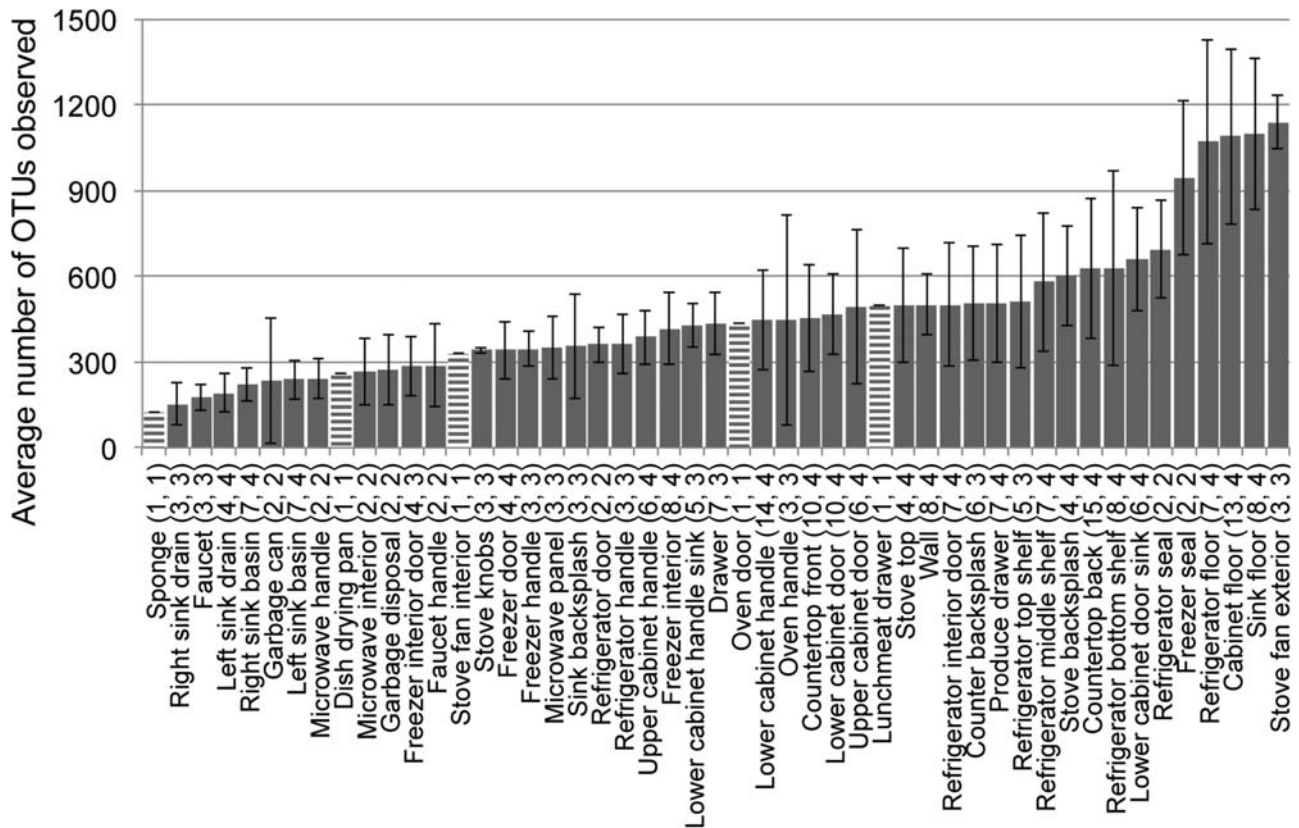


**Fig. 2.** Distribution and average relative abundances of bacterial genera commonly associated with food-borne illnesses. Darker shades of colour in each panel indicate a relatively higher abundance of the bacterial genus on that individual surface. Note that while each genus was observed in each kitchen, these patterns are a composite of the four kitchens studied and do not reflect the distribution patterns in any single kitchen. Grey indicates surfaces that were only successfully sampled in one kitchen while white surfaces were not sampled. Numbers in parentheses indicate the percentage of all sequences assigned to each genus. The triangle next to the sink represents the dish-drying rack while the oval on the stove exhaust fan represents the interior of the fan.

The kitchen surfaces that hosted the most diverse bacterial communities were the outside of the stove exhaust fans and the various floor surfaces (Fig. 3, Table S1). The relatively high bacterial diversity on the stove exhaust fan is likely a product of both passive (i.e. settling) and active (e.g. fan forcing) deposition of particulates, coupled with infrequent cleaning. Other surfaces that are likely cleaned infrequently, including floors and freezer door seals, also harboured diverse communities, pointing to surface hygiene as an important factor influencing bacterial alpha diversity in residential kitchens. The least diverse communities observed were associated with metallic surfaces around the kitchen sink and included the faucet, faucet handles, sink drains and sink basins (three of four sinks were stainless steel). These communities tended to be dominated by Gram-negative bacteria, including several known biofilm-forming organisms such as the *Sphingomonadaceae* (Fig. 1) (Kelley *et al.*, 2004). Interestingly, previous cultivation-based studies have found moist surfaces around sinks to harbour among the highest densities of cultivable bacteria (Scott *et al.*, 1982; Rusin *et al.*, 1998; Ojima *et al.*, 2002a,b; Sinclair and Gerba, 2011). Thus, although the diversity of sink surfaces may be low, the proportion of cultivable organisms harboured by these environments is actually high. It is also likely that sinks are

among the few surfaces in our kitchens where microorganisms are actively growing because moisture is more available than on other surfaces.

Kitchen surface communities were generally different based on the kitchen of origin (ANOSIM Global  $R = 0.175$ ,  $P = 0.001$ ), indicating that communities from the same kitchen were, on average, more similar than communities from different kitchens. This result may arise because the inhabitants of each home possess unique skin communities, eat different foods, have different surface disinfection routines and have a number of other different behaviours likely to influence surface-associated bacterial communities. Furthermore, individual kitchens are not identical with respect to their design, usage patterns, surface materials and environmental conditions (e.g. temperature, moisture and ventilation rates) and any of these factors could influence the composition of bacterial communities found on kitchen surfaces. Surface communities also differed based on general sampling area (ANOSIM Global  $R = 0.282$ ,  $P = 0.001$ ) (Fig. S1), and were driven by the abundances of the two most abundant phyla, the *Proteobacteria* and *Firmicutes*, both of which were strongly correlated with the first axis of the principal coordinates plot ( $r = -0.926$  and  $r = 0.923$  respectively) (Fig. S2). The Gram-negative *Proteobacteria* were more abundant on

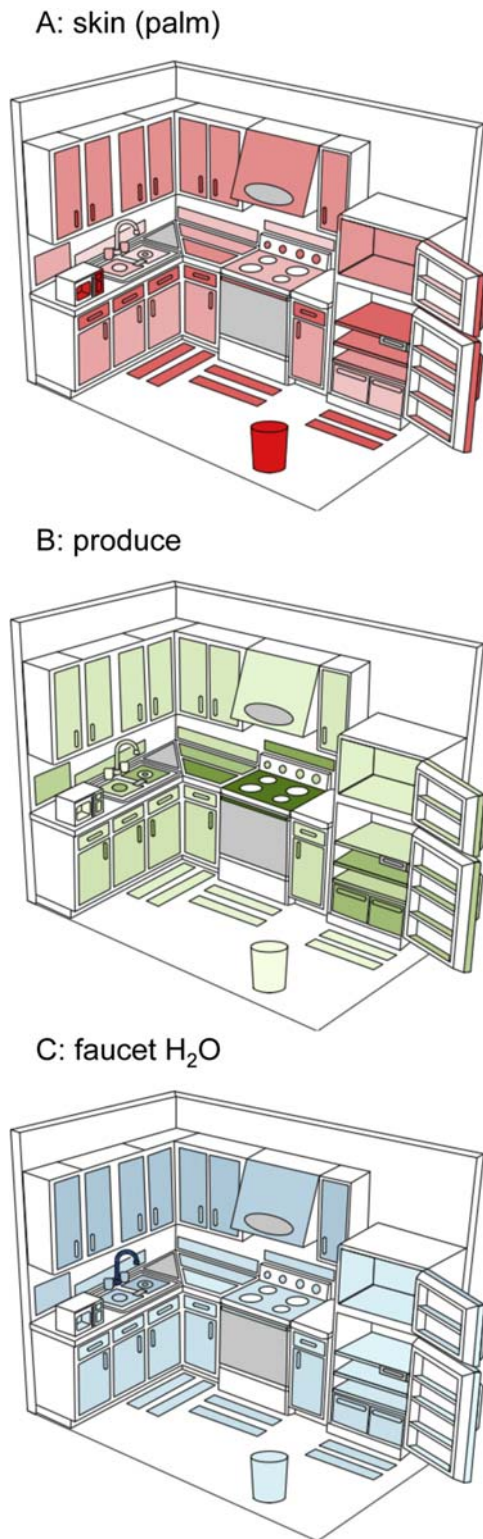


**Fig. 3.** Average number of bacterial OTUs observed on different residential kitchen surfaces determined from 10 000 randomly selected sequences from each sample. Bars are ordered from least to most diverse. Numbers in parentheses indicate the total number of samples characterized and the number of homes from which samples originated. Error bars are  $\pm$  one standard deviation. Striped bars are surfaces for which only one sample yielded quality sequence data and thus do not have error bars.

moist surfaces, while the Gram-positive, spore-forming *Firmicutes* were more abundant on dry (e.g. floors, cabinets, microwaves) and/or cold (e.g. refrigerator/freezer interior) surfaces. Again, these distribution patterns could be indicative of differences in the survivability, growth or frequency of transmission of particular organisms as moist surfaces could lead to the preferential growth of certain taxa and spore formers may survive longer on dry or cold surfaces.

To determine the relative importance of different sources of bacteria on kitchen surfaces, we identified three indicator taxa from raw produce (*Enterobacteriaceae*, *Microbacteriaceae* and *Bacillales*), four from human skin (*Propionibacteriaceae*, *Corynebacteriaceae*, *Staphylococcaceae* and *Streptococcaceae*) and three from faucet water samples (*Sphingomonadaceae*, *Methylobacteriaceae* and *Gallionellaceae*) using SIMPER (Clarke and Gorley, 2006) (Fig. S3). The most important source across all surfaces was clearly human skin with relatively larger contributions to those surfaces routinely touched with our hands (Tables S2–S4, Fig. 4). This is similar to what has previously been observed in public

restrooms where skin was also the principal source of bacteria (Flores *et al.*, 2011). Contributions from the other sources (faucet water and produce) tended to follow predictable patterns as illustrated by the relatively larger contribution of faucet water to sink surfaces and the importance of food-associated bacteria on surfaces that regularly come into contact with food (e.g. counter/stove tops, refrigerator shelves, produce drawer) (Fig. 4). Indicator taxa from faucet water were also found to be relatively abundant on upper cabinets, possibly suggesting transport of bacteria in aerosolized water. We confirmed these overall patterns using the community-level SourceTracker approach, which, despite its different mathematical and conceptual basis, exhibited similar relative contributions of sources to the various kitchen surfaces (Fig. S4). Although these results mirror patterns we might expect based on usage patterns within the kitchen or proximity to bacterial sources, they do highlight the spread of bacteria from human skin to surfaces in our kitchens and the potential transfer of bacteria from other sources to the human body after touching contaminated surfaces.



**Fig. 4.** Average relative abundances of indicator taxa from three potential sources of bacteria to residential kitchen surfaces. Figures are independent of each other and are coloured so that the darker shades indicate a relatively higher abundance of bacteria derived from that particular source. For information about what taxa were used as indicators, see text or Fig. S1. Figures not drawn to scale.

## Conclusions

This study shows that kitchen surfaces host remarkably diverse bacterial communities that differ both between kitchens and across surface types found within kitchens. Bacteria belonging to genera that include common pathogens comprise only a very small fraction of these communities (and even within these genera, most of the bacteria detected are probably not pathogenic, underscoring the rarity of pathogens as members of kitchen-associated microbial communities). Moreover, these results demonstrate that these bacterial communities are structured in ways that likely reflect expected dispersal from bacterial sources (i.e. human skin, food and faucet water) in ways related to how each surface is used or its proximity to each type of source. The baseline characterization of kitchen-associated microbial communities presented here, in combination with future experimental studies that show how specific behaviours or treatments affect the survivability, growth and transmission of bacteria on particular kitchen surfaces, will further improve our understanding of the microbial ecology of residential kitchens.

## Experimental procedures

### *Sampling, DNA extraction and sequencing*

At least 82 kitchen surfaces (Table S1) in the homes of four families living in Boulder, Colorado were sampled in September 2011 using sterile cotton swabs as described previously (Fierer *et al.*, 2008; 2010; Flores *et al.*, 2011). Because each kitchen was unique in design and contained surfaces of different dimensions, we sampled surfaces based on general features (e.g. countertops, stoves, sinks) rather than by strict surface area measurements. The duration of swabbing individual surfaces, however, was uniform across kitchens at 10–15 s per location. One litre of cold and hot faucet water was also collected from each home, and filtered through a 0.2 µm bottle top filters (Nalgene, Rochester, NY, USA) to capture bacteria from this potential source. Kitchens A and B were in second-storey apartments, kitchen C was in a single-family home and kitchen D was in a garden-level apartment of a different single-family home, providing a range of representative building types.

Genomic DNA was extracted from both cotton swabs and filters using the MoBio PowerSoil DNA isolation kit following the protocol of Fierer and colleagues (2008). A portion of the 16S rRNA gene spanning the variable region 4 (V4) was amplified using the barcoded, universal primer set (515F/806R), PCR mixture and thermal cycling conditions described in Caporaso and colleagues (2012). This primer set was designed to cover a wide diversity of both archaea and bacteria with few biases (Bates *et al.*, 2011; Bergmann *et al.*, 2011). PCR reactions were performed in triplicate 25 µl reactions that were subsequently combined and quantified using the PicoGreen dsDNA assay kit (Invitrogen, Carlsbad, CA, USA). Quantified reactions were pooled in equimolar concentrations and cleaned using MoBio UltraClean PCR Clean-up Kit following the manufacturer's instructions. Pools



were submitted for sequencing on an Illumina HiSeq2000 instrument at the University of Colorado Biofrontiers Institute Advanced Genomics Facility. All sequence data and sample metadata are publicly available through the European Bioinformatics Institute (EBI) under ERP001751.

### Sequence analysis

Because Illumina amplicon sequencing generates tens of millions of sequences, *de novo* picking of operational taxonomic units (OTUs, defined by pairwise sequence similarity) was not practical. Instead, we used a closed reference-based OTU picking approach as previously described (Hamady *et al.*, 2010; Caporaso *et al.*, 2011; 2012) using QIIME (Caporaso *et al.*, 2010). Briefly, after sequences were demultiplexed and quality filtered, OTUs at the 97% sequence similarity level were picked using UCLUST (Edgar, 2010) against the Greengenes database pre-clustered at 97% identity (DeSantis *et al.*, 2006). Sequences were assigned to OTUs with corresponding taxonomy based on their best match to a sequence in the Greengenes reference database. Sequences were discarded if they had less than a 97% match to any sequence in the database (34% of the sequences were discarded by this filter). For phylogenetic diversity metrics, the Greengenes tree was used.

After removing sequences of poor quality and those that did not match the Greengenes reference database, a total of 18 989 626 partial 16S rRNA gene sequences remained. An additional 3 537 685 sequences were determined to be from chloroplasts and were removed prior to further analysis, because we were only interested in the bacterial and archaeal communities. The remaining sequences were rarefied to 10 000 sequences per sample, resulting in a total of 248 kitchen samples used in all downstream analyses (Table S1). From these sequences, a total of 9049 unique OTUs (range 62–1557 per sample) were observed. Of these, approximately 20% (1838/9049) were singletons (observed only once).

To determine which surfaces hosted the most diverse communities, both OTU-based (taxonomic richness) and phylogenetic-based (phylogenetic diversity – PD; Faith and Baker, 2006) alpha diversity metrics were calculated for 10 resampling events of 10 000 sequences per sample using QIIME (Caporaso *et al.*, 2010). Values corresponding to surfaces present in multiple kitchens were then averaged across kitchens. Because both metrics showed similar patterns, only taxonomic richness results are presented here. The taxonomic compositions of the different surface communities were averaged across kitchens at multiple taxonomic levels and the relative abundances of individual taxa were projected onto a generic kitchen diagram using SitePainter (Gonzalez *et al.*, 2012). To compare the surface-associated communities both across kitchens and by general kitchen area, we used the phylogenetically based weighted UniFrac metric (Lozupone and Knight, 2005). The resulting distance matrix was visualized using principal coordinates analysis (PCoA), and sample categories were tested to determine whether they harboured distinct communities using analysis of similarity (ANOSIM) in PRIMER v6 (Clarke and Gorley, 2006). Pearson correlations between taxon abundances and principal coordinates were also conducted in PRIMER v6.

In order to determine the relative importance of potential sources of bacteria to the kitchen environment, we used two complementary approaches: a traditional indicator taxon approach, which examines individual taxa that are common in one environment while rare in others, and a Bayesian community-level source tracking approach, which uses features of the entire community with a Dirichlet model to take into account variability in individual source environments (Knights *et al.*, 2011). For both approaches, OTUs were picked using the same reference-based approach described above for a variety of produce items ( $n = 192$ , Table S5), human palms (Costello *et al.*, 2009) ( $n = 64$ ) and faucet water (this study;  $n = 5$ ). Indicator taxa were identified using the family-level taxonomy determined from 200 randomly selected sequences from each source environment using SIMPER in Primer v6 (Clarke and Gorley, 2006). SIMPER identifies taxa that are far more abundant in one source environment than in other source environments under consideration (Fig. S3). Contributions of sources to kitchen surface communities were determined based on the average abundance of these indicator taxa across the four kitchens (Tables S2–S4). For the Bayesian approach, a composite OTU table of each environmental sample and source samples (produce, faucet water, skin) was used as input for the SourceTracker algorithm (Knights *et al.*, 2011) in R (Ihaka and Gentleman, 1996). Output from SourceTracker was averaged for each surface type across all kitchens for each source environment. Relative contributions determined from both approaches were mapped onto a generic kitchen diagram using SitePainter (Gonzalez *et al.*, 2012).

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### Supporting information

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** Principal coordinate plots of weighted UniFrac distances showing clustering of individual surface types across the four kitchens examined. Letters in each plot indicate the kitchen of origin.

**Fig. S2.** Principal coordinate plots of weighted UniFrac distances overlaid with the abundance of the *Proteobacteria* (A) and *Firmicutes* (B). Bubbles are scaled according to abundance of each phylum.

**Fig. S3.** Indicator taxa identified by SIMPER for raw produce (A), human skin (palms) (B) and faucet water (C).

**Fig. S4.** Results of SourceTracker showing relative contributions of skin (A), produce (B) and faucet water (C) to kitchen surface bacterial communities. Figures are independent of each other and are coloured so that the darker shades indicate a relatively higher abundance of bacteria derived from that particular source. Figures not drawn to scale.

**Table S1.** Summary of kitchen surfaces for which over 10 000 quality 16S rRNA gene sequence fragments were obtained and used to examine bacterial biogeography of residential kitchens.

**Table S2.** Average percentage abundance of produce indicator taxa across replicate kitchen surfaces.

**Table S3.** Average percentage abundance of palm indicator taxa across all kitchen surfaces.

**Table S4.** Average percentage abundance of faucet water indicator taxa across all kitchen surfaces.

**Table S5.** The bacterial communities of the food items listed were characterized using barcoded pyrosequencing and averaged across all foods to identify bacterial taxa indicative of raw produce (J. W. L. and N. F., submitted). Note that for all produce items, both conventionally and organically grown produce was characterized.