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Microbial analyses of airborne dust collected from dormitory rooms predict the sex of occupants

Abstract We have long known that human occupants are a major source of microbes in the built environment, thus raising the question: How much can we learn about the occupants of a building by analyzing the microbial communities found in indoor air? We investigated bacterial and fungal diversity found in airborne dust collected onto heating, ventilation, and air-conditioning (HVAC) air filters and settling plates from 91 rooms within a university dormitory. The sex of the room occupants had the most significant effect on the bacterial communities, while the room occupants had no significant effect on fungal communities. By examining the abundances of bacterial genera, we could predict the sex of room occupants with 79% accuracy, a finding that demonstrates the potential forensic applications of studying indoor air microbiology. We also identified which bacterial taxa were indicators of female and male rooms, and found that those taxa often identified as members of the vaginal microbiome were more common in female-occupied rooms while taxa associated with human skin or the male urogenital microbiota were more common in male-occupied rooms.

J. C. Luongo[1], A. Barberán[2], R. Hacker-Cary[3], E. E. Morgan[2], S. L. Miller[1], N. Fierer[2,4]

[1]Department of Mechanical Engineering, University of Colorado, Boulder, CO, USA, [2]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO, USA, [3]Department of Integrative Physiology, University of Colorado, Boulder, CO, USA, [4]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA

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Noah Fierer, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA
Tel.: (303) 492-5615
Fax: (303) 492-1149
e-mail: noah.fierer@colorado.edu

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Practical Implications

This work presents bacterial and fungal analyses of indoor air from a unique perspective comparing male-occupied vs. female-occupied rooms within a university dormitory. Our study confirms the importance of human occupants in shaping bacterial communities found in indoor air and shows that the sex of the occupants can alter those communities. Results indicate that dust samples from HVAC filters can be identifying of sex-specific source environments, representing a novel forensic approach for identifying the sex of the occupants of a given room.

Introduction

We spend 90% of our lives indoors (Jenkins et al., 1992), and the quality of the air we breathe indoors is critical to human health and well-being (EPA, 2015). In addition to chemical and particulate pollutants, microorganisms also impact indoor air quality. Airborne microorganisms that are allergens or pathogens are of primary concern. Bacteria, fungi, and viruses are ubiquitous in indoor air with concentrations that typically exceed 100 000 cells or viral particles per cubic meter of air (Prussin et al., 2015). Most microbes cannot be identified using standard techniques (Amann et al., 1995), and only recently have researchers begun using molecular methods to comprehensively assess the amounts and types of bacteria and fungi found in indoor air (Adams et al., 2013, 2014, 2015a; Kembel et al., 2012; Meadow et al., 2014a).

Building-related factors such as ventilation, relative humidity, temperature, and occupants can influence the diversity and composition of microbes found indoors (Dannemiller et al., 2016; Kembel et al., 2012; Kettleson et al., 2015; Meadow et al., 2014a). Although the fungi found indoors are primarily influenced by what fungi are found outside the home (Adams et al., 2013; Barberán et al., 2015b), the occupants of a given building can have a significant influence on the types of bacteria found indoors. It has long been known that

humans shed bacteria from their skin and other body sites into their surrounding environments (Davies and Noble, 1962; Flores et al., 2011; Meadow et al., 2014b; Noble, 1975) as do indoor pets (Dunn et al., 2013; Fujimura et al., 2010; Kettleson et al., 2015). More recently, chamber experiments have detected distinct personal microbial 'clouds' associated with individuals, with one female subject being strongly associated with a *Lactobacillus* phylotype nearly identical to *Lactobacillus crispatus*, a bacterium commonly found in healthy vaginal samples (Meadow et al., 2015). Another recent study found that the female-to-male ratio of occupants living in a home influenced the types of bacteria found in the home (Barberán et al., 2015a). Despite this accumulating evidence, we still lack a specific understanding of how the sex of the occupants influences the diversity, composition, and abundance of microbes found indoors. Given that humans are known to be one of the dominant sources of bacteria in the indoor environment (Barberán et al., 2015a; Täubel et al., 2009), we took the next step and sought to determine whether we could predict the sex of occupants from information on the amounts and types of microbes found in indoor dust samples. We used high-throughput sequencing of bacterial and fungal taxonomic marker genes along with quantitative PCR (qPCR) to study the types and abundances of bacteria and fungi found in settled dust and HVAC filters in university dormitory rooms. We used multivariate statistical techniques to identify how, and to what extent, the number of occupants, sex of occupants, HVAC system operation, or other measured factors influenced microbial community composition and bioaerosol abundances.

Materials and methods

We assessed the microbial communities found in the air of 91 rooms in a dormitory on the University of Colorado campus (Boulder, USA) that houses undergraduate students (85% of participants were between 18 and 20 years of age). Each room housed 1–2 individuals per room, either males or females according to the University's two-sex system used to assign housing. Thus, results are confined to the assumption that the majority of occupants are neither transsexual nor intersexual and cannot speak to a more nuanced sex system (Fausto-Sterling, 2000). Each room had a fan coil unit that provided heating or air conditioning to recirculated room air (no outside air). The dormitory HVAC system was a constant volume system and supplied 100% outdoor air at a constant volumetric flow rate to each room. For each of the 91 rooms (65 male and 26 female), we collected airborne dust samples from fan coil unit filters (MERV 8 rating). These filters had been installed one year prior to collection and only filtered the air from each individual room, allowing us to collect a time-integrated sample from each room. For a subset of these rooms (38 rooms in total, 23 male and 15 female), we also installed two passive samplers per room, following the procedure described in (Emerson et al., 2015). Passive samplers from the same room were pooled in our analyses. Passive samplers were suspended 2 to 2.5 m above the floor in each room to collect settled airborne dust from each room. The passive samplers were installed for 2.5 months, from mid-February to mid-May 2015.

DNA was extracted from each of the 91 fan coil unit filters and the 76 passive samplers using the approach described in Emerson et al. (2015). DNA was PCR amplified using barcoded primers targeting the V4 region of the 16S rRNA gene (for bacterial analyses) or the ITS1 region of the rRNA operon (for fungal analyses). Amplicons were pooled in equimolar concentrations and sequenced on an Illumina MiSeq instrument. Details on the primers, PCR conditions, and the sequencing approach are provided in Emerson et al. (2015) and Lauber et al. (2013).

Sequences were demultiplexed and forward reads were analyzed for both 16S and ITS rRNA gene sequences. All sequences were quality-filtered and singletons were removed using a combination of QIIME, UPARSE, and in-house python scripts, following the pipeline described previously (Barberán et al., 2015b). All statistical analyses were performed in R (https://www.r-project.org/). Filter and passive samples were statistically analyzed separately. Bacterial samples were rarefied to 5000 sequences per sample, and fungal samples were rarefied to 7500 sequences per sample. After removing potential contaminants (i.e., operational taxonomic units, OTUs, with abundances greater than 5% in the blanks and no-template controls), we generated Bray–Curtis dissimilarity community matrices after Hellinger transformation of the rarefied OTU tables. We assessed whether variables such as sex of the room occupants affected bacterial community composition using permutational multivariate analysis of variance (PerMANOVA). Variables were tested individually; interactions were not considered. In total, 12 measured or reported variables were investigated including sex of occupants, number of occupants, room type, wing, floor, outdoor air delivery rate from the HVAC system (in cubic feet per minute), average overnight steady-state CO_2 concentration from one week of sampling, proportion of time the fan coil unit was operating over three months, self-reported window opening frequency, self-reported cleaning frequency, estimated skin surface area from self-reported height and weight, and self-reported dandruff diagnosis. A detailed list of measurements and statistical results are found in Table S2.

We used a machine learning approach to identify the relationship between the response (female-inhabited or male-inhabited room) and the predictors (relative abundance of bacterial genera). Machine learning techniques focus on algorithms to identify relationships

between variables rather than starting with a given model. In particular, we applied boosted regression trees to predict the sex of the inhabitants based on the bacterial community composition. Boosted regression tree models were trained with 70% of the samples, and the remaining 30% were used to assess the predictive performance (Elith et al., 2008). To identify OTUs associated with female vs. male rooms, we used indicator value analyses (Dufrêne and Legendre, 1997), as implemented in Barberán et al. (2015b), to identify those taxa indicative of different sample categories from information on taxa abundances and frequencies of occurrence.

DNA extracted from the passive samplers was used for qPCR analyses following the method described in Emerson et al. (2015) so we could also assess variation in the amounts of bacteria and fungi recovered in the air of the sampled dormitory rooms. For these analyses, we only focused on the passive samplers as it would have been difficult to extract DNA from the HVAC filters in a manner suitable for quantitative analyses of fungal and bacterial loads. Results for total bacterial and fungal abundances are reported in *E. coli* or *Aspergillus fumigatus* genome equivalents, respectively, but results should be interpreted as genome equivalents of bacterial or fungal cells per passive sampler.

Results and discussion

The most abundant bacterial and fungal taxa observed in our samples generally matched those identified from previously published studies of the indoor microbiome (Adams et al., 2013, 2015a; Barberán et al., 2015a). Both passive and filter sample types were dominated by the same suite of bacterial taxa including *Streptococcus*, *Micrococcus*, *Corynebacterium*, *Lactobacillus*, *Haemophilus*, *Finegoldia*, Staphylococcaceae, and Oxalobacteraceae. Many of these taxa are likely associated with human skin (e.g., *Staphylococcus*, *Corynebacterium*, *Streptococcus* (Grice and Segre, 2011)) and the vaginal microbiota (e.g., *Lactobacillus* (Ravel et al., 2011)). The most abundant fungal taxa in both sample types was *Davidiella*, a teleomorph of *Cladosporium* (Hawksworth, 2003), a fungus commonly reported in house dust samples and indoor air (Adams et al., 2013; Barberán et al., 2015a; Noris et al., 2011). Other abundant fungal taxa included common household molds such as *Aureobasidium*, *Penicillium*, *Cryptococcus*, and *Alternaria* (Adams et al., 2013; Bloom et al., 2009; Pitkäranta et al., 2008) as well as the gastronomically relevant fungi *Pleurotus* (genus of edible mushrooms).

None of the measured or recorded room characteristics were significant predictors of the types of fungi found in either the passive or filter samples. Previous work has shown that outdoor air fungi typically dominate the fungi found indoors (Adams et al., 2013; Barberán et al., 2015a) so it is not surprising that there would be minimal variation in the fungal communities identified from samples within the same building. Likewise, the amounts of fungi found in the collected dust samples, as determined via qPCR, were not significantly correlated with any of the measured variables (Kruskal–Wallis tests, $P > 0.1$). Although fungi were found to be, on average, 27% more abundant in rooms occupied by males than in rooms occupied by females, this difference was not statistically significant (Kruskal–Wallis test, $P = 0.12$) (Figure 1).

In contrast to the fungi, we found notable, and predictable, differences in the types of bacteria found across the sampled rooms. Sex of the room occupants was the best predictor of bacterial community composition for both sample types (PerMANOVA, passive: $P = 0.001$, $R^2 = 0.039$, filter: $P = 0.001$, $R^2 = 0.021$). The number of occupants (ranging from 1 to 2 individuals per room) was also found to be a significant predictor of the types of bacterial communities found in both sample types (PerMANOVA, passive: $P = 0.029$, $R^2 = 0.032$, filter: $P = 0.013$, $R^2 = 0.014$) with the location of the room (categorized by wing) significantly correlated with bacterial community composition across the collected filter samples (PerMANOVA, $P = 0.017$, $R^2 = 0.026$). Each wing had a separate HVAC system supplying outdoor air, which may have contributed to differences in community composition. However, we note that the wing and number of occupants was not correlated with the sex of the room occupants (Fisher test, $P > 0.05$). In other words, the effect of the sex of the occupants on bacterial community composition is unlikely to be driven by differences in the number of room occupants or differences in room location within the dormitory.

The qPCR-based estimates of bacterial abundances in the collected passive samples were not significantly correlated with any of the measured factors, except for the sex of the room occupants. In particular, we found that bacteria were, in general, 67% more abundant in male- vs. female-occupied rooms (Kruskal–Wallis test, $P = 0.006$) (Figure 1). Although the reasons for these differences remain uncertain, our guess is that these differences are driven by differences in the rates at which skin-associated bacteria are resuspended into room air given the importance of skin as a source of bacteria in the collected samples. Males may simply shed more skin bacteria into their surrounding environments than females, a hypothesis that has some support in the literature (Davies and Noble, 1962; Noble, 1975; Noble et al., 1976), although additional research is warranted to determine whether this is a valid explanation for the higher abundances of bacteria observed in male-occupied rooms. Estimated skin surface area based on occupant height and weight was not a significant predictor of bacterial abundances, eliminating that parameter as a confounder for sex differences in bacterial shedding. Other factors, however, such as the use of skin lotion

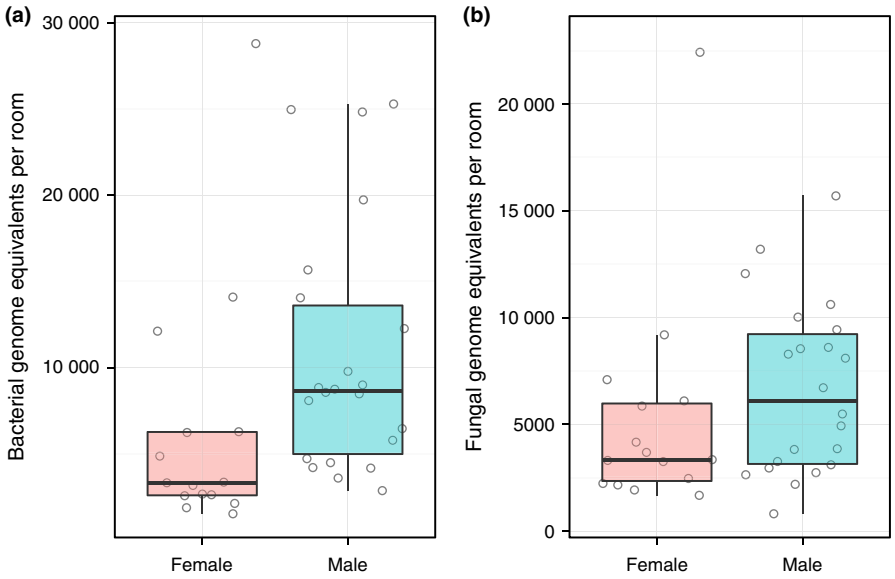

Fig. 1 Results from quantitative PCR analyses of airborne dust samples showing differences in amounts of bacteria (a) and fungi (b) collected onto settling plates over 2.5 months of sampling

(Hall et al., 1986) or clothing type (Doig, 1972), may contribute to differences in bacterial dispersal.

Given the significant effect that the sex of occupants had on bacterial community composition in both the passive and filter samples, we set out to determine how accurately we could predict the sex of occupants from information on bacterial community composition alone. To do this, we used machine learning models to assess the probability of whether a sample originated from a female-inhabited or male-inhabited room by examining the relative abundance of bacterial genera. Given the smaller number of passive samples (38 rooms sampled), this analysis was only conducted on filter samples (91 rooms sampled). We found that we could predict, with 79% accuracy, the sex of the room occupants from the relative abundances of different bacterial genera. The bacterial genera that had the highest contribution in the model, that is, those that were most differentially abundant between male and female-occupied rooms, are shown in descending order of model contribution in Figure 2. Note that the genus *Lactobacillus* had the largest contribution to the model and the relative abundance of this genus was the most useful for discriminating between male- and female-occupied rooms. Members of this genus can be found in a wide range of habitats and are often abundant in environments as varied as human skin (Fierer et al., 2008), the gut (Meadow et al., 2014b), the vagina (Ravel et al., 2011), or in dairy products (Bernardeau et al., 2008).

Although the genus level assignments proved useful for identifying male- vs. female-occupied rooms, we looked at the data at a finer level of taxonomic resolution to identify which specific OTUs were differentially abundant between the male- and female-occupied

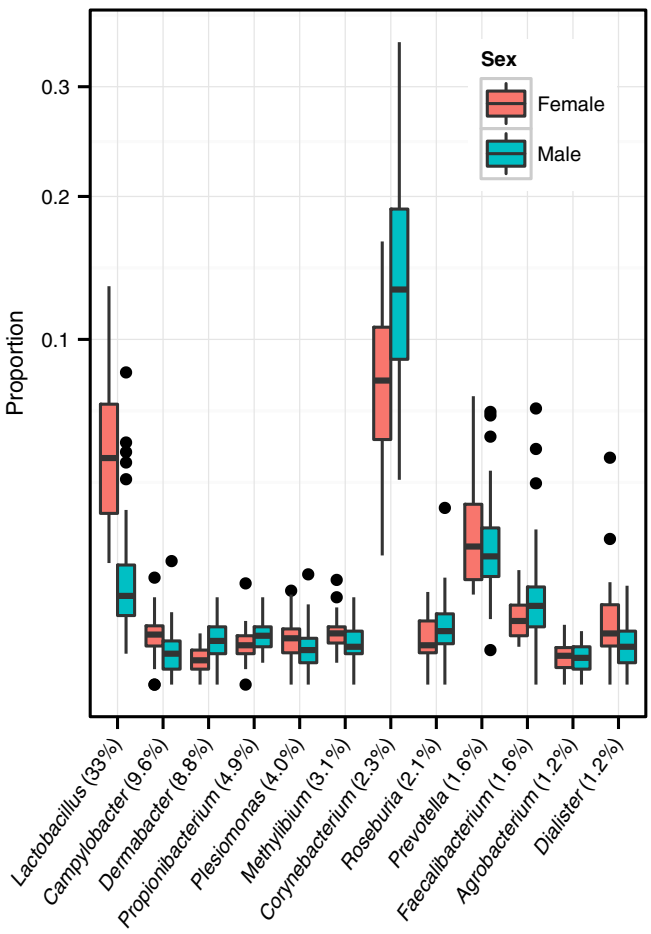

Fig. 2 Proportional abundances of bacterial genera from the HVAC filter samples listed in descending order of their contribution to the boosted regression tree model (model contributions are listed in the *x*-axis labels)

rooms. Indicator value analyses revealed specific OTUs that were indicators of female- vs. male-occupied rooms. Table 1 displays the top five indicator OTUs for each sampling and occupant type. While those individual OTUs identified as being differentially abundant between male- and female-occupied rooms varied depending on whether we examined the results from the passive or filter samples, a number of these taxa overlapped between the two sample types. Specifically, *Lactobacillus iners* was consistently more abundant in female-occupied rooms while *Dermabacter hominis*, *Facklamia*, and *Corynebacterium* were consistently more abundant in male-occupied rooms, regardless of the sample type (Figure S1). *Lactobacillus iners* is a relatively abundant member of the vaginal microbiome, being detected in 83.5% of subjects in a recent cross-sectional study of 396 healthy asymptomatic women and dominating 34.1% of the communities analyzed (Ravel et al., 2011). Although the source of *Dermabacter hominis* in these rooms remains difficult to determine, members of this species are commonly found in semen (Türk et al., 2014). Three male-associated OTUs classified as *Corynebacterium* are common skin inhabitants (Grice and Segre, 2011) and members of this genus have previously been shown to be significantly more abundant on male than on female hand surfaces (Fierer et al., 2008).

Table 1 Top OTUs that most effectively distinguished between male- and female-occupied rooms, as determined by the indicator value analyses. OTUs with high indicator values indicate that they were more common and more abundant in rooms occupied by either men or women. For details on the proportional abundances of these OTUs in male vs. female-occupied rooms, see Figure S1

OTU number	Taxonomic identity	Indicator value	*P*-value	Occupant sex	Sample type
OTU 14	*Lactobacillus iners*	0.73	0.008	Female	Passive
OTU 317	*Dialister microaerophilus*	0.63	0.003	Female	Passive
OTU 179	*Prevotella* sp.	0.53	0.003	Female	Passive
OTU 353	*Sphingobacterium multivorum*	0.45	0.01	Female	Passive
OTU 6078	*Mycoplana* sp.	0.43	0.01	Female	Passive
OTU 11	*Lactobacillus crispatus*	0.83	0.001	Female	Filter
OTU 14	*Lactobacillus iners*	0.78	0.003	Female	Filter
OTU 5851	*Corynebacterium* sp.	0.70	0.001	Female	Filter
OTU 65	*Anaerococcus* sp.	0.67	0.005	Female	Filter
OTU 78	*Dialister* sp.	0.65	0.003	Female	Filter
OTU 234	*Dermabacter hominis*	0.91	0.001	Male	Passive
OTU 6181	*Facklamia* sp.	0.86	0.001	Male	Passive
OTU 8580	*Corynebacterium* sp.	0.78	0.001	Male	Passive
OTU 35	*Corynebacterium* sp.	0.75	0.001	Male	Passive
OTU 28	*Corynebacterium aurimucosum*	0.68	0.001	Male	Passive
OTU 170	*Corynebacterium* sp.	0.81	0.001	Male	Filter
OTU 8580	*Corynebacterium* sp.	0.77	0.001	Male	Filter
OTU 6181	*Facklamia* sp.	0.72	0.001	Male	Filter
OTU 234	*Dermabacter hominis*	0.70	0.001	Male	Filter
OTU 28	*Corynebacterium aurimucosum*	0.68	0.001	Male	Filter

To quantitatively compare the potential sources of bacteria in male vs. female-occupied rooms, we compiled a list from the literature of bacterial taxa indicative of specific source habitats (Table S1). This list includes many of the taxa we identified as indicators of male and female environments. We found that male rooms had significantly higher proportions of skin-associated bacteria and female rooms had significantly higher proportions of vagina-associated bacteria (Kruskal–Wallis test, $P < 0.01$) (Figure 3). Male rooms yielded significantly higher proportions of stool-associated bacteria only in filter samples (Kruskal–Wallis test, $P < 0.01$).

There has recently been a call for more standardized sample collection protocols to improve meta-analysis of microbiota in the built environment (Adams et al.,

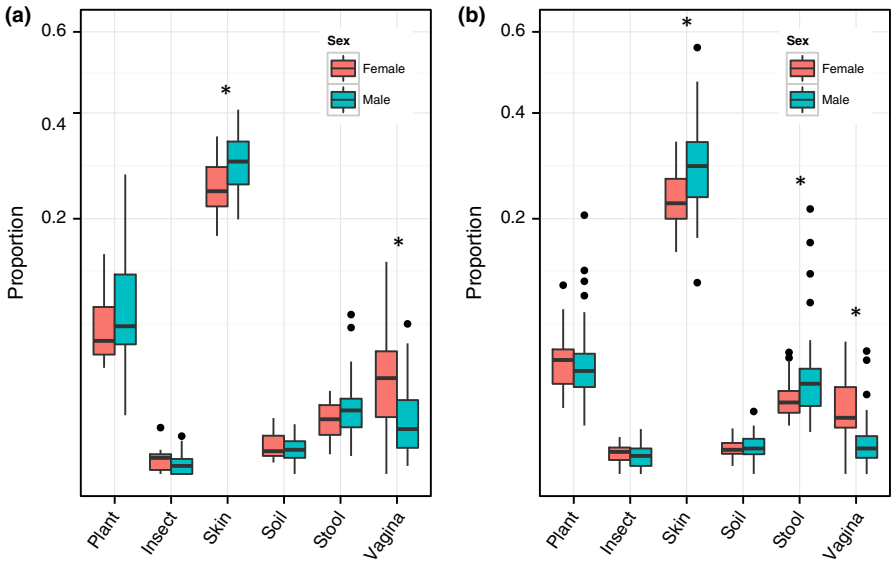

Fig. 3 Differences in the relative abundances of bacterial taxa indicative of potential source environments (listed in Table S1) between female and male rooms. Results are based on analyses of either the passive samplers (a) or the HVAC filters (b). Significantly different groups are labeled with an asterisk

2015a). Passive airborne dust collectors are frequently used as a way to monitor bioaerosol exposures (Adams et al., 2015b) given their ease of deployment and low cost. Preliminary evidence suggests that HVAC filters may represent another, relatively low-cost, option for longer-term investigations of airborne microbial communities (Emerson et al., 2015; Noris et al., 2011). With this dataset, we could assess whether the two sampling strategies (passive vs. HVAC filter samples) yielded similar assessments of room microbiomes given that we had 26 rooms that were sampled using both strategies. In general, the two sampling strategies yielded qualitatively similar results as the community similarity patterns between the two sampling strategies were correlated (Mantel test; r_M = 0.43; $P < 0.01$). The most common bacterial and fungal OTUs were similar across the two sample types in the 26 overlapping rooms (Figure S2) and various OTUs found in the two sample types overlapped as bacterial indicators of the sex of occupants (see above), reinforcing the idea that the microbial communities sampled from HVAC filters are similar to longer-term indoor air samples (Noris et al., 2011). Interestingly, a few of the more common OTUs had significantly different relative proportions between the two sample types. *Streptococcus, Lactobacillus,* and *Haemophilus* were relatively more abundant in passive samplers while *Micrococcus, Corynebacterium,* and *Staphylococcus* were relatively more abundant in HVAC filters (Kruskal–Wallis test, $P < 0.05$). This subtle pattern could be driven by differences in sampling time or by differences between the sampling strategies in the size distributions of the collected particles. It is also possible that sampling from HVAC filters may have introduced some mechanical microbial lysis, which has the potential to selectively change community composition, as discussed in Emerson et al. (2015). Together, these results highlight that both sampling strategies are useful and yield generally similar assessments of the indoor microbiome, but caution must be considered when quantitatively comparing results that were obtained using different sampling strategies, a point that has been made in a previous meta-analysis of indoor microbiomes (Adams et al., 2015a).

This work not only confirms the importance of human occupants in shaping the bacterial communities found in indoor air, and it also shows that even the sex of the occupants can alter those communities. *Lactobacillus* is the genus that most contributed to the differences between female-inhabited and male-inhabited environments. More generally, taxa often identified as members of the vaginal microbiota were more common in female-occupied rooms while taxa associated with human skin or the male urogenital microbiota were more common in male-occupied rooms. The results presented here have potential relevance to forensics as it shows that we can predict the sex of the occupants with fairly high accuracy. Just as other studies have shown that skin-associated bacterial communities are highly personalized and could be used for forensic identification of items touched by an individual (Fierer et al., 2010), these results show that dust samples can also be identifying. In cases where human DNA cannot be obtained, the bacterial cells dispersed in the indoor environment may represent a novel forensic approach for identifying the sex of the occupants of a given room, but additional work is required to determine the potential applications of such an approach.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Proportional abundances of top OTUs identified using indicator value analysis (listed in Table 1) comparing female and male rooms from passive samplers (left panel) and HVAC filters (right panel).

Figure S2. Proportional abundances of the most common bacterial (left panel) and fungal (right panel) taxa between the two sample collection strategies.

Table S1. Bacterial taxa, or chloroplasts, were used as indicators of the potential source environments to identify the relative importance of each source environment in each of the collected samples.

Table S2. List of measurements and results from various statistical analyses.

References

Adams, R.I., Miletto, M., Taylor, J.W. and Bruns, T.D. (2013) Dispersal in microbes: fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances, *ISME J.*, **7**, 1262–1273.

Adams, R.I., Miletto, M., Lindow, S.E., Taylor, J.W. and Bruns, T.D. (2014) Airborne bacterial communities in

residences: similarities and differences with fungi, *PLoS One*, **9**, e91283.
Adams, R.I., Bateman, A.C., Bik, H.M. and Meadow, J.F. (2015a) Microbiota of the indoor environment: a meta-analysis, *Microbiome*, **3**, 1–18.
Adams, R.I., Tian, Y., Taylor, J.W., Bruns, T.D., Hyvärinen, A. and Täubel, M. (2015b) Passive dust collectors for assessing airborne microbial material, *Microbiome*, **3**, 1–11.
Amann, R.I., Ludwig, W. and Schleifer, K. (1995) Phylogenetic identification and *in situ* detection of individual microbial cells without cultivation, *Microbiol. Rev.*, **59**, 143–169.
Barberán, A., Dunn, R.R., Reich, B.J., Pacifici, K., Laber, E.B., Menninger, H.L., Morton, J.M., Henley, J.B., Leff, J.W., Miller, S.L. and Fierer, N. (2015a) The ecology of microscopic life in household dust, *Proc. R. Soc. B*, **282**. doi: 10.1098/rspb.2015.1139.
Barberán, A., Ladau, J., Leff, J.W., Pollard, K.S., Menninger, H.L., Dunn, R.R. and Fierer, N. (2015b) Continental-scale distributions of dust-associated bacteria and fungi, *Proc. Natl Acad. Sci.*, **112**, 5756–5761.
Bernardeau, M., Vernoux, J.P., Henri-Dubernet, S. and Guéguen, M. (2008) Safety assessment of dairy microorganisms: the Lactobacillus genus, *Int. J. Food Microbiol.*, **126**, 278–285.
Bloom, E., Grimsley, L.F., Pehrson, C., Lewis, J. and Larsson, L. (2009) Molds and mycotoxins in dust from water-damaged homes in New Orleans after hurricane Katrina, *Indoor Air*, **19**, 153–158.
Dannemiller, K.C., Gent, J.F., Leaderer, B.P. and Peccia, J. (2016) Influence of housing characteristics on bacterial and fungal communities in homes of asthmatic children, *Indoor Air*, **26**, 179–192.
Davies, R.R. and Noble, W.C. (1962) Dispersal of bacteria on desquamated skin, *Lancet*, **280**, 1295–1297.
Doig, C.M. (1972) The effect of clothing on the dissemination of bacteria in operating theatres, *Br. J. Surg.*, **59**, 878–881.
Dufrêne, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach, *Ecol. Monogr.*, **67**, 345–366.
Dunn, R.R., Fierer, N., Henley, J.B., Leff, J.W. and Menninger, H.L. (2013) Home life: factors structuring the bacterial diversity found within and between homes, *PLoS One*, **8**, e64133.
Elith, J., Leathwick, J.R. and Hastie, T. (2008) A working guide to boosted regression trees, *J. Anim. Ecol.*, **77**, 802–813.
Emerson, J.B., Keady, P.B., Brewer, T.E., Clements, N., Morgan, E.E., Awerbuch, J., Miller, S.L. and Fierer, N. (2015) Impacts of flood damage on airborne bacteria and fungi in homes after the 2013 Colorado Front Range flood, *Environ. Sci. Technol.*, **49**, 2675–2684.
EPA (2015) The Inside Story: A Guide to Indoor Air Quality, Publications and Resources, Available from: http://www.epa.gov/iaq/pubs/insidestory.html (accessed 1 March 2015).
Fausto-Sterling, A. (2000) The five sexes, revisited, *Sciences*, **40**, 18–23.
Fierer, N., Hamady, M., Lauber, C.L. and Knight, R. (2008) The influence of sex, handedness, and washing on the diversity of hand surface bacteria, *Proc. Natl Acad. Sci.*, **105**, 17994–17999.
Fierer, N., Lauber, C.L., Zhou, N., McDonald, D., Costello, E.K. and Knight, R. (2010) Forensic identification using skin bacterial communities, *Proc. Natl Acad. Sci.*, **107**, 6477–6481.
Flores, G.E., Bates, S.T., Knights, D., Lauber, C.L., Stombaugh, J., Knight, R. and Fierer, N. (2011) Microbial biogeography of public restroom surfaces, *PLoS One*, **6**, e28132.
Fujimura, K.E., Johnson, C.C., Ownby, D.R., Cox, M.J., Brodie, E.L., Havstad, S.L., Zoratti, E.M., Woodcroft, K.J., Bobbitt, K.R., Wegienka, G., Boushey, H.A. and Lynch, S.V. (2010) Man's best friend? The effect of pet ownership on house dust microbial communities, *J. Allergy Clin. Immunol.*, **126**, 410.
Grice, E.A. and Segre, J.A. (2011) The skin microbiome, *Nat. Rev. Microbiol.*, **9**, 244–253.
Hall, G.S., Mackintosh, C.A. and Hoffman, P.N. (1986) The dispersal of bacteria and skin scales from the body after showering and after application of a skin lotion, *Epidemiol. Infect.*, **97**, 289–298.
Hawksworth, D.L. (2003) Davidiella, a new generic name for the teleomorph of Cladosporium S. Str., *Mycol. Res.*, **107**, 1250–1250.
Jenkins, P.L., Phillips, T.J., Mulberg, E.J. and Hui, S.P. (1992) Activity patterns of Californians: use of and proximity to indoor pollutant sources, *Atmos. Environ.*, **26A**, 2141–2148.
Kembel, S.W., Jones, E., Kline, J., Northcutt, D., Stenson, J., Womack, A.M., Bohannan, B.J., Brown, G.Z. and Green, J.L. (2012) Architectural design influences the diversity and structure of the built environment microbiome, *ISME J.*, **6**, 1469–1479.
Kettleson, E.M., Adhikari, A., Vesper, S., Coombs, K., Indugula, R. and Reponen, T. (2015) Key determinants of the fungal and bacterial microbiomes in homes, *Environ. Res.*, **138**, 130–135.
Lauber, C.L., Ramirez, K.S., Aanderud, Z., Lennon, J. and Fierer, N. (2013) Temporal variability in soil microbial communities across land-use types, *ISME J.*, **7**, 1641–1650.
Meadow, J.F., Altrichter, A.E., Kembel, S.W., Moriyama, M., O'Connor, T.K., Womack, A.M., Brown, G.Z., Green, J.L. and Bohannan, B.J.M. (2014a) Bacterial communities on classroom surfaces vary with human contact, *Microbiome*, **2**, 7.
Meadow, J.F., Altrichter, A.E., Kembel, S.W., Kline, J., Mhuireach, G., Moriyama, M., Northcutt, D., O'Connor, T.K., Womack, A.M., Brown, G.Z., Green, J.L. and Bohannan, B.J.M. (2014b) Indoor airborne bacterial communities are influenced by ventilation, occupancy, and outdoor air source, *Indoor Air*, **24**, 41–48.
Meadow, J.F., Altrichter, A.E., Bateman, A.C., Stenson, J., Brown, G., Green, J.L. and Bohannan, B.J.M. (2015) Humans differ in their personal microbial cloud, *PeerJ*, **3**, e1258.
Noble, W.C. (1975) Dispersal of skin microorganisms*, *Br. J. Dermatol.*, **93**, 477–485.
Noble, W.C., Habbema, J.D.F., Van Furth, R., Smith, I. and De Raay, C. (1976) Quantitative studies on the dispersal of skin bacteria into the air, *J. Med. Microbiol.*, **9**, 53–61.
Noris, F., Siegel, J.A. and Kinney, K.A. (2011) Evaluation of HVAC filters as a sampling mechanism for indoor microbial communities, *Atmos. Environ.*, **45**, 338–346.
Pitkäranta, M., Meklin, T., Hyvärinen, A., Paulin, L., Auvinen, P., Nevalainen, A. and Rintala, H. (2008) Analysis of fungal flora in indoor dust by ribosomal DNA sequence analysis, quantitative PCR, and culture, *Appl. Environ. Microbiol.*, **74**, 233–244.
Prussin, A.J., Garcia, E.B. and Marr, L.C. (2015) Total concentrations of virus and bacteria in indoor and outdoor air, *Environ. Sci. Technol. Lett.*, **2**, 84–88.
Ravel, J., Gajer, P., Abdo, Z., Schneider, G.M., Koenig, S.S.K., McCulle, S.L., Karlebach, S., Gorle, R., Russell, J., Tacket, C.O., Brotman, R.M., Davis, C.C., Ault, K., Peralta, L. and Forney, L.J. (2011) Vaginal microbiome of reproductive-age women, *Proc. Natl Acad. Sci. USA*, **108**(Suppl 1), 4680–4687.
Täubel, M., Rintala, H., Pitkäranta, M., Paulin, L., Laitinen, S., Pekkanen, J., Hyvärinen, A. and Nevalainen, A. (2009) The occupant as a source of house dust bacteria, *J. Allergy Clin. Immunol.*, **124**, 834–840.
Türk, S., Mazzoli, S., Stšepetova, J., Kuznetsova, J. and Mändar, R. (2014) Coryneform bacteria in human semen: inter-assay variability in species composition detection and biofilm production ability, *Microb. Ecol. Health Dis.*, **25**, 1–6.