

RESEARCH ARTICLE

Open Access



# Temporary establishment of bacteria from indoor plant leaves and soil on human skin

Gwynne Á. Mhureach<sup>1\*</sup> , Ashkaan K. Fahimipour<sup>1,2,3</sup>, Roo Vandegrift<sup>1,4</sup>, Mario E. Muscarella<sup>5</sup>, Roxana Hickey<sup>1</sup>, Ashley C. Bateman<sup>1</sup>, Kevin G. Van Den Wymelenberg<sup>1</sup> and Brendan J. M. Bohannan<sup>2</sup>

## Abstract

**Background:** Plants are found in a large percentage of indoor environments, yet the potential for bacteria associated with indoor plant leaves and soil to colonize human skin remains unclear. We report results of experiments in a controlled climate chamber to characterize bacterial communities inhabiting the substrates and leaves of five indoor plant species, and quantify microbial transfer dynamics and residence times on human skin following simulated touch contact events. Controlled bacterial propagule transfer events with soil and leaf donors were applied to the arms of human occupants and repeatedly measured over a 24-h period using 16S rRNA gene amplicon sequencing.

**Results:** Substrate samples had greater biomass and alpha diversity compared to leaves and baseline skin bacterial communities, as well as dissimilar taxonomic compositions. Despite these differences in donor community diversity and biomass, we observed repeatable patterns in the dynamics of transfer events. Recipient human skin bacterial communities increased in alpha diversity and became more similar to donor communities, an effect which, for soil contact only, persisted for at least 24 h. Washing with soap and water effectively returned communities to their pre-perturbed state, although some abundant soil taxa resisted removal through washing.

**Conclusions:** This study represents an initial characterization of bacterial relationships between humans and indoor plants, which represent a potentially valuable element of biodiversity in the built environment. Although environmental microbiota are unlikely to permanently colonize skin following a single contact event, repeated or continuous exposures to indoor biodiversity may be increasingly relevant for the functioning and diversity of the human microbiome as urbanization continues.

**Keywords:** Microbiome, Human skin, 16S, Phyllosphere, Indoor plants, Soil, Potting mix, Microbial transmission

## Introduction

Keeping indoor potted plants is common across the world and has recently increased in popularity [1, 2]. Indoor plants may provide various benefits, including perceived air quality improvement, interior aesthetics, and psychological and cognitive health benefits [3–7]. It has been speculated that potted houseplants may also contribute to the diversity of plant- and soil-associated

microorganisms encountered by building occupants [8], which may impact the human immune system or reduce risk of chronic disorders, such as allergies and asthma [9–16]. It has been shown that plants can alter microbial community diversity and composition of indoor environments [17–19]. Yet, the effects of such environmental engineering on human-associated microbial communities remain poorly understood.

Modern lifestyles tend to decrease exposure to soil- and plant-associated microorganisms. Urbanization homogenizes the outdoor environmental microbial assemblage to which residents are exposed [20] and most people in industrialized nations spend the vast

\*Correspondence: gwynhwyf@uoregon.edu

<sup>1</sup> Biology and the Built Environment Center, University of Oregon, Eugene, OR, USA

Full list of author information is available at the end of the article



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

majority of their lives indoors [21], which significantly moderates their microbial exposures. Typical indoor environments include more human-associated taxa than outdoor environments [22–25] due to constant microbial shedding by building occupants [26] and filtering of outdoor microbiota by building envelopes and air filtration systems. This situation has prompted experiments with other means of increasing exposure to soil- and plant-associated microbiomes [27]. Keeping indoor plants and participating in backyard gardening and nature-based activities are hypothesized to increase interactions with soil- and plant-associated microbes [28–30], potentially providing a 'microbiome rewilding' effect [31] or protecting against human pathogens through competitive advantage [32]. Such exposures may drive temporary or long-term changes in human skin microbial community composition, although empirical data remain scarce.

Despite their potential to affect human-associated microbiomes and hence human health, little is known about the variation of indoor plant microbiomes by plant type, source nursery, or substrate (henceforth, we use the term 'substrate' to encompass both outdoor soil and commercial potting mix; not to be confused with 'growth media,' which refers to substrates used in microbial cultures). Abundant research has investigated microbiome assembly and dynamics of outdoor plants, including agricultural crops, wild and urban trees and shrubs, and ornamental flowers, but only a few studies (for example, [33] and [18]) have focused on indoor plant microbiomes or whether and how potting mix microbial communities differ from those found in natural soils. Furthermore, the transmissibility of microbiota from these environmental sources and their ability to remain on human skin is poorly understood. Here we characterize the diversity of bacterial communities inhabiting the substrates and leaves of five indoor plant species, and quantify microbial transfer dynamics and residence time on human skin following simulated touch contact events with outdoor soil and leaf top surfaces. We hypothesized that (1) both soil and leaf donor microbial communities would transfer new bacterial taxa to the recipient skin community, and that these initial transfer effects would likely persist on the order of hours; (2) the effects would largely vanish within 24 h; and (3) washing with soap and water would remove the signature of the experimental transfer. With the high prevalence of indoor plants and the likelihood that people physically interact with their leaves and substrates, a basic understanding of the indoor plant microbiome may help guide interior design decisions, including the number, type, and placement of plants, that could be beneficial for building occupants.

## Methods

### Overview

In this study, we collected microbial samples from substrates and leaves of five different indoor plant types (Additional file 1: Fig. S1), and forearm skin of human subjects before and after transferring microbial propagules from outdoor soil and plant leaves. The study was performed on June 20–21 and 27–28 and July 13–14, 2016, at the Energy Studies in Buildings Laboratory (ESBL) facility in Portland, Oregon, from approximately 9:00 am–7:00 pm on the study days listed. Outdoor soil was sourced from a farm in Mohawk, Oregon, USA, while potting mix samples were taken directly from pots containing the plants used in the study; the potting mix (Gray's Organic Potting Soil) was originally sourced from Gray's Garden, Eugene, Oregon, USA. Indoor plant types studied were *Spathiphyllum* (Peace Lily), *Dieffenbachia* (Dumb Cane), *Dracaena* (Dragon Tree), *Sanseveria* (Snake Plant), and *Calathea* (Prayer Plant). Plants were purchased on April 10 and May 15, 2016, and were repotted into the same potting mix (Gray's Organic Potting Soil) after purchase. Plants were kept in a climate-controlled chamber at a constant temperature of 24.4 °C and relative humidity of 42.6% until the day of sample collection. Sixteen adult subjects between the ages of 18–35 were recruited to participate in the transfer experiments. Eligibility requirements for participation in the study included (1) that the individual was in generally good health, (2) free of skin conditions or infections, and (3) had not taken antibiotics within the prior 6 months. Subjects were asked to refrain from bathing or applying topical items to the skin for a 12-h period preceding the experiment. The subjects were informed as to the full nature and design of the study and gave written consent to be participants. This study and its associated research protocols were approved by the IRB at the University of Oregon on December 23, 2013 (Reference #: 03112016.016). All researchers assigned to this protocol were CITI certified to work with human subjects.

### Baseline microbial sample collection

We used sterile nylon-flocked swabs (Copan Diagnostics; Murrieta, CA, USA) to collect microbial communities from substrates (outdoor soil, potting mix), plant leaves (top and bottom surfaces), and forearm skin. Prior to use, swabs were moistened with a sterile saline solution (0.15 M NaCl; 0.1% Tween20) and then excess moisture was removed by flicking the swab carefully. Outdoor soil was 2-mm sieved and passively air-dried prior to aliquoting subsamples; each subsample was assigned as a donor for one recipient subject for the transfer experiment. A baseline sample was collected from each outdoor soil subsample prior to performing the transfer. Potting mix samples

were collected from pots containing the plants used in the transfer experiment, as well as one sample from an unopened potting mix bag. Due to qualitative differences in texture and moisture at the time of sampling, in comparison to outdoor soil, potting mix samples were not subjected to sieving or air-drying. To collect outdoor soil and potting mix samples, pre-moistened swabs were briefly dipped into a 8 mL aliquot of substrate, resulting in approximately 0.0075 g soil/mix per swab. For leaf samples, a 10 × 10 cm area of the top surface of a single healthy plant leaf from each type of indoor plant was swabbed for approximately 15 s while rotating the swab; this procedure was repeated for the bottom surface of each leaf with a different swab. Similarly, skin surface samples were collected by swabbing from standardized sampling grids measuring 1 × 3 cm drawn on each subject using ethanol-disinfected custom plastic vinyl stencils and thin-tipped permanent markers (Additional file 1: Fig. S2). Five equal and distinct grid cells were designated for sampling the skin at five time points: before transfer (0); 2-, 4-, and 8-h post-transfer; and a spot for either a 24-h post-transfer or post-wash sampling time point for each donor type; a larger area served as a donor for the skin-to-skin control (Additional file 1: Fig. S2). For the baseline skin samples, one cell was swabbed in each row of the grid, corresponding to Soil Recipient Areas, Leaf Recipient Areas, and Skin Recipient Areas at time point 0 (T00).

### Microbial propagule transfer experiment

Following collection of baseline soil, leaf, and skin samples, microbial propagules were immediately transferred from a subsample of outdoor soil, a donor plant leaf, and an adjacent area of skin to the dry inner forearm of an individual human recipient subject. Propagule transfer was accomplished by collecting donor soil/leaf/skin microbiota using the same swabbing techniques described above, then immediately applying the swab to the recipient area of skin (the entire row of the sampling grid corresponding to each donor type; Additional file 1: Fig. S2) and again rotated while swabbing firmly for approximately 10–15 s. Swabs were used in lieu of direct contact to standardize the microbial propagule size transferred to each subject from soil and leaf sources.

Only outdoor soil and top leaf surfaces of three plant types (*Spathiphyllum*, *Dieffenbachia*, and *Calathea*) were used in the transfer experiment in an effort to minimize potential sources of variability. Outdoor soil was used in the transfer experiment because (1) contact with outdoor soil is more common than contact with potting soil; (2) microbial biomass in outdoor soil is known to be high, whereas commercial potting mix is typically sterilized during manufacture; and (3) outdoor soil is frequently

used to pot indoor plants. Top surfaces of leaves were used in an effort to eliminate surface location as a potential source of variation and because they are more likely to be contacted by people than bottom surfaces. A unique donor leaf was selected and swabbed (both for the baseline sample collection and for the transfer experiment) for each human subject volunteer and, similarly, a unique soil subsample was used for each subject; donor leaf/soil samples were linked with recipient skin samples for downstream analyses. Subjects S01–S06 received a leaf donor community from *Spathiphyllum*, Subjects S07–S12 received a leaf donor community from *Dieffenbachia*, and Subjects S13–S16 received a leaf donor community from *Calathea*. Skin-to-skin control transfers were performed using a designated area of dry skin on the arm to inoculate an adjacent area of dry skin. After the transfer procedure was complete, a sterile gauze dressing was lightly taped over the area with minimal occlusion and replaced between sampling periods. Subjects remained sedentary in the climate-controlled chamber for 8 h.

Swabs were also used for subsequent time-series sampling, as they have been demonstrated to be an effective method for sampling microbial diversity of the skin [34]. At each post-transfer time point, one grid cell for each donor type was swabbed. Grid columns for each time point were randomized between subjects in an effort to reduce spatial autocorrelation. To achieve both a post-wash (TW, time after wash) sampling time point and a 24-h time point (T24), we asked half of the subjects to wash the recipient skin area with Castile soap and gently pat dry with sterile paper towels just after the 8-h sampling time point for immediate re-sampling. The remaining eight subjects did not wash the recipient skin area but were sampled the following day for a 24-h post-transfer sampling time point. Between the time that the subjects left the research facility and returned the following day for the 24-h sampling time point, they were asked to refrain from thoroughly wetting the now-exposed inner forearm area, but otherwise were allowed to resume normal daily activities. For each of the three transfer types on each subject at the requisite time point 2, 4, 8, and 24-h post-transfer and post-wash, a swab sample was collected using a sterile swab (dampened with sterile saline solution: 0.15 M NaCl; 0.1% Tween20) applied to the skin and rotated while swabbing firmly for approximately 10–15 s. All baseline transfer swabs (T00) and following time-series swab samples (T02, T04, T08, T24, TW) were collected and frozen at  $-20^{\circ}\text{C}$  for subsequent DNA extraction.

### 16S rRNA gene sequencing

A total of 331 swab samples were processed and submitted for sequencing. Negative swab, extraction kit, and

polymerase chain reaction (PCR) controls were included to identify possible sources of contamination during library preparation. DNA from all samples was manually extracted using the MoBio PowerLyzer PowerSoil DNA Isolation Kit according to manufacturer's instructions. Amplicons of the V3–V4 region (319f–806r) of the 16S rRNA gene were prepared in 50  $\mu$ L PCR reactions with one PCR step using dual-barcoded primers (see description in Supplementary Information), cleaned with Ampure beads, quantified using Quant-iT dsDNA assay kit, and pooled with equal concentrations of amplicons using an Eppendorf epMotion 5075 robot. Libraries were sequenced across two runs on an Illumina MiSeq generating 250 bp paired end reads.

Illumina sequence data were filtered, trimmed, and denoised using the DADA2 v1.5.2 statistical inference algorithm [35, 36], which identifies amplicon sequence variants (ASVs). Due to poor quality of the reverse reads, only forward reads were used. Reads were trimmed and truncated at 10 nt and 240 nt, and each read was required to have fewer than three expected errors based on quality scores. Taxonomy was assigned to ASVs using the RDP classifier implemented in DADA2 and the Silva version 132 reference database [37], with an 80% bootstrapped threshold for retaining classifications. We omitted sequence variants classified as chloroplasts or mitochondria, and those that were unclassified beyond the kingdom level. Putative contaminants were identified with *decontam* [38] and removed prior to downstream analyses, resulting in elimination of 71,467 reads. We also removed samples that failed to meet our minimum size threshold of 1000 reads. No significant batch effect of sequencing run was observed.

#### Absolute abundance estimation with qPCR

We estimated absolute abundance as total counts of 16S rRNA gene copies per swab for donor skin, outdoor soil, and leaf top surface microbiomes using real-time quantitative PCR (qPCR; Applied Biosystems StepOnePlus System). Swabs represent approximately 0.0075 g of soil, 100 cm<sup>2</sup> of leaf surface, or 3 cm<sup>2</sup> of skin surface. As the primary intent of this study was to quantify changes in the skin microbial community abundance, diversity, and composition after a simulated touch contact event, rather than to compare skin microbial biomass with that of soil or plant leaves, we did not attempt to normalize samples by dry weight or surface area. The reaction mixture was prepared according to guidelines provided by ABS PowerUp SYBR Green PCR Master Mix for a 20  $\mu$ L reaction and run in triplicate: ABS PowerUp SYBR Green PCR Master Mix (10  $\mu$ L), 10  $\mu$ M Total Bacteria F SYBR Primer 5'-gtgStgcaYggYgtgctgca-3' (0.8  $\mu$ L), 10  $\mu$ M Total Bacteria R SYBR Primer 5'-acgtcRtccMcaccttctc-3' (0.8  $\mu$ L), PCR

grade water (6.4  $\mu$ L) and undiluted DNA template (2  $\mu$ L) [39]. We also used the suggested ABS PowerUP thermocycling conditions for primers with  $T_m < 60^\circ\text{C}$ : initial denaturation for 2 min at 50  $^\circ\text{C}$ , 2 min at 95  $^\circ\text{C}$ ; 40 cycles of 15 s at 95  $^\circ\text{C}$ , 15 s at 60  $^\circ\text{C}$ , 60 s 72  $^\circ\text{C}$ ; followed by a melt curve in the range of 60  $^\circ\text{C}$  to 95  $^\circ\text{C}$ . Standard curves were generated using 10-fold serial dilutions of synthetic 167 bp gBlocks Gene Fragments (Integrated DNA Technologies, Coralville, Iowa, USA) of the same region amplified with the above primers, with known gene sequence copy numbers. To correct for differing reaction efficiencies across the different source community sample types, particularly since soil contains PCR inhibitors that reduce amplification efficiency [40], we used LinReg-PCR [41] to quantify 16S rRNA gene copies from fluorescence values.

#### Statistical analysis

All analyses were conducted in the R statistical programming language [42]. Differences between qPCR-based estimates of initial taxon abundances within and across groups (outdoor soil, leaf top surfaces, baseline skin) were examined using analysis of variance (ANOVA) on log-transformed corrected counts and Tukey's post-hoc test. Estimating alpha diversity from amplicon sequencing data is an area of active research and discussion [43–46]. The Shannon diversity index, despite its wide usage, is particularly sensitive to numbers of unseen members of the true community, which are notoriously difficult to accurately estimate in environmental microbiome studies due to inadequate sampling effort relative to the true diversity of microbial communities [47, 48]. To address these limitations, we first examined sample coverage using species accumulation curves, as implemented in *iNEXT* [49, 50], then compared effective numbers of species (Hill numbers) based on Shannon entropy and Simpson diversity index to robustly characterize alpha diversity of pre-transfer skin, leaf, and soil samples. The *iNEXT* algorithm adjusts for unseen taxa by subsampling without replacement, then extrapolating from successively smaller subsamples to construct a curve representing expected alpha diversity for a given community as a function of sampling effort. This type of asymptotic species richness estimation is preferable to interpolation or rarefaction, which downsamples to the lowest sample size and discards a potentially large amount of data [51]. To quantify effects of soil and leaf propagule transfers on skin alpha diversity, we used the paired sample t-test, with the exception of the leaf transfer comparison between T00 and T02, which failed to meet requirements of normality and sphericity and was tested with the non-parametric Friedman test.

To examine beta diversity of outdoor soil, potting mix, plant leaves, and skin, we visualized clustering in a principal coordinates analysis (PCoA) ordination and performed permutational multivariate analysis of variance (PERMANOVA) using the `adonis` function in `vegan` [52] on Morisita-Horn dissimilarities. The abundance-based Morisita-Horn dissimilarity index was selected because it is robust against differences in sampling depth and undersampling [53, 54], both of which conditions are present in these data. Due to the high level of dissimilarity observed for the two types of substrates, we further investigated taxonomic differences between outdoor soil and potting mix using a negative binomial generalized linear model, as implemented in DESeq2 [55]. Degree of dissimilarity between donor communities and recipient skin communities at different post-transfer time points was tested with ANOVA using Morisita-Horn index.

We assessed persistence of specific soil- and leaf-associated bacterial taxa on skin by first selecting ASVs present in skin experimental samples after the transfer event (T02) that were also present in soil/leaf donor samples, but not present in skin baseline samples. Each skin sample was compared only with the corresponding soil/leaf donor sample; that is, samples were not aggregated by type. From this list of transferred ASVs, we filtered out those that had less than 0.001 relative abundance, sample-wise, and then visualized occurrence and abundance as a heatmap.

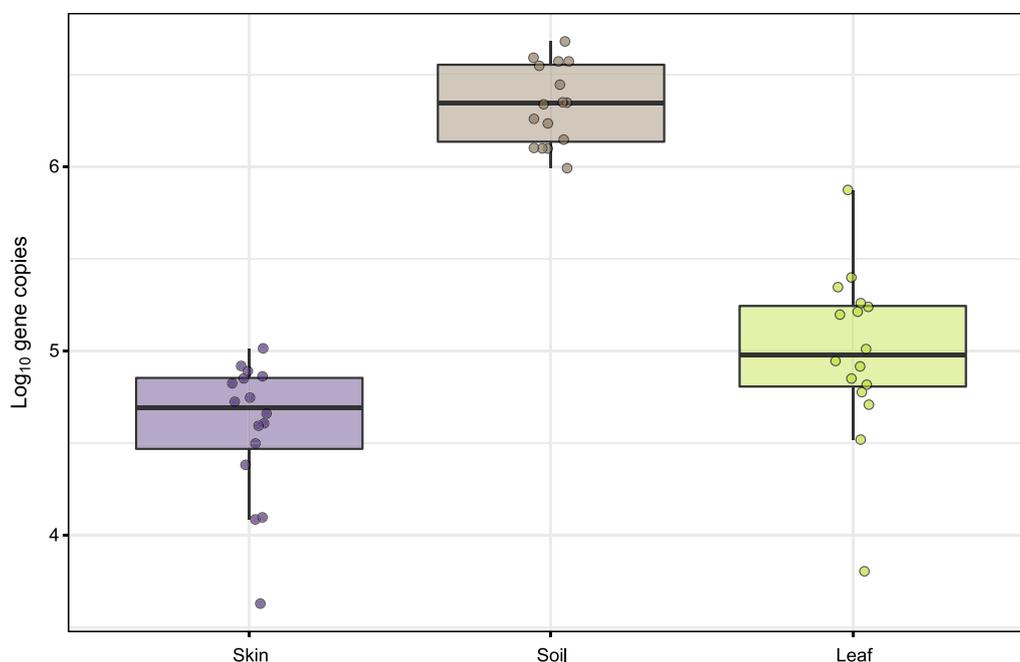
## Results

### Bacterial community structure of indoor plant leaves, substrates, and baseline skin samples

#### Overview

We collected microbial samples from two types of plant substrates (outdoor soil and potting mix), leaf tops and bottoms of 14 indoor plants, representing five different genera—*Calathea*, *Dieffenbachia*, *Dracaena*, *Sanseveria*, and *Spathiphyllum*, and human skin before and after transferring soil and leaf microbiota. After quality filtering, we observed a total of 6,622,107 reads, representing 12,864 unique amplicon sequence variants (ASVs) across 22 bacterial Phyla. Outdoor soil samples had, on average, over an order of magnitude greater estimated bacterial abundance (i.e. 16S rRNA gene copy numbers) compared to leaf top surface samples (Fig. 1; Tukey’s HSD:  $\beta_{\text{soil}} = 1.3$ ,  $P < 0.005$ ). Prior to swab transfers, skin had lower absolute abundance of bacterial cells than either outdoor soil (Tukey’s HSD:  $\beta = -1.7$ ,  $P < 0.005$ ) or leaf top surfaces (Tukey’s HSD:  $\beta = -0.41$ ,  $P = 0.01$ ) with the caveat that samples were not normalized by dry weight or surface area and are intended to be interpreted as estimates of propagule size for the simulated touch transfer event. Potting mix and leaf bottom surfaces were not included in qPCR assays.

Substrate (outdoor soil and potting mix samples aggregated) communities were dominated by Actinobacteria



**Fig. 1** Log<sub>10</sub> bacterial 16S gene copy abundances for skin, outdoor soil, and leaf samples prior to the transfer event. Note that samples were not normalized by dry weight or surface area; skin samples represent a 3 cm<sup>2</sup> surface area, soil samples represent 0.0075 g of soil, and leaf samples represent a 100 cm<sup>2</sup> surface area

(44%), Proteobacteria (25.7%), Gemmatimonadetes (19.1%), and Verrucomicrobia (3.89%). Leaf communities (top and bottom surfaces aggregated) were inhabited primarily by members of Actinobacteria (41.4%), Deinococcus-Thermus (30%), Proteobacteria (15.4%), and Bacteroidetes (8.63%). Baseline skin samples were largely dominated by Actinobacteria (65.1%), Proteobacteria (21.8%), Bacteroidetes (9.45%), and Firmicutes (2.31%).

The most abundant ASV found in substrate samples was identified as a member of *Sphingomonas*, comprising 3.36% of all sequences; on leaves *Aeromicrobium* sp. was the most abundant ASV, comprising 4.17% of all sequences. The most abundant ASV observed in pre-transfer skin samples was *Propionibacterium* sp., comprising 44.7% of sequences. At baseline, leaf and skin samples shared 327 ASVs, while soil and skin samples shared only 54 ASVs (Fig. 2). Leaf bacterial communities had the highest number of unique ASVs, more than double the number observed in either skin or soil communities. Effectively all baseline skin samples were characterized by high relative abundances of four genera—*Streptococcus*, *Staphylococcus*, *Corynebacterium*, and *Propionibacterium*.

**Alpha diversity**

In general, sample coverage was high and species accumulation curves showed that most samples were close to the asymptotic estimates of community richness (Additional file 1: Fig. S3). Leaf samples had the highest average observed numbers of species and the widest variance, however, soil had higher effective numbers of species than leaves, based on Shannon entropy (Table 1; Tukey’s HSD:  $\beta = 42, P = 0.01$ ) and Simpson index (Tukey’s HSD:  $\beta = 38, P < 0.005$ ). Estimates for the effective numbers of

species are lower than observed richness because microbial communities are typically characterized by having a long tail of rare species, which are more difficult to detect in high-biomass communities [25]. Thus, the number of equally-abundant species needed to achieve the same Shannon entropy value as the observed community is much lower. Since leaf communities had higher numbers of observed ASVs but lower effective numbers of ASVs, we conclude that leaves tended to have greater bacterial richness but lower evenness than soil. Baseline skin samples had the lowest average observed and effective numbers of species, based on Shannon entropy (Table 1; Tukey’s HSD:  $\beta_{\text{skin-soil}} = -87.7, P < 0.005, \beta_{\text{skin-leaf}} = -45.7, P < 0.005$ ) and Simpson index (Tukey’s HSD:  $\beta_{\text{skin-soil}} = 57.3, P < 0.005, \beta_{\text{skin-leaf}} = 19.3, P < 0.005$ ).

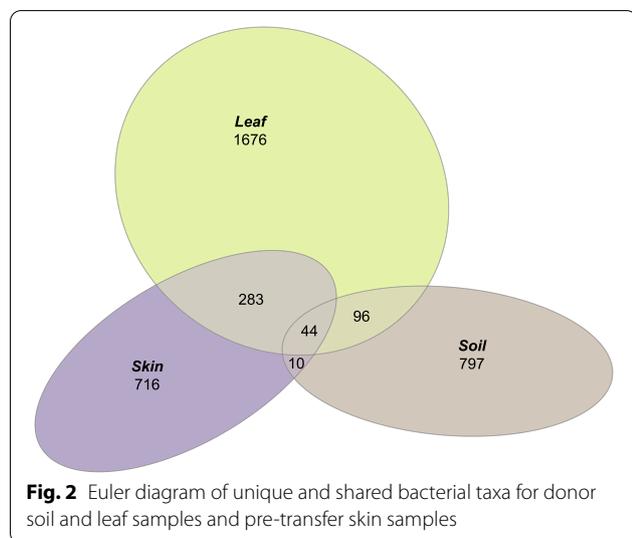
**Beta diversity**

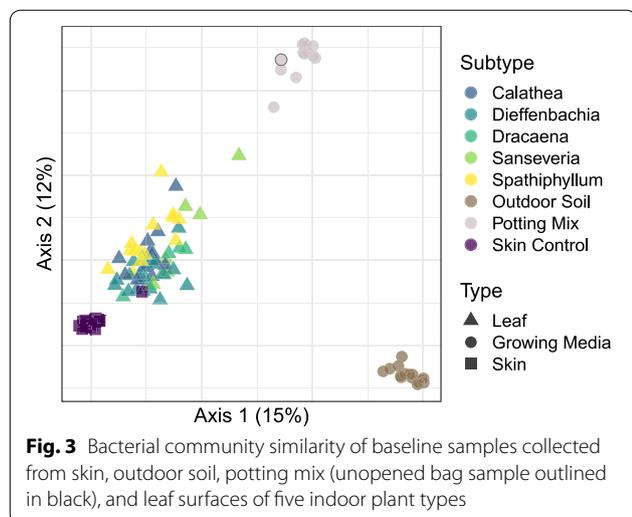
Bacterial communities found in potting mix samples were compositionally dissimilar from those found in outdoor soil samples (PERMANOVA:  $R^2 = 0.74, P < 0.005$ ) and both were distinct from skin and plant leaf communities (Fig. 3; PERMANOVA:  $R^2 = 0.21, P < 0.005$ ). Despite collecting potting mix samples from pots containing plants, we did not observe an effect of plant type on community dissimilarity (PERMANOVA:  $R^2 = 0.06, P = 0.14$ ). Additionally, the sample from an unopened potting mix bag was indistinguishable from other potting mix samples, suggesting that the effect of watering and proximity to plant roots was minimal or overshadowed by the differences between potting mix and outdoor soil.

**Table 1** Mean observed and estimated effective numbers of bacterial ASVs (based on Shannon entropy and Simpson index) of bacterial ASVs for leaf, soil, and skin samples prior to the transfer event

Type	N	Observed	Eff. Species <sub>shan</sub>	Eff. Species <sub>simp</sub>
Leaf	59	215.6 (±38.4)	63.3 (±11.7)	26.0 (±4.4)
Calathea	14	133.3 (±25.6)	37.6 (±9.3)	15.4 (±4.3)
Dieffenbachia	18	299.5 (±90.2)	94.5 (±34.5)	32.5 (±11.7)
Dracaena	7	334.3 (±212.0)	50.1 (±9.9)	26.6 (±7.8)
Sanseveria	6	206.0 (±37.3)	87.0 (±24.2)	42.1 (±13.4)
Spathiphyllum	14	134.9 (±21.9)	45.3 (±13.6)	21.0 (±7.3)
Soil	28	176.0 (±7.5)	105.3 (±5.0)	64.0 (±3.2)
Outdoor.	16	179.2 (±10.9)	113.8 (±7.5)	69.0 (±4.6)
Soil	12	171.8 (±10.3)	93.9 (±4.5)	57.2 (±3.6)
Skin	47	124.8 (±7.4)	17.6 (±1.8)	6.7 (±1.1)
Female	24	134.8 (±13.1)	18.0 (±2.9)	7.6 (±1.9)
Male	23	114.5 (±6.1)	17.1 (±2.3)	5.7 (±0.9)

Standard error of the mean shown in parentheses





A number of genera distinguished microbial communities in potting mix versus outdoor soil (Additional file 1: Figs. S4 and S5).

Different indoor plant genera and, to a lesser extent, individuals within the same genus tended to have different leaf surface microbiome composition (Additional file 1: Figs. S6 and S7). Even within the same individual plant (in particular, *Dieffenbachia* plant P16), samples from different leaves sometimes had wide variation in genus-level composition. In addition to the effect of plant type, leaf surface location (top vs. bottom) also had a small but significant effect on community dissimilarity, and there was a weak interaction effect with host species (Table 2). We did not detect an effect of plant nurseries on microbial community dissimilarity (PERMANOVA:  $R^2 = 0.02$ ,  $P = 0.15$ ).

**Magnitude and persistence of microbial transfer to skin depend on source type**

Alpha diversity of recipient skin receiving soil propagules increased dramatically after the transfer event (Fig. 4; paired t-test:  $t_{15} = - 8.1$ ,  $P < 0.005$ ) and remained elevated for 24 h (paired t-test:  $t_7 = - 3.7$ ,  $P = 0.01$ ). Subjects who were assigned to the hand-washing group had a substantial decrease in alpha diversity following the wash,

resulting in levels that were not significantly different from baseline (paired t-test:  $t_7 = - 2.0$ ,  $P = 0.08$ ). Recipient skin that received microbial propagules from leaves had only a small increase in alpha diversity following transfer (Friedman test:  $\chi^2_1 = 8.1$ ,  $P < 0.005$ ), which disappeared after both the wash (paired t-test:  $t_7 = 0.62$ ,  $P = 0.55$ ) and the 24-h period (paired t-test:  $t_6 = - 1.7$ ,  $P = 0.14$ ). Alpha diversity for skin-to-skin controls did not increase after the transfer event (paired t-test:  $t_{15} = - 0.94$ ,  $P = 0.36$ ).

Following the transfer event, community composition of skin areas that received soil microbial propagules strongly resembled donor soil compared to the pre-transfer state (Fig. 5 and Additional file 1: Fig. S8). Communities observed on the skin remained significantly more similar to soil communities, even after 24 h (ANOVA:  $F_{1,29} = 161.4$ ,  $P < 0.005$ ) and through a soap and water wash (ANOVA:  $F_{1,29} = 7.6$ ,  $P = 0.02$ ). Post-transfer samples from skin areas that received leaf microbial propagules also resembled donor communities more than baseline skin, although this change was commensurately smaller compared to the soil transfer experiments. At the 24-h census, leaf recipient skin communities were not more similar to donor communities than baseline skin (ANOVA:  $F_{1,27} = 3.0$ ,  $P = 0.10$ ). After washing, recipient skin was more dissimilar from leaf donors than baseline skin (ANOVA:  $F_{1,27} = 10.5$ ,  $P = 0.01$ ). Control skin samples, which received propagules from an adjacent area of skin, became less similar to the initial pre-transfer (T00) sample over time, possibly due to spatial variation.

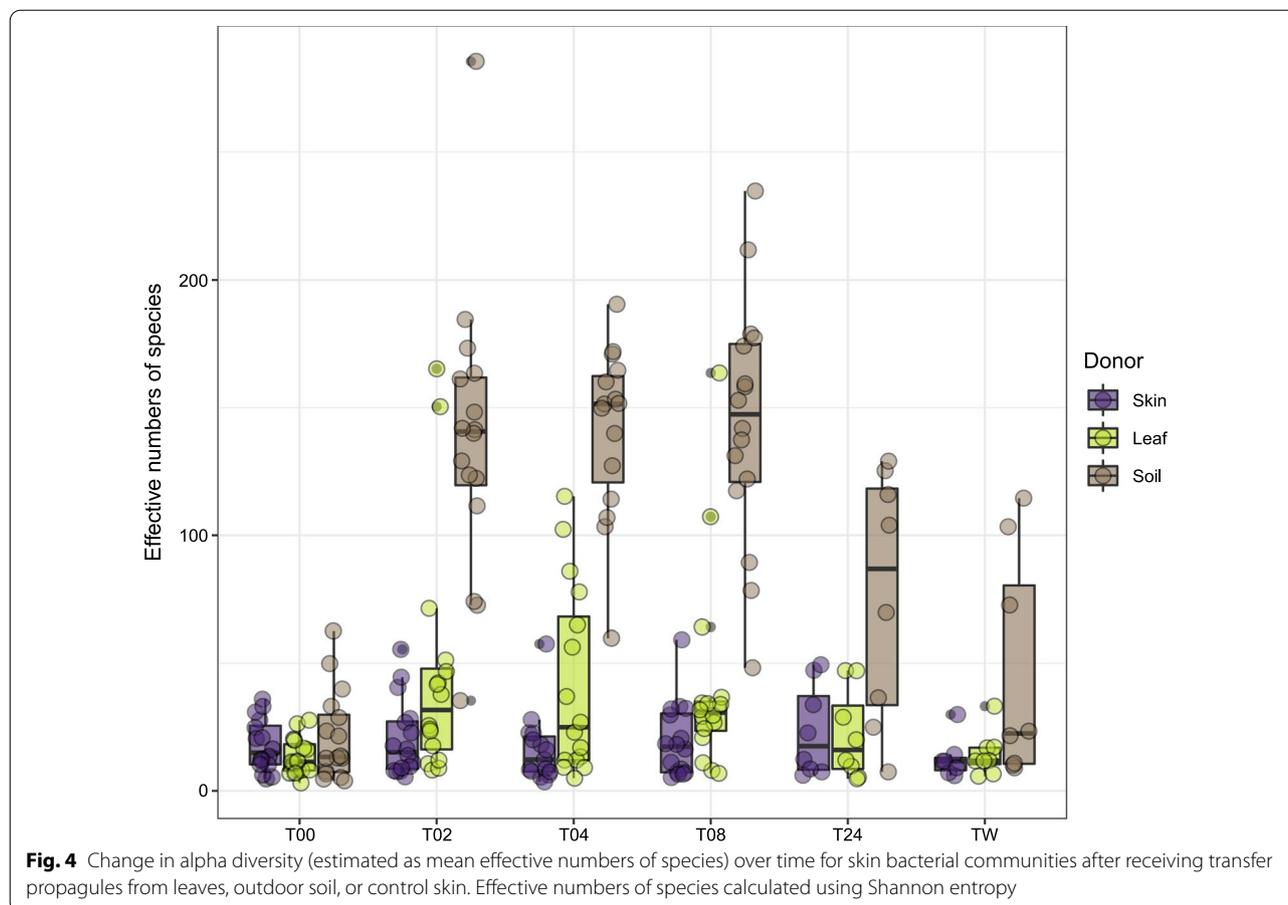
In total, 291 ASVs found in soil donor samples, but not observed in baseline skin samples of the corresponding individual, were enriched on the skin 2 h after the soil transfer event (Additional file 1: Fig. S9). Many of these persisted at least 8 h post-transfer, and some were not completely removed even after washing or after a 24-h period. In contrast, few ASVs associated with leaf donor samples were substantially enriched on skin at the 2-h or later censuses (Additional file 1: Fig. S10).

**Discussion**

It has been suggested that modifying the indoor microbiome through 'bioinformed design' [56] could help promote human well-being by engineering exposures to

**Table 2** Plant type and leaf surface (top vs. bottom) were significant predictors of bacterial community dissimilarity

Variable	Df	Sums of Sqs	Mean Sqs	F. Model	R2	P value
Plant type	4	3.73	0.93	3.10	0.17	0.0002
Leaf surface	1	1.37	1.37	4.55	0.064	0.0001
Type:Surface	4	1.50	0.38	1.25	0.07	0.024
Residuals	49	14.76	0.30	NA	0.69	NA
Total	58	21.37	NA	NA	1.00	NA



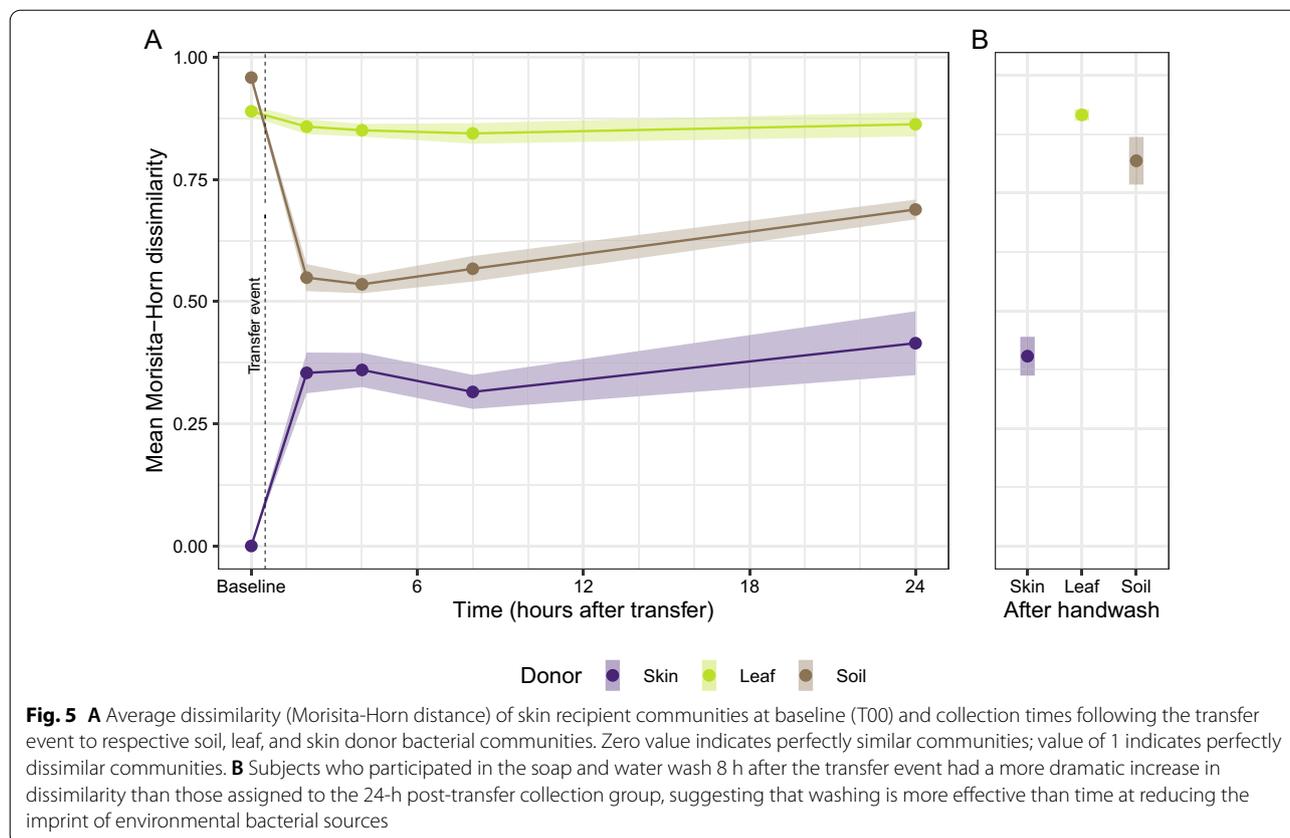
potentially-beneficial microorganisms. In particular, built environments that are highly controlled and sanitized, such as hospitals and cleanrooms, may experience a loss of microbiome diversity and development of antibiotic resistance as a result of stringent cleaning regimes [57]. One possible avenue for re-establishing indoor microbial diversity is through the addition of houseplants [8, 17, 18]. However, characterizing the innate microbiome of houseplants is a necessary first step towards achieving such goals. This study represents an initial effort to describe the microbial communities associated with leaves and substrates of several common houseplants, as well as their ability to transfer to human skin.

#### Houseplant microbiome characteristics

In this study, we found that community composition of outdoor soil was distinct from potting mix, an effect driven by the enrichment of 40 bacterial taxa, including *Arthrobacter*, *Gaiella*, *Gemmatimonas*, *Massilia*, and *Sphingomonas* in soil samples, and enrichment of 33 other taxa, including *Actinospica*, *Gordonia*, *Hyphomicrobium*, *Mucilaginibacter*, *Nocardia*, and *Rhodanobacter*,

in potting mix (Additional file 1: Figs. S4 and S5). Interestingly, close relatives of many taxa enriched in potting mix are known to inhabit acidic, nutrient-deficient, and/or polluted soil environments [58–60]. *Rhodanobacter* and *Hyphomicrobium*, in particular, have been previously recovered from potting media [61, 62], sometimes associated with *Spathiphyllum* plants where they may play a protective role against root-rot pathogens [63]. Some researchers have suggested that microorganisms abundant in houseplant substrates are responsible for VOC removal in living biofilters, due to their ability to degrade a wide range of organic pollutants [62].

Indoor plant leaf microbiomes characterized in this study were dominated by members of Actinobacteria, Deinococcus-Thermus, Proteobacteria, and Bacteroidetes, which are the same highly abundant phyla (with the exception of Deinococcus-Thermus) typically present in the phyllosphere in outdoor settings [64–66]. Genera commonly found on plant leaves in outdoor studies, such as *Pseudomonas*, *Sphingomonas*, *Methylobacterium*, *Bacillus*, *Massilia*, *Arthrobacter*, and *Pantoea* [67], were also highly abundant in this



study, though several genera appeared to be preferentially associated with certain types of indoor plants (Additional file 1: Fig. S7). Specifically, we noted that genus *Aurantimonas* was enriched on *Calathea* plants, *Devosia* on *Dieffenbachia*, and *Methylobacterium* on *Spathiphyllum* plants. Close relatives of these bacterial genera are known for their stress-resistance [65, 68], allowing them to inhabit harsh environmental conditions, such as those generally ascribed to leaf surfaces. A speculative explanation for the greater richness but lower evenness in leaf samples compared with substrate samples is the likelihood of more transient taxa (i.e., taxa deposited from air) present on leaf surfaces than in the substrate matrix. This is a likely possibility, since some plant leaves were visibly dusty prior to sampling. Previous surveys of indoor air have found up to  $10^6$  bacterial cells per  $m^3$ , roughly similar to bacterial abundance in outdoor air [69]. Alpha diversity of indoor air may be lower [69, 70], equal [71], or higher than outdoor air [72], depending on building type and ventilation system. Studies focusing on indoor dust have found between  $10^3$ – $10^6$  bacterial particles (variously quantified as gene copies, genomes, or CFUs) per mg of dust [25, 73, 74] and greater alpha diversity than outdoor dust [75]. Thus, deposition from indoor air is expected

to be a significant source of the diversity observed in leaf samples.

**Transfer and persistence on human skin**

Alpha diversity of skin receiving soil microbial propagules increased immediately after the transfer event and remained elevated for at least 24 h, though not through washing; effects of leaf propagules were much less pronounced and did not last as long. These effects are likely a function of donor community absolute abundance, as Shmida and Wilson [76] stated that mass effects will always increase alpha diversity.

Community similarity between donor propagules and skin also increased following the transfer event, again, more so for soil transfer than for leaf. This may be partly explained by a combination of the initial dissimilarity of donor microbial communities to baseline skin communities and donor propagule absolute abundance. Soil microbial communities were highly distinct from those inhabiting baseline skin (Fig. 3) and also had well over an order of magnitude greater absolute abundance (Fig. 1), whereas leaf microbial communities were much more similar to baseline skin and had only marginally greater absolute abundance. We speculate that leaf and skin microbiomes were more similar to each other than to soil

because they shared many similar characteristics, such as being relatively dry and exposed to air and UV radiation. Both the indoor plants and human subjects in this study spent much of their time inside buildings and, therefore, may have harbored many transient bacterial taxa associated with indoor air. In contrast, the soil used for simulated touch contact events was collected directly from a farm approximately 180 km away.

Of the 291 ASVs that were transferred from soil to skin, a number of genera, including *Arthrobacter*, *Bradyrhizobium*, *Gaiella*, *Massilia*, *Mycobacterium*, and *Sphingomonas*, remained detectable on the recipients' skin for the entire 24-h study period, through resumption of daily activities and even a soap and water wash (Additional file 1: Fig. S9). On average, the relative abundance of taxa on skin post-transfer was correlated to their relative abundance in the donor community, indicating that, for many taxa, transfer occurs proportionally to relative abundance in the donor community. This finding is consistent with existing theoretical frameworks of metacommunity ecology and invasion biology; namely, the mass effects paradigm in metacommunity ecology, which describes the ability of organisms to establish in sites where they cannot self-maintain [76], and a parallel concept in invasion biology—propagule pressure [77]. Most exogenous taxa remained on human skin for only several hours, whereas a small number were detected on subjects for at least 24 h, dependent on their abundance in the donor community. Similarly, other research has indicated that the probability of successful colonization by microorganisms from environmental sources depends largely on their absolute abundances in source habitats [78, 79]. Ultimately, washing the recipient area with soap and water proved most effective at removing the imprint of donor bacterial propagules. Both of these results are consistent with prior research demonstrating that direct skin contact with soil leads to a substantial, but transient, alteration of skin microbiome diversity and composition [80]. The practical effect of this is that the propagule pressure for abundant taxa emigrating to the skin is higher; on longer time scales, this implies that the probability of colonization (as distinct from the probability of acquisition, studied here) is likely to be higher for those taxa that maintain high abundance in source communities that are often contacted [81–83].

### Relevance

Touch contact with substrates such as soil or plants, which bear their own complex assemblages of microbial residents, may lead to the wholesale transmission of microbial communities, a phenomenon known as community coalescence [84]. It is possible that regular acquisition through dispersion (e.g., contact) events and

the transient dynamics of resetting the microbiome are enough to explain the increased variation observed on the skin relative to the gut and oral microbiomes [85]. That is, the skin microbiome may be always in a non-equilibrium state, 'recovering' from a recent coalescence event. Differential persistence through time for different microbes (potentially driven by differential abundance in the source communities) means that there will be complex behavior resulting from the interaction of different time scales: the time scales on which microbes are lost (which vary by microbe, and by other disturbance events like washing or skin sloughing), and the time scales on which new contact events happen. Thus, explaining microbial community composition of skin at a given moment must take into account, not only long-term commensal microbiota, but also the transient dynamics of multiple, interacting coalescence events—the current microbial assemblage is the result of the combination of multiple immigration events in time, with each microbe acquired having its own particular decay curve, all of which must be considered together to explain any given assemblage.

Although environmental microbiota are unlikely to permanently colonize skin [86], they may be able to indirectly influence human health by interacting with commensal skin microbiota, which can then modulate the immune system [87], or even perform the same role directly [88]. Given the observed importance of source biomass on the transfer and persistence of environmentally-acquired microbiota, these results suggest that continued study of hand hygiene [89] and substrates commonly encountered in the built environment [22, 90–95] may help promote safe and salutogenic buildings in the future.

### Conclusion

Exposure to indoor biodiversity is an increasingly relevant topic as human populations continue to urbanize and individuals spend increasingly more of their lives inside buildings. In addition to their well-researched beneficial effects on mental well-being, indoor plants may also interact with human health by contributing soil- and plant-associated microbial diversity to indoor environments. However, much remains to be understood about the microbial communities inhabiting houseplants and their substrates, as well as their potential interactions with our own commensal microbiomes. This study characterized the microbial communities of several common houseplants and is one of the first culture-independent studies comparing microbial communities of outdoor soil and manufactured potting mix. It also provides a first glimpse of the bacterial relations between humans and houseplants.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40793-022-00457-7>.

**Additional file 1.** Supplementary information.

### Acknowledgements

The authors would like to thank Dr. Jessica L. Green, who provided laboratory space, mentorship, and aid in study design while serving as a dissertation co-advisor (with BB) for ACB. We would also like to thank Hannah Wilson and Clarisse Betancourt for sample processing and sequence library preparation, and Maggie Weitzman (University of Oregon's Genomics & Cell Characterization Core Facility) for sequencing and advice. A special thanks to the Energy Studies in Buildings Laboratory (ESBL) for use of their climate-controlled chamber, and to Jason Stenson in particular for his assistance in using the chamber. We also thank Marshall Bockrath for statistical consulting, and Isabelle O'Neal for graphic design assistance.

### Author contributions

GM analyzed the data, prepared the figures and tables, and wrote and revised the manuscript. AKF helped analyze the data, prepare the figures and tables, and write and/or revise the manuscript. RV helped analyze the data, prepare the figures and tables, and write and/or revise the manuscript. MEM helped analyze the data, prepare the figures and tables, and write and/or revise the manuscript. RH helped execute the study and write and/or revise the manuscript. ACB conceived, designed, and executed the study, and helped analyze the data, prepare the figures and tables, and write and/or revise the manuscript. KGV DW helped analyze the data and write and/or revise the manuscript. BJMB helped conceive, design, and execute the study and helped write and/or revise the manuscript. All authors read and approved the final manuscript.

### Funding

This work was funded by a grant to the Biology and the Built Environment Center from the Alfred P. Sloan Foundation Microbiology for the Built Environment Program (no. G-2015-14023).

### Availability of data and materials

The 16S rRNA raw sequence data have been deposited in the NCBI SRA database under accession number PRJNA767119. All other data used in this study have been deposited in the open access data repository Figshare (DOI: 10.6084/m9.figshare.16655140).

### Declarations

#### Ethics approval and consent to participate

The subjects were informed as to the full nature and design of the study and gave written consent to be participants. This study and its associated research protocols were approved by the Institutional Review Board at the University of Oregon on December 23, 2013 (Approval Number 03112016.016). All researchers assigned to this protocol were CITI certified to work with human subjects. Identities of participants were never recorded on samples or in resulting datasets.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

#### Author details

<sup>1</sup>Biology and the Built Environment Center, University of Oregon, Eugene, OR, USA. <sup>2</sup>Institute of Ecology and Evolution, University of Oregon, Eugene, OR, USA. <sup>3</sup>Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL, USA. <sup>4</sup>United States Department of Agriculture, APHIS, PPQ, Miami, FL, USA. <sup>5</sup>Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA.

Received: 4 January 2022 Accepted: 15 December 2022

Published online: 26 December 2022

### References

- Knuth MJ, Khachatryan H, Hall CR. How consistent are consumers in their decisions? Investigation of houseplant purchasing. *Behav Sci*. 2021;11(5):73.
- Bulgari R, Petrini A, Cocetta G, Nicoletto C, Ertani A, Sambo P, et al. The impact of COVID-19 on horticulture: critical issues and opportunities derived from an unexpected occurrence. *Horticulturae*. 2021;7(6):124.
- Aydogan A, Cerone R. Review of the effects of plants on indoor environments. *Indoor Built Environ*. 2021;30(4):442–60.
- Moya TA, van den Dobbelaer A, Ottelé M, Bluyssen PM. A review of green systems within the indoor environment. *Indoor Built Environ*. 2019;28(3):298–309.
- Han KT, Ruan LW. Effects of indoor plants on self-reported perceptions: a systemic review. *Sustainability*. 2019;11(16):4506.
- Raanaas RK, Evensen KH, Rich D, Sjøstrøm G, Patil G. Benefits of indoor plants on attention capacity in an office setting. *J Environ Psychol*. 2011;31(1):99–105.
- Park SH, Mattson RH. Effects of flowering and foliage plants in hospital rooms on patients recovering from abdominal surgery. *HortTechnology*. 2008;18(4):563–8.
- Berg G, Mahner A, Moissl-Eichinger C. Beneficial effects of plant-associated microbes on indoor microbiomes and human health? *Front Microbiol*. 2014;5:15.
- von Hertzen L, Haahtela T. Disconnection of Man and the Soil: Reason for the Asthma and Atopy Epidemic? *Journal of Allergy and Clinical Immunology*. 2006;117(2):334–44.
- Haahtela T. A biodiversity hypothesis. *Allergy*. 2019;74:1445–56.
- Gilbert J, Knight R. *Dirt is good: the advantage of germs for your child's developing immune system*. New York: St. Martin's Press; 2017.
- Hanski I, von Hertzen L, Fyhrquist N, Koskinen K, Torppa K, Laatikainen T, et al. Environmental biodiversity, human microbiota, and allergy are inter-related. *Proc Natl Acad Sci*. 2012;109(21):8334–9.
- Lehtimäki J, Sinkko H, Hielm-Björkman A, Salmela E, Tiira K, Laatikainen T, et al. Skin microbiota and allergic symptoms associate with exposure to environmental microbes. *Proc Natl Acad Sci*. 2018;115(19):4897–902.
- Ege MJ, Mayer M, Normand AC, Genuneit J, Cookson WO, Braun-Falder C, et al. Exposure to environmental microorganisms and childhood asthma. *N Engl J Med*. 2011;364(8):701–9.
- Stein MM, Hrusch CL, Gozdz J, Igartua C, Pivniouk V, Murray SE, et al. Innate immunity and asthma risk in Amish and Hutterite farm children. *N Engl J Med*. 2016;375(5):411–21.
- Rook GA. Regulation of the immune system by biodiversity from the natural environment: an ecosystem service essential to health. *Proc Natl Acad Sci USA*. 2013;110(46):18360–7.
- Mahner A, Moissl-Eichinger C, Berg G. Microbiome interplay: plants alter microbial abundance and diversity within the built environment. *Front Microbiol*. 2015;6:887.
- Mahner A, Haratani M, Schmuck M, Berg G. Enriching beneficial microbial diversity of indoor plants and their surrounding built environment with biostimulants. *Front Microbiol*. 2018;9:2985.
- Ding LJ, Zhou XY, Zhu YG. Microbiome and antibiotic resistance in household dust from Beijing, China. *Environ Int*. 2020;139: 105702.
- Parajuli A, Grönroos M, Siter N, Puhakka R, Vari HK, Roslund MI, et al. Urbanization reduces transfer of diverse environmental microbiota indoors. *Front Microbiol*. 2018;9:84.
- Klepeis NE, Nelson WC, Ott WR, Robinson JP, Tsang AM, Switzer P, et al. The national human activity pattern survey (NHAPS): a resource for assessing exposure to environmental pollutants. *J Expo Anal Environ Epidemiol*. 2001;11(3):231–52.
- Meadow JF, Altrichter AE, Kembel SW, Moriyama M, O'Connor TK, Womack AM, et al. Bacterial communities on classroom surfaces vary with human contact. *Microbiome*. 2014;2(1):7.
- Martin LJ, Adams RI, Bateman A, Bik HM, Hawks J, Hird SM, et al. Evolution of the indoor biome. *Trends Ecol Evol*. 2015;30(4):223–32.
- National Academies of Sciences, Engineering, and Medicine. *Microbiomes of the built environment: a research agenda for indoor*

- microbiology, human health, and buildings. Washington, DC: The National Academies Press; 2017.
25. Fahimipour AK, Hartmann EM, Siemens A, Kline J, Levin DA, Wilson H, et al. Daylight exposure modulates bacterial communities associated with household dust. *Microbiome*. 2018;6(1):1–13.
  26. Meadow JF, Altrichter AE, Bateman AC, Stenson J, Brown G, Green JL, et al. Humans differ in their personal microbial cloud. *PeerJ*. 2015;3: e1258.
  27. Nurminen N, Lin J, Grönroos M, Puhakka R, Kramna L, Vari HK, et al. Nature-derived microbiota exposure as a novel immunomodulatory approach. *Future Microbiol*. 2018;13(7):737–44.
  28. Parajuli A, Hui N, Puhakka R, Oikarinen S, Grönroos M, Selonen VAO, et al. Yard vegetation is associated with gut microbiota composition. *Sci Total Environ*. 2020;713: 136707.
  29. Roslund MI, Puhakka R, Grönroos M, Nurminen N, Oikarinen S, Gazali AM, et al. Biodiversity intervention enhances immune regulation and health-associated commensal microbiota among daycare children. *Sci Adv*. 2020;6(42):eaba2578.
  30. Selway CA, Mills JG, Weinstein P, Skelly C, Yadav S, Lowe A, et al. Transfer of environmental microbes to the skin and respiratory tract of humans after urban green space exposure. *Environ Int*. 2020;145: 106084.
  31. Mills JG, Brookes JD, Gellie NJC, Liddicoat C, Lowe AJ, Sydnor HR, et al. Relating urban biodiversity to human health with the ‘Holobiont’ concept. *Front Microbiol*. 2019;10:550.
  32. Wicaksono WA, Reisenhofer-Grabert T, Erschen S, Kusstatscher P, Berg C, Krause R, et al. Phyllosphere-associated microbiota in built environment: do they have the potential to antagonize human pathogens? *J Adv Res*. 2022;52090123222000467.
  33. Ortega RA, Mahnert A, Berg C, Müller H, Berg G. The plant is crucial: specific composition and function of the phyllosphere microbiome of indoor ornamentals. *FEMS Microbiol Ecol*. 2016;92(12):fw173.
  34. Grice EA, Kong HH, Conlan S, Deming CB, Davis J, Young AC, et al. Topographical and temporal diversity of the human skin microbiome. *Science* (New York, NY). 2009;324(5931):1190–2.
  35. Callahan BJ, Sankaran K, Fukuyama JA, McMurdie PJ, Holmes SP. Bioconductor workflow for microbiome data analysis: from raw reads to community analyses. *F1000Research*. 2016;5:1492.
  36. Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP. DADA2: high-resolution sample inference from illumina amplicon data. *Nat Methods*. 2016;13(7):581–3.
  37. Quast C, Pruesse E, Yilmaz P, Gerken J, Schweer T, Yarza P, et al. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res*. 2013;41(Database issue):D590–6.
  38. Davis NM, Proctor DM, Holmes SP, Relman DA, Callahan BJ. Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. *Microbiome*. 2018;6(1):1–14.
  39. Maeda H, Fujimoto C, Haruki Y, Maeda T, Kokeguchi S, Petelin M, et al. Quantitative real-time PCR using TaqMan and SYBR green for *Actinobacillus actinomycetemcomitans*, *Porphyromonas gingivalis*, *Prevotella intermedia*, tetQ gene and total bacteria. *FEMS Immunol Med Microbiol*. 2003;39(1):81–6.
  40. Braid MD, Daniels LM, Kitts CL. Removal of PCR inhibitors from soil DNA by chemical flocculation. *J Microbiol Methods*. 2003;52(3):389–93.
  41. Ramakers C, Ruijter JM, Deprez RHL, Moorman AFM. Assumption-free analysis of quantitative real-time polymerase chain reaction (PCR) data. *Neurosci Lett*. 2003;339(1):62–6.
  42. R Development Core Team. R: a language and environment for statistical computing; 2010.
  43. Haegeman B, Hamelin J, Moriarty J, Neal P, Dushoff J, Weitz JS. Robust estimation of microbial diversity in theory and in practice. *ISME J*. 2013;7(6):1092–101.
  44. Chiu CH, Chao A. Estimating and comparing microbial diversity in the presence of sequencing errors. *PeerJ*. 2016;4: e1634.
  45. Willis A. Rarefaction, alpha diversity, and statistics. *bioRxiv*; 2017.
  46. Willis AD. Rigorous statistical methods for rigorous microbiome science. *mSystems*. 2019;4(3):e00117-19.
  47. Bullington LS, Lekberg Y, Larkin BG. Insufficient sampling constrains our characterization of plant microbiomes. *Sci Rep*. 2021;11(1):3645.
  48. Grey EK, Bernatchez L, Cassey P, Deiner K, Deveney M, Howland KL, et al. Effects of sampling effort on biodiversity patterns estimated from environmental DNA metabarcoding surveys. *Sci Rep*. 2018;8(1):8843.
  49. Hsieh TC, Ma KH, Chao A. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol*. 2016;7(12):1451–6.
  50. Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, et al. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr*. 2014;84(1):45–67.
  51. Colwell RK, Coddington JA, Hawksworth DL. Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond B Biol Sci*. 1994;345(1311):101–18.
  52. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. *Vegan: community ecology package*; 2018.
  53. Huse S, Welch DBM, Sogin ML. Sequencing errors, diversity estimates, and the rare biosphere. In: Choffnes RE, Olsen L, Wizemann T, editors. *The science and applications of microbial genomics*. Washington, D.C.: National Academies Press; 2012.
  54. Beck J, Holloway JD, Schwanghart W. Undersampling and the measurement of beta diversity. *Methods Ecol Evol*. 2013;4(4):370–82.
  55. Love MI, Huber W, Anders S. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biol*. 2014;15(12):1–21.
  56. Green JL. Can bioinformed design promote healthy indoor ecosystems? *Indoor Air*. 2014;24(2):113–5.
  57. Mahnert A, Moissl-Eichinger C, Zojer M, Bogumil D, Mizrahi I, Rattei T, et al. Man-made microbial resistances in built environments. *Nat Commun*. 2019;10(1):968.
  58. Golinska P, Zucchi TD, Silva L, Dahm H, Goodfellow M. *Actinospica durhamensis* Sp. Nov. isolated from a spruce forest soil. *Antonie van Leeuwenhoek*. 2015;108(2):435–42.
  59. Arenskötter M, Bröker D, Steinbüchel A. Biology of the metabolically diverse genus *Gordonia*. *Appl Environ Microbiol*. 2004;70(6):3195–204.
  60. Moore RL. The biology of hyphomicrobium and other prosthecate, budding bacteria. *Ann Rev Microbiol*. 1981;35(1):567–94.
  61. Al-Sadi AM, Al-Zakwani HA, Nasehi A, Al-Mazroui SS, Al-Mahmooli IH. Analysis of bacterial communities associated with potting media. *Springerplus*. 2016;5(1):74.
  62. Russell JA, Hu Y, Chau L, Pauliushchik M, Anastopoulos I, Anandan S, et al. Indoor-biofilter growth and exposure to airborne chemicals drive similar changes in plant root bacterial communities. *Appl Environ Microbiol*. 2014;80(16):4805–13.
  63. De Clercq D, Van Trappen S, Cleenwerck I, Ceustermans A, Swings J, Coosemans J, et al. *Rhodanobacter spathiphylli* Sp. Nov., a gammaproteobacterium isolated from the roots of spathiphyllum plants grown in a compost-amended potting mix. *Int J System Evolut Microbiol*. 2006;56(8):1755–9.
  64. Vorholt JA. Microbial life in the phyllosphere. *Nat Rev Microbiol*. 2012;10(12):828–40.
  65. Delmotte N, Knief C, Chaffron S, Innerebner G, Roschitzki B, Schlapbach R, et al. Community proteogenomics reveals insights into the physiology of phyllosphere bacteria. *Proc Natl Acad Sci*. 2009;106(38):16428–33.
  66. Wagner MR, Lundberg DS, del Rio TG, Tringe SG, Dangel JL, Mitchell-Olds T. Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. *Nat Commun*. 2016;7(1):12151.
  67. Bulgarelli D, Schlaeppli K, Spaepen S, van Themaat EVL, Schulze-Lefert P. Structure and functions of the bacterial microbiota of plants. *Annu Rev Plant Biol*. 2013;64(1):807–38.
  68. Talwar C, Nagar S, Kumar R, Scaria J, Lal R, Negi RK. Defining the environmental adaptations of genus *devosia*: insights into its expansive short peptide transport system and positively selected genes. *Sci Rep*. 2020;10(1):1151.
  69. Kembel SW, Jones E, Kline J, Northcutt D, Stenson J, Womack AM, et al. Architectural design influences the diversity and structure of the built environment microbiome. *ISME J*. 2012;6(8):1469–79.
  70. Prussin AJ, Garcia EB, Marr LC. Total concentrations of virus and bacteria in indoor and outdoor air. *Environ Sci Technol Lett*. 2015;2(4):84–8.
  71. Meadow JF, Altrichter AE, Kembel SW, Kline J, Mhuireach G, Moriyama M, et al. Indoor airborne bacterial communities are influenced by ventilation, occupancy, and outdoor air source. *Indoor Air*. 2013;24(1):41–8.
  72. Kodama AM, McGee RL. Airborne microbial contaminants in indoor environments. naturally ventilated and air-conditioned homes. *Arch Environ Health Int J*. 1986;41(5):306–11.

73. Dannemiller KC, Weschler CJ, Peccia J. Fungal and bacterial growth in floor dust at elevated relative humidity levels. *Indoor Air*. 2017;27(2):354–63.
74. Chęcinska A, Probst AJ, Vaishampayan P, White JR, Kumar D, Stepanov VG, et al. Microbiomes of the dust particles collected from the international space station and spacecraft assembly facilities. *Microbiome*. 2015;3(1):50.
75. Barberán A, Dunn RR, Reich BJ, Pacifci K, Laber EB, Menninger HL, et al. The ecology of microscopic life in household dust. *Proc R Soc B*. 2015;282(1814):20151139.
76. Shmida A, Wilson MV. Biological determinants of species diversity. *J Biogeogr*. 1985;12(1):1.
77. Brown BL, Barney JN. Rethinking biological invasions as a metacommunity problem. *Front Ecol Evol*. 2021;8: 584701.
78. Acosta F, Zamor RM, Najjar FZ, Roe BA, Hambright KD. Dynamics of an experimental microbial invasion. *Proc Natl Acad Sci USA*. 2015;112(37):11594–9.
79. Klein G, MacIntosh K, Kaczmarska I, Ehrman JM. Diatom survivorship in ballast water during trans-pacific crossings. *Biol Invasions*. 2010;12(5):1031–44.
80. Grönroos M, Parajuli A, Laitinen OH, Roslund MI, Vari HK, Hyöty H, et al. Short-term direct contact with soil and plant materials leads to an immediate increase in diversity of skin microbiota. *MicrobiologyOpen*. 2018;8(3): e00645.
81. Williamson MH, Fitter A. The characters of successful invaders. *Biol Cons*. 1996;78(1):163–70.
82. Simberloff D. The role of propagule pressure in biological invasions. *Annu Rev Ecol Syst*. 2009;40(1):81–102.
83. Cassey P, Delean S, Lockwood JL, Sadowski JS, Blackburn TM. Dissecting the null model for biological invasions: a meta-analysis of the propagule pressure effect. *PLoS Biol*. 2018;16(4): e2005987.
84. Rillig MC, Antonovics J, Caruso T, Lehmann A, Powell JR, Veresoglou SD, et al. Interchange of entire communities: microbial community coalescence. *Trends Ecol Evol*. 2015;30(8):470–6.
85. Caporaso JG, Lauber CL, Costello EK, Berg-Lyons D, Gonzalez A, Stombaugh J, et al. Moving pictures of the human microbiome. *Genome Biol*. 2011;12(5):R50.
86. Oh J, Byrd AL, Park M, Kong HH. Temporal stability of the human skin microbiome. *Cell*. 2016;165(4):854–66.
87. Naik S, Bouladoux N, Linehan JL, Han SJ, Harrison OJ, Wilhelm C, et al. Commensal-dendritic-cell interaction specifies a unique protective skin immune signature. *Nature*. 2015;520(7545):104–8.
88. Fyhrquist N, Ruokolainen L, Suomalainen A, Lehtimäki S, Veckman V, Vendelin J, et al. *Acinetobacter* species in the skin microbiota protect against allergic sensitization and inflammation. *J Allergy Clin Immunol*. 2014;134(6):1301–1309.e11.
89. Vandegrift R, Bateman AC, Siemens KN, Nguyen M, Wilson HE, Green JL, et al. Cleanliness in context: reconciling hygiene with a modern microbial perspective. *Microbiome*. 2017;5(1):1–12.
90. Mhuireach GA, Dietz L, Griffiths W, Horve PF, Laguerre A, Northcutt D, et al. Differing effects of four building materials on viable bacterial communities and VOCs. *Dev Built Environ*. 2021;7: 100055.
91. Chase J, Fouquier J, Zare M, Sonderegger DL, Knight R, Kelley ST, et al. Geography and location are the primary drivers of office microbiome composition. *mSystems*. 2016;1(2):e00022-16.
92. Hu J, Ben Maamar S, Glawe AJ, Gottel N, Gilbert JA, Hartmann EM. Impacts of indoor surface finishes on bacterial viability. *Indoor Air*. 2019;29:551–62.
93. Hui N, Grönroos M, Roslund MI, Parajuli A, Vari HK, Soininen L, et al. Diverse environmental microbiota as a tool to augment biodiversity in urban landscaping materials. *Front Microbiol*. 2019;10:536.
94. Lax S, Smith DP, Hampton-Marcell J, Owens SM, Handley KM, Scott NM, et al. Longitudinal analysis of microbial interaction between humans and the indoor environment. *Science*. 2014;345(6200):1048–52.
95. Stephens B. What have we learned about the microbiomes of indoor environments? *mSystems*. 2016;1(4):e00083-16.

## Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more [biomedcentral.com/submissions](https://biomedcentral.com/submissions)

