Microbial Ecology (2025) 88:7
https://doi.org/10.1007/s00248-025-02505-4

RESEARCH

Yeasts Prefer Daycares and Molds Prefer Private Homes

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Received: 28 November 2024 / Accepted: 12 February 2025

Abstract

Worldwide, people spend most of their time indoors; in their homes, workplaces, schools, and daycares. Indoor fungi can cause negative health effects due to the production of toxins or volatiles that trigger the immune system of the occupants. To what degree indoor fungi (mycobiomes) differ between buildings with different usage is poorly known. Here, we compare the indoor mycobiomes in 123 children's daycare centers and 214 private homes throughout Norway, as revealed by metabarcoding of DNA extracted from dust samples collected by community scientists. Although the fungal richness per se was similar in dust samples from daycares and homes, the fungal community composition differed. Yeast fungi, distributed mainly across the orders Saccharomycetales, Filobasidiales, and Tremellales, were proportionally more abundant in the daycares, while filamentous fungi, including spore-producing molds such as *Aspergillus, Penicillum*, and *Cladosporium*, were relatively more abundant in homes. Number of occupants, which is considerably higher in daycares, correlated significantly with the fungal community shift. We hypothesize that the density of occupants and their age distribution drive the systematic difference of yeasts and filamentous fungi in the two building types.

Keywords Buildings · Citizen science · DNA metabarcoding · Dust · Indoor fungi · Kindergarten

Introduction

Within buildings, conditions for microbial growth are generally harsh due to limited humidity and scarce nutrient availability. However, some microorganisms are adapted to these adverse conditions and can grow and proliferate indoors. Molds and yeasts, both polyphyletic assemblages representing different fungal growth forms, are especially tolerant for the harsh indoor conditions and are often found in surveys of indoor fungal communities [1–9]. Molds are known to affect our health through the volatiles they produce or their aerially spread spores that may trigger our immune system or cause respiratory disease [10–12]. Many yeasts, such as *Candida* and *Malassezia,* are associated with the human body, where they mainly grow as commensals [13]. However, both yeasts and molds can cause superficial infections such as dandruff, atopic dermatitis/eczema, ringworm, and nail infections [14], as well as serious infections in immuno-compromised people, e.g., invasive aspergillosis, mucormycosis, and candidemia [15, 16]. The latter ones increased considerably during the COVID-19 pandemic [17, 18].

In addition to the fungi that can grow and survive indoors, fungal spores are transported indoors from outdoor sources and are detected in DNA-based surveys from the built environment [6–9, 19–21]. Fungal spores spread easily by air into buildings through windows, doors, and the ventilation system. Further, people and pets may function as vectors and transport fungal spores. The proportion of outdoor fungi spreading into buildings varies throughout the year, with a

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Published online: 20 February 2025

higher influx during the plant growth seasons, when fungi also are sporulating outdoors [5, 6, 20, 22].

In parts of the world, children of age 1–6 years spend considerable time inside daycare centers. Daycares are often characterized by a high density of people, which potentially influences air quality and humidity. Intensively used rooms have been suggested to allow higher yeast diversity in a study where yeasts were cultured from schools in Poland [3]. In Norway, outdoor play is highly evaluated and children in daycares spend up to 70% and 31% of their time outside during the summer and winter, respectively [23, 24]. Thus, outdoor materials, such as sand, soil, dust, feces from birds and other animals, and plant debris, might easily be brought into daycares, constituting important biomass inputs for the indoor environment. Other elements usually not present in daycares, like potted plants and pets, are more common in homes, where the number of occupants is generally lower. In these respects, daycares may represent somewhat different environmental conditions for indoor fungal growth than homes. The indoor mycobiomes of daycares and private homes in Norway have previously been surveyed in separate studies, revealing a high prevalence of molds and yeasts in both building types [7, 8]. However, a direct comparison between these two settings is still lacking.

The main differences between the homes and daycares are the number of occupants and their age distribution, while the buildings themselves often can be similar, including similar architecture and the same building materials. In addition, the temporal usage of homes and daycares differs; while daycares are used intensively over a few hours by many people, homes are often used by fewer people more throughout the whole day. Logistically, it is challenging to obtain samples from a high number of buildings representative of a wide geographic region. In this study, we therefore used a community science approach, recruiting inhabitants or daycare personnel to collect dust samples in a predefined simple manner, which allowed us to obtain a high number of samples throughout Norway for statistical comparisons. The central objective of this study was to compare indoor dust mycobiomes from homes and daycares distributed throughout Norway. More specifically, we aimed (i) to reveal whether different indoor mycobiomes can be found in the two building types and which fungal groups may differ, as well as (ii) to identify the factors that may be associated with these differences.

Methods

Context and Original Datasets

We compared two DNA metabarcoding datasets of indoors and outdoors dust samples from homes and daycares located throughout Norway (Supplementary Fig. S1), which have been recently published [7, 8]. To recruit community scientists for sampling work, daycares were contacted by mail, while home inhabitants were largely approached through social media and scientific networks. Since the sampling scheme, material, and methods were thoroughly described in the original publications, we provide a condensed version here. Altogether 271 homes and 125 daycares throughout Norway were originally selected for sampling. However, the combined dataset of this study includes a more balanced number of indoor samples (428 from 214 homes and 411 from 123 daycares) and corrects the overrepresentation of Oslo area in the original home dataset. During spring 2018, inhabitants (homes) or personnel (daycares) collected dust samples on doorframes at three specific locations: (1) the main entrance outdoors, (2) main central room (living room in homes), and (3) bathroom. Large daycares sampled from two main central rooms and two bathrooms. The dust samples were obtained using the same sampling kits including sterile FLOQSwabs (Copan Italia spa, Brescia, Italy) and instructions. The returned swabs were stored at − 80 °C until DNA extraction. The inhabitants/personnel also provided metadata about the buildings such as the number of occupants, building features, and previously reported pests and water damages by responding to a questionnaire. In addition, based on the geographical coordinates of the buildings, data for some relevant environmental variables related to climate, geology, and topography were extracted from WorldClim 2 or provided by [25] (see Supplementary Table S1 for metadata). In brief, the DNA metabarcoding workflow included five steps: (i) DNA extraction from the swabs using chloroform and the EZNA Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA); (ii) PCR amplification of the ITS2 region using the primers gITS7 [26] and ITS4 [27], both including sample specific tags at the 5'-end; (iii) clean up and normalization of PCR products using SequalPrep Normalization Plates (Thermo Fisher Scientific, Waltham, MA, USA), and subsequent pooling of 96 uniquely barcoded samples including technical replicates, negative samples (unused swabs), extraction blanks, PCR negatives, and a mock community; and (v) library preparation and 250 bp paired-end MiSeq Illumina sequencing carried out at Fasteris SA (Plan-les-Ouates, Switzerland).

Bioinformatics

The bioinformatic analyses for the combined dataset from homes and daycares, whose raw sequences are available on ENA at EMBL-EBI (https://www.ebi.ac.uk/ena/browser/view/PRJEB42161) and Dryad (https://doi.org/https://doi.org/10.5061/dryad.sn02v6x5s), respectively, were performed as described by Martin-Sanchez et al. [7] and Estensmo et al. [8] with slight modifications. Shortly, raw

sequences were demultiplexed using CUTADAPT [28] and sequences shorter than 100 bp discarded. DADA2 [29] was used to filter low quality reads, error correction, merging in contigs, and chimera removal. ITSx [30] was used to exclude the non-fungal sequences and trim the conserved regions of flanking rRNA genes. To account for intraspecific variability [31], the generated amplicon sequence variants (ASVs) were clustered into operational taxonomic units (OTUs) using VSEARCH [32] at 97% similarity. LULU [33] was used with default settings to correct for potential OTU over-splitting. Taxonomy of OTUs was assigned using the BLASTn algorithm [34] against the UNITE and INSD dataset for fungi (v. 04.02.2020) [35]. Ecological trophic modes and guilds for the identified taxa were annotated using the FUNGuild tool [36]. OTUs with less than 10 reads and those that were not assigned to the kingdom Fungi were discarded from downstream analyses. For comparing daycares and homes, we downscaled the original datasets by excluding 2 daycares and 57 homes, hereby providing a more balanced dataset in terms of geographical location (15 homes per municipality maximum), collection date (all samples in April–May 2018), and number of indoor samples from homes vs. daycares (428 vs. 411 in the rarefied matrix). The OTU table was rarefied to 2540 reads per sample using the function *rrarefy* of the VEGAN R package v. 2.6–4 [37], keeping the majority of samples (only 18 samples were excluded). The final quality-filtered and rarefied matrix, without technical replicates, negative controls, and mock samples, contained 9107 OTUs from 1169 samples. Those OTUs with taxonomic assignment at species, genus, or family level were further annotated into growth forms (filamentous, yeast, dimorphic, lichen, and chytrid) based on literature surveys.

Statistics

Initially, we assessed OTU richness per sample, as well as the total number of OTUs and their overlaps for the two types of building (homes vs. daycares) and compartments (indoor vs. outdoor). For comparison of the indoor mycobiomes, beta diversity was assessed with NMDS ordination of dust samples using *metaMDS* from VEGAN R package v. 2.6–4, Bray–Curtis dissimilarity index and 200 random starts in search of stable solution on the Hellinger-transformed rarefied OTU tables. Continuous environmental variables were regressed against NMDS ordination and added as vectors on the ordination plots using *gg_envfit* from GGORDIPLOTS R package v 0.3.0 [38] to visualize their association with the indoor dust mycobiomes. To evaluate the correlation between environmental variables and the observed variance in fungal community composition, permutational multivariate analysis of variance (PERMANOVA; 999 permutations) was performed individually on each variable using *adonis2* from VEGAN R package v. 2.6–4. Relative abundances of taxa at order and genus level were assessed to highlight the differences between homes and daycares. To reveal significant associations ($p < 0.05$) between OTUs and the type of building, an indicator species analysis was performed using *multipatt* from INDICSPECIES R package v. 1.7.14 [39]. Significant differences in the variance of OTU richness per sample and the relative abundances of selected genera were evaluated with the analysis of variance (ANOVA) and *t*-test.

Results

OTU Richness

A weak, but significant difference in indoor fungal richness between the two building types was detected; we obtained on average 160 and 149 OTUs per sample for the indoor samples from homes and daycares, respectively (*t*-test, $p = 0.02$; Fig. 1a). Further, for homes, the fungal richness within the buildings was significantly higher than in the outdoor dust samples ($p = 1.4e\text{-}14$). Comparably, this increase was not significant for daycares ($p = 0.34$; Fig. 1a). In total, the daycare dataset had more OTUs than the homes dataset (7419 and 6408 OTUs, respectively; Fig. 1b). For both homes and daycares, only 11–12% of the fungal OTUs appeared uniquely outdoors, while 41–47% were uniquely found indoors. In addition, the 49% of indoor fungi (OTUs) were found in both types of buildings, while 20% and 31% of them were uniquely associated with homes and daycares, respectively (Supplementary Fig. S2).

Indoor Community Composition

The community composition of the indoor mycobiomes was distinctly different in daycares and homes (Fig. 2a). A high number of factors were significantly correlated to the mycobiome composition, but accounted only for small proportions of the variation (Fig. 2b). The building type (daycare vs. homes) accounted for most of the variation in the indoor mycobiomes (6.3%), followed by the number of occupants (4.2%), and the ventilation system of the building (balanced versus mechanical or natural; 3.5%). In addition, climate variables related to outdoor temperature and precipitation each explained less than 2.1% of the variation in the indoor mycobiome composition.

We observed distinct differences in the taxonomic composition between the two building types (Fig. 3a). The orders Saccharomycetales, Filobasidiales, and Tremellales were proportionally more abundant in daycares. Further, on genus level, ascomycetous yeasts, like *Saccharomyces, Candida*, and *Debaryomyces*, as well as basidiomycetous yeasts like *Cryptococcus, Filobasidium, Malassezia, Naganishia*, and *Rhodotorula,* were proportionally more abundant in daycares

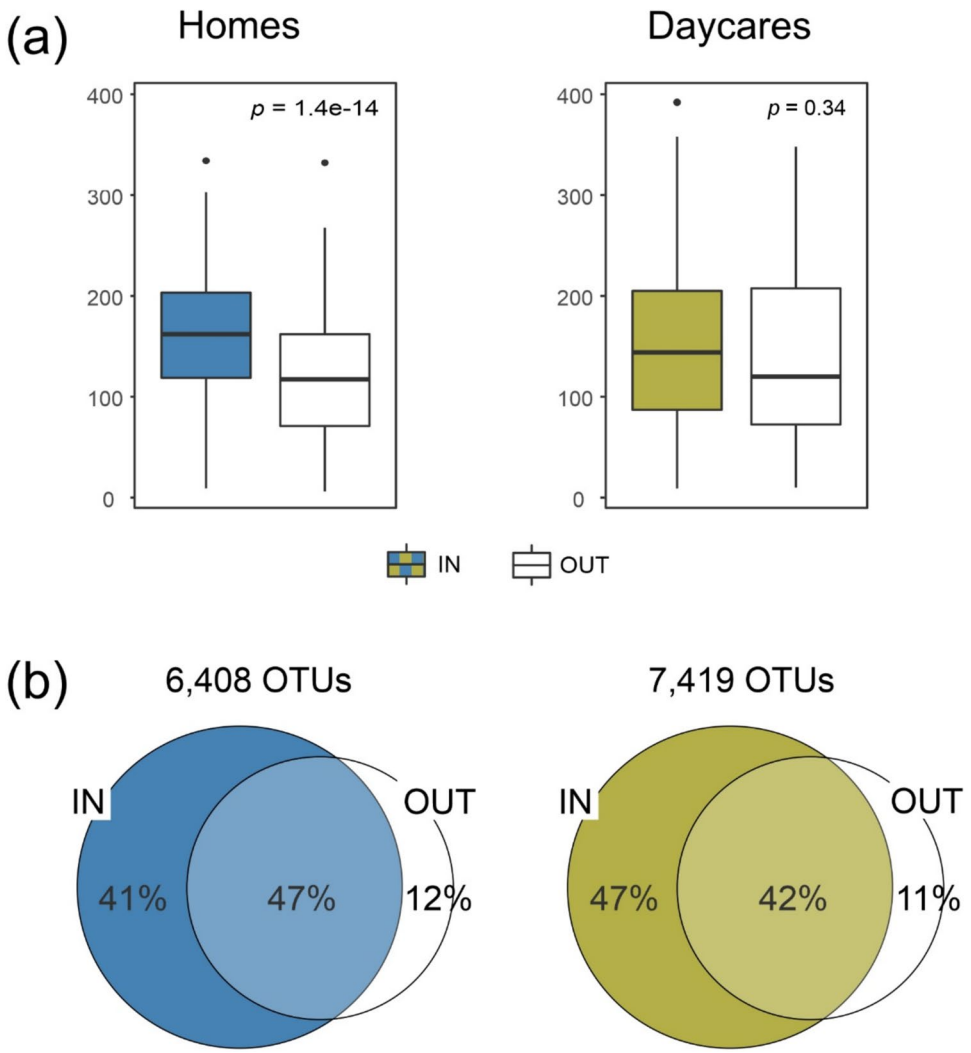

Fig. 1 Comparison indoor vs. outdoor samples for each type of building. **a** OTU richness per sample and **b** number of OTUs and overlaps. All statistics were calculated from a rarefied matrix that includes 9107 OTUs and 1169 dust samples collected from homes ($n = 636$) and daycares ($n = 533$). Significance of richness differences between outdoor and indoor samples was assessed by *t*-test

compared to homes (Fig. 4, *t*-test $p < 10e\text{-}5$). In homes, saprotrophic and plant pathogenic filamentous ascomycetes in the orders Capnodiales, Dothideales, Eurotiales, and Helotiales were relatively more abundant (Fig. 3a). These orders include mold genera such as *Alternaria, Aspergillus, Cladosporium*, and *Penicillium*, all proportionally more abundant in homes (Fig. 4). In contrast, the two mold genera *Wallemia* (Basidiomycota) and *Mucor* (Mucoromycota) were proportionally more abundant in daycares (Fig. 4). Indicator species analysis also supported these findings and identified some yeasts (*Filobasidium*, *Cryptococcus*, *Saccharomyces*, and *Cyberlindnera*) and *Mucor* species as the strongest daycare indicators (IndVal > 50%), and the typical molds (*Penicillium*, *Alternaria*, *Aspergillus*, *Cladosporium* species) as home indicators (Supplementary Table S2).

When annotating the OTUs in the final rarefied matrix (6971 of 9107 OTUs; 76.5%) into growth forms, we observed a clear difference in the distribution of yeasts, mycelial fungi, and dimorphic fungi between the two building types (Fig. 3b), where yeasts are relatively more abundant in daycares while mycelial fungi are relatively more abundant in homes.

Discussion

Previous dust-mycobiome studies have also observed a higher diversity (richness) of fungi indoors [40, 41]. This phenomenon can be explained by the fact that many outdoor fungi have the ability to enter buildings, while the reverse is apparently not the case to the same degree. Hence, the outdoor environment represents a major source of inoculum to the indoor environment, as also observed in previous studies [21, 40, 42].

The clear differences in indoor community composition between daycares and homes suggest that the number of occupants, and possibly their age profiles, are important drivers for the indoor dust mycobiomes. Previous research has also reported higher airborne fungal loads (measured in colony forming units per m^3) in daycares compared to homes

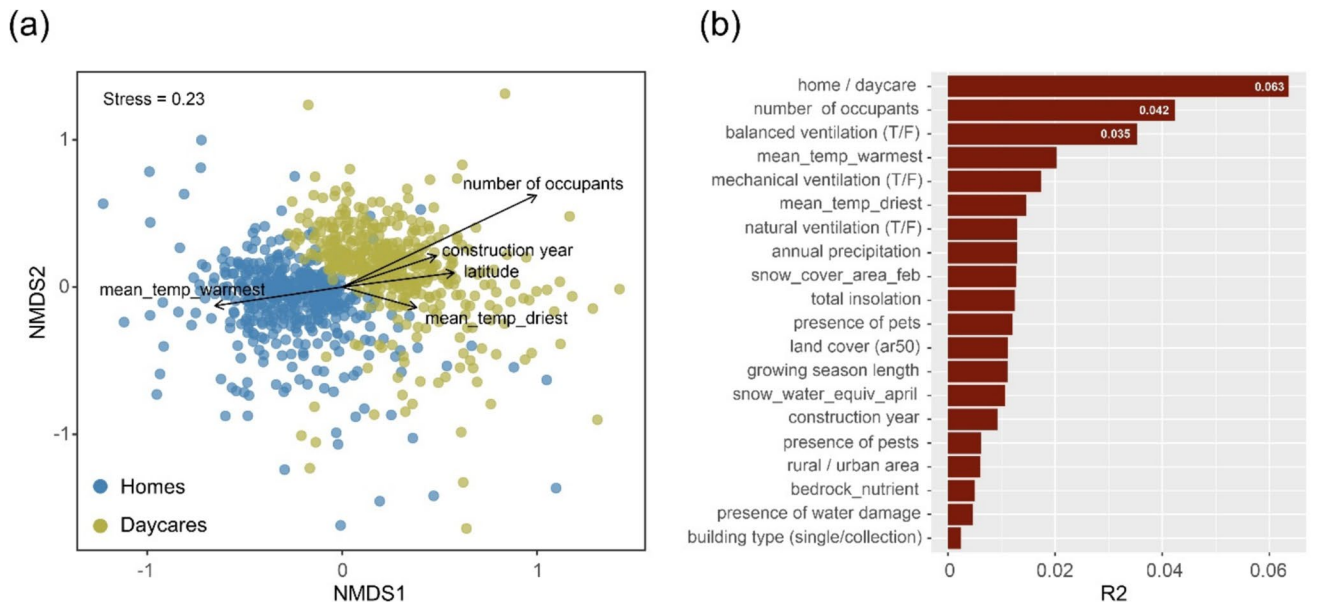

Fig. 2 Factors correlated with compositional changes the indoor mycobiome in homes and daycares. **a** NMDS ordination plot displaying compositional variation between homes and daycare centers. Each point represents one dust sample, and its color indicates its origin (home vs. daycare). **b** The main explanatory variables for the observed variance according to PERMANOVA results (R2 values with $p < 0.001$). Statistics were based on the indoor rarefied matrix that includes 8181 OTUs and 839 dust samples collected from homes ($n = 428$) and daycare centers ($n = 411$)

[43]. The fact that the included environmental factors only account for a small part of the variation in community composition is a common feature in fungal community studies. The assembly process of fungal communities is probably strongly influenced by random processes, such as spore dispersal and colonization [44, 45], making exact predictions of mycobiome composition difficult. Furthermore, there is a high temporal (within-year) variation in fruiting and sporulation of outdoor fungi, especially in temperate regions, which is also reflected in the indoor mycobiomes due to the influx of spores [6, 46, 47]. In our previous temporal study of the mycobiomes in two daycares [6], dust samples were collected throughout a year in order to evaluate the effect of seasonality on the indoor mycobiomes using DNA metabarcoding. This showed a strong seasonal pattern in the mycobiome composition, with higher fungal richness in summer and fall. Hence, in analyses of indoor fungi, it is important to consider the temporal variability by obtaining samples at approximately the same time or conducting repeated sampling. In the present study, the samples were collected throughout Norway at the same time period (April–May). Thus, even if the climate varies across the country, both the daycare and the home dataset are affected by the same climate variables.

As for all environmental DNA-based studies, the taxonomic annotation here might show low resolution and/or errors due to both the short barcode and the correctness of the used sequence database. Thus, we decided to not report or discuss taxonomy at the species level. Even at the genus level, we are aware of the possible misidentification between certain genera, e.g., those belonging to Saccharomycetales (*Candida*, *Debaryomyces*, and *Saccharomyces*). However, this potential limitation would not affect to the overall pattern observed between molds and yeasts in the two building types. We suggest two different hypotheses that may explain this proportional difference. First, more yeasts may be associated with young children, driving the difference. It has been documented that children have a more diverse fungal skin community compared to adults, including genera such as *Aspergillus*, *Epicoccum*, *Cladosporium*, *Candida*, *Rhodotorula*, *Cryptococcus*, and *Phoma*, in addition to the obligatory lipophilic yeast genus *Malassezia* that dominates on the skin of adults [48]. Moreover, the higher density of people per se may drive the proportional difference, since yeasts are more associated with the human body than molds [49]. Besides, Adams et al. [9] reported a significant overlap between the mycobiomes associated with indoor environmental samples (dust and surfaces) and those from the occupants' skin. Several fungal genera with yeast growth such as *Candida*, *Malassezia*, and *Saccharomyces* can also be found in the gastrointestinal tract [50, 51]. A higher density of people may therefore lead to a proportional difference between yeasts and molds, which may be mediated in part by the deposition of occupants' dead skin cells on the indoor surfaces. There seemed to be an even stronger difference in community composition between homes and daycares with

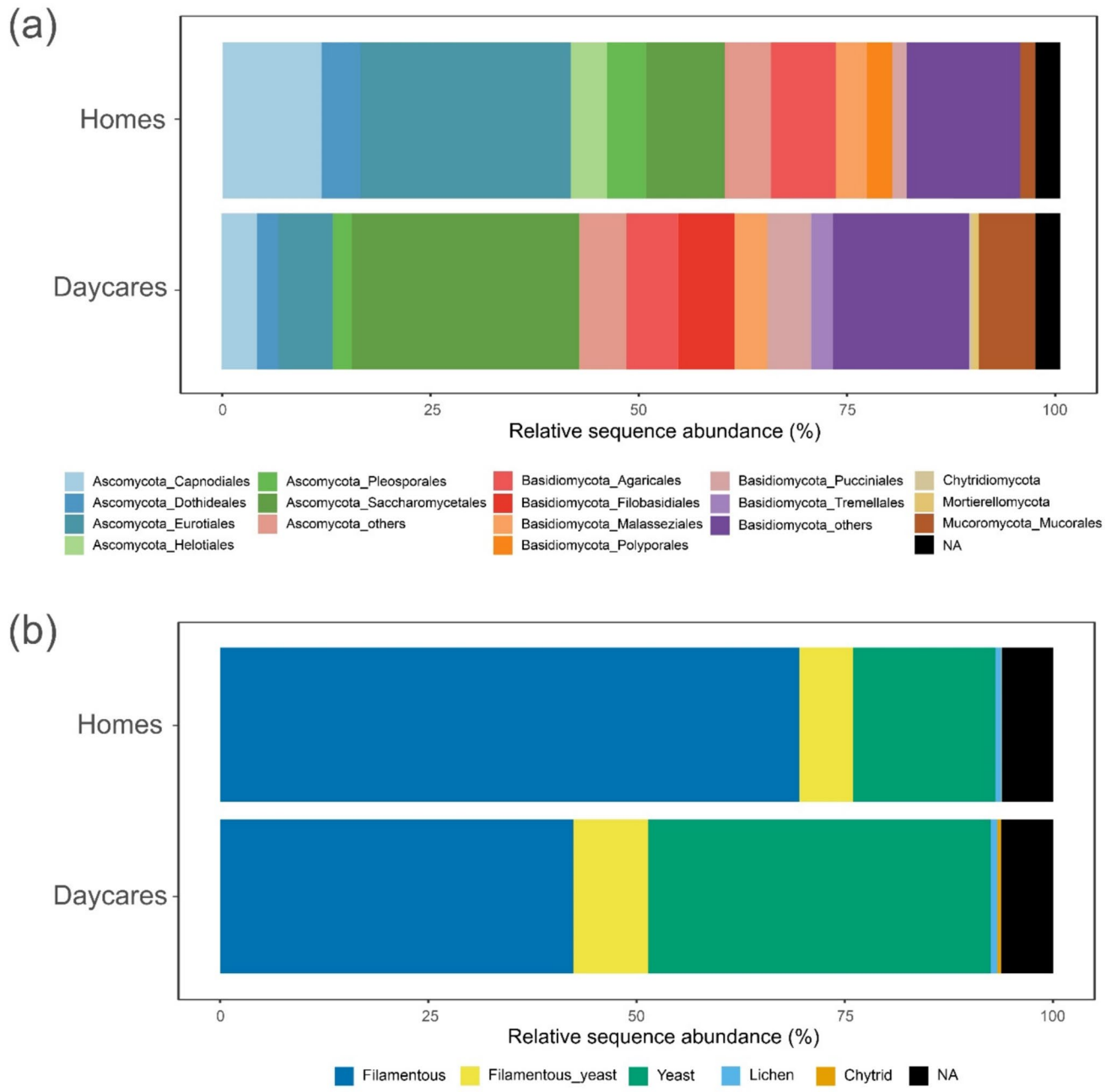

Fig. 3 Relative sequence abundance of fungi detected in indoor dust samples from homes and daycares. **a** The most abundant Orders sorted by Phyla. The less abundant Orders were collapsed and labeled as "Phylum_others". **b** Annotation of the main fungal growth forms: filamentous, filamentous and yeast (dimorphic fungi), yeast, lichen, and chytrid. NA: not assigned

many children (Fig. 2a), which may further support the latter hypothesis. However, to be able to conclude on this topic, more in-depth studies with cross-factorial, balanced study design, tentatively also including investigations of the skin/body mycobiome, are needed. In addition, other possible factors that may differ between private houses and daycares, such as food preferences [52], or possibly, the abundance of invertebrates such as dust mites, could be taken into consideration.

Previous research has also shown that indoor environments, such as healthcare centers [2], homes [53], and schools [3, 54], exhibit high yeast diversity. While Marques do Nascimento et al. [2], Hashimoto et al. [53], and Ejdys et al. [3] specifically investigated yeasts by culturing, Park et al. [54] conducted metagenomic sequencing of all organisms in 500 classrooms. Both approaches identified a substantial level of yeast diversity including

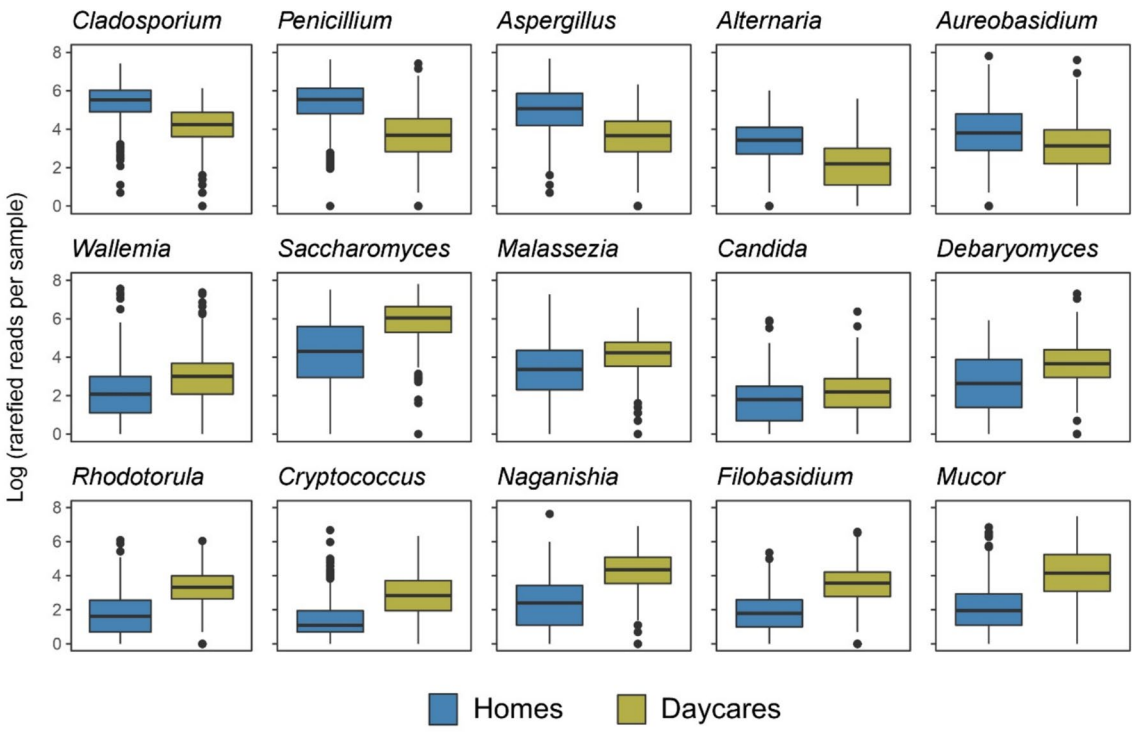

Fig. 4 Selected genera showing significant differences ($p < 10E\text{-}5$; *t*-test) in abundance (Log (rarefied reads per sample)) when comparing indoor samples from homes ($n = 428$) and daycares ($n = 411$)

the genera *Candida*, *Debaryomyces*, *Rhodotorula*, *Cryptococcus*, *Naganishia*, *Filobasidium*, and *Cyberlindnera*.

Overall, this study showed a striking difference in the relative distribution of yeasts and filamentous fungi in daycares and homes, where yeasts were proportionally more abundant in daycares and vice versa. Whether this difference is directly coupled to health effects is unknown. Molds have been shown to cause asthma and other respiratory diseases in humans in moist environments [55, 56]. Furthermore, moisture in homes, in addition to the level of fungal spores outdoors, were the best predictors to indoor fungal spore concentrations in 190 homes in Paris, France [57]. Moisture in schools, but not microbes, was the best predictor of respiratory problems in school children in the Netherlands and Finland [58]. However, a recent birth cohort study in Finnish homes reported that early-life exposure to home dust mycobiomes do not have clear negative or positive effects on asthma development in children [59]. Despite the clear association between some yeasts (e.g., *Malassezia* and *Candida*) and skin disorders (atopic dermatitis and mucocutaneous candidiasis, respectively) [14], some studies have pointed out a potential protective role of the dust yeast exposure against allergies and asthma in children [60]. Thus, the marked difference in the proportional abundance of molds and yeasts in the different building types may not lead to negative effects for the occupants. To gain further insight on this topic, future studies should assess inhabitant's health status coupled to the indoor mycobiomes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00248-025-02505-4.

Acknowledgements We acknowledge the personnel of the daycare centers and the inhabitants of the homes for sampling and for providing metadata of the building and occupancy features. Mycoteam AS contributed to the sampling and provided sampling equipment.

Author Contributions Conceptualization: HK, PMM-S, ELE and IS; Investigation: PMM-S and ELS; Methodology: PMM-S, ELS and SM; Formal analysis: PMM-S, LM and KH; Visualization: PMM-S; Data curation: PMM-S; Software: LM; Resources: SM; Writing – original draft: HK; Writing – review & editing: all authors; Supervision: HK and IS; Funding acquisition: HK, PMM-S, ELE and IS.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. The research was financially supported by the University of Oslo, the Norwegian Asthma and Allergy Association (NAAF), and the European Union's Horizon 2020 research and innovation program (Marie Skłodowska-Curie Individual Fellowship to PMM-S; grant agreement *MycoIndoor* No 741332). PMM-S also thanks the grant PID2021-123184OA-I00 funded by MCIN/AEI/https://doi.org/10.13039/501100011033 and ERDF—A way of making Europe.

Data Availability Our initial combined OTU table, as well as the final rarefied matrix for fungi, are available at Zenodo (https://doi.org/10.5281/zenodo.14049800) together with information about metadata of environmental variables, taxonomic assignment, as well as annotations

of trophic modes/guilds and growth forms. Raw sequence data from homes and daycares are available on ENA at EMBL-EBI (https://www.ebi.ac.uk/ena/browser/view/PRJEB42161) and Dryad (https://doi.org/10.5061/dryad.sn02v6x5s), respectively.

Declarations

Competing Interests The authors declare no competing interests.

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