Forensic Science International 370 (2025) 112451

Contents lists available at ScienceDirect

Forensic Science International

journal homepage: www.elsevier.com/locate/forsciint

Molecular identification of fungi associated with advanced decomposition at a human taphonomy facility in Canada

Steven Richard Beaulieu [a], Agathe Ribéreau-Gayon [a,b], Theo Devèze [a], Shari L. Forbes [c,*,1], Hugo Germain [a,*,1]

[a] Department of Biochemistry, Chemistry, Physics and Forensic Science, Université du Québec à Trois-Rivières, 3351 Boulevard des Forges, Trois-Rivières, QC G9A-5H7, Canada
[b] Groupe de Recherche en Science Forensique, Université du Québec à Trois-Rivières, Canada
[c] Department of Chemistry and Biochemistry, University of Windsor, 401 Sunset Ave, Windsor, ON N9B 3P4, Canada

ARTICLE INFO

Keywords:
Forensic taphonomy
Forensic mycology
Fungal communities
Necrobiome
DNA barcoding
Nested PCR, Illumina MiSeq

ABSTRACT

Forensic taphonomy investigates the postmortem processes of human remains, focusing on the environmental factors that influence decomposition. Recent studies have highlighted the potential forensic relevance of fungi in this context, but the knowledge base remains limited. This study explored fungal communities associated with outdoor human decomposition at the REST[ES] facility in Quebec. Nested PCR amplification and Illumina MiSeq sequencing were used to identify fungal species on discolored patches of twelve samples of desiccated soft tissues from three donors. Twelve fungal species were putatively identified, some of which were previously unknown on human remains, including *Leucosporidium yakuticum*, *Tausania pullulans*, and Fusicolla species. These fungi may contribute to tissue discoloration and following longitudinal investigation, could serve as biomarkers for forensic reconstructions, including place and time of death. This study emphasizes the need for further research into the role of fungi in human decomposition processes and their applications in forensic science.

1. Introduction

Forensic taphonomy, an interdisciplinary field within forensic science, focuses on studying the postmortem processes of human remains [1,2]. This fast-developing discipline investigates the physical, chemical, and biological changes during soft and hard tissue decomposition along with environmental factors and interactions with fauna and flora influencing these changes in order to reconstruct the sequence of events from the time of death to the recovery of the remains [3–6]. It is traditionally considered that the process of decomposition progresses through five main stages: the fresh stage, typically characterized by the immediate onset of enzymatic, microbial and entomological activity; the bloat stage, marked by the accumulation of gases resulting in the bloated appearance of the body; the active decay stage, whereby microbial activity accelerates, leading to further degradation of soft tissues; the advanced decay stage, during which the majority of soft tissues are lost, leaving behind primarily skeletal remains; and finally, the dry/skeleton stage, where mostly only bones persist after the partial or complete loss of soft tissue following decomposition [7]. However, recent experimental studies in various environments have shown that decomposition is rather a continuum with no clear-cut stages [8,9], thus further highlighting the need to conduct more experimental research in controlled settings, including in nordic climates that suffer from a paucity of data compared to other environments such as temperate climates.

Despite extensive exploration of various environmental variables such as insects, vertebrate scavengers, bacteria and diatoms [10–15], other variables of potential forensic relevance, including fungi and lichens, have seldom been studied in the published literature [16–26]. Fungi are a vast and diverse kingdom of eukaryotic organisms. Within the Fungi kingdom, it is estimated that there are up to 5.1 million different species [27]. This substantial diversity and abundance has sparked interest in their application in forensic science. Numerous applications of fungi have been described in the forensic literature, ranging from trace determination to estimating the post-mortem interval (PMI), detecting clandestine graves, and contributing to diagnosing the circumstances surrounding suspicious deaths [21,23,26]. While the

* Corresponding authors.
E-mail addresses: steven.richard.beaulieu@usherbrooke.ca (S. Richard Beaulieu), agathe.ribereau-gayon@uqtr.ca (A. Ribéreau-Gayon), shari.forbes@uwindsor.ca (S.L. Forbes), hugo.germain@uqtr.ca (H. Germain).
[1] These authors contributed equally to this work

https://doi.org/10.1016/j.forsciint.2025.112451
Received 10 December 2024; Received in revised form 7 March 2025; Accepted 18 March 2025
Available online 24 March 2025

presence of fungal growth on human remains has been proposed as a potential indicator for estimating PMI, it is not considered an accurate technique and can only suggest that a body has been deceased for weeks or months as this represents the timeframe required for fungal growth to occur. The use of fungi as a PMI tool is influenced by many factors such as the accurate classification of the fungi, the preservation method of the remains, and the environmental conditions, including temperature and moisture levels, at the site where the remains were found. Despite the considerable interest and the potential forensic relevance, there is still a limited number of studies that have explored the use of fungi in forensic science, thus providing opportunities for a more in-depth exploration of fungal applications as potential taphonomic markers.

The published literature highlights a limited experimental knowledge base on fungal species capable of growing on decomposing human corpses [18,21]. Few research or medicolegal case studies have identified fungal species on decomposing bodies and even fewer have used molecular biology techniques. For example, van de Voorde and van Dijck identified multiple genera and species, including *Geotrichum candidum*, *Mortiella sp*, *Fusarium sp.*, *Cladosporium sp.*, *Penicillium notatum* and *Hormodendrum sp*., on a body found indoors to estimate PMI [28]. Ishii *et al*. also identified different fungi species on two bodies with PMIs of 6 and 10 months, with one species (*Eurotium repens*) more abundant on both bodies [16]. A case study by Hitosugi *et al*. reported *Penicillium sp.* and *Aspergillus sp.* on a corpse with a PMI of approximately 10 days [17]. Schwarz *et al*. employed ITS amplification followed by DNA sequencing (barcoding) to identify 24 fungal species from 23 autopsied cadavers where macroscopically visible fungal growth was observed [18]. The PMIs of the bodies analyzed in the study were mostly unknown or $<$ 2 months when PMI was known. Becktell *et al*. identified *Aureobasidium melanogenum* and *Didymella glomerata* using molecular barcoding techniques, these were not previously described in the literature on bodies with a PMI of over 4 years [29]. Kato *et al.* reported two cases where fungal colonies were found on cadavers. In the first case, *Penicillium commune* and *Cladosporium cladosporioides* were isolated, while in the second case, fungi such as *Epicoccum nigrum*, *Mucor sp., Cladosporium sp.*, and *Pestalotiopsis sp*. were identified [30]. All these studies have used classical microbiology to grow the fungi and, in some cases, performed DNA sequencing from the pure culture or colonies. The downside of using microbiological media is that many fungi may not grow on the chosen media.

The current literature therefore outlines a need for further experimental knowledge of fungal species involved in the decomposition process of human remains at various decomposition stages. Moreover, a recent study conducted by Ribéreau-Gayon *et al*. [9] highlighted the presence of discolored patches on the desiccated skin of donors from the site for Research in Experimental and Social Thanatology/ *Recherche en Science Thanatologiques [Experimental and Social*] (REST[ES]). Although the biological nature of these discolored patches was not examined in that study, it reported that the often brightly discolored areas appeared exclusively on desiccated soft tissues and not on fresh tissues nor skeletonized remains and were present in all three bodies (donors) included in the present study (out of the six analyzed). The colored patches were first observed on donors' bodies included in the present study between days 16 and 25 [9]. A likely hypothesis is that the discolored patches are linked with some microbe, potentially a fungi. Fungi are known to be more resistant to desiccation than other microorganisms that may cause discoloration of tissues, such as bacteria [31]. The aim of this study was to identify fungal taxa that appeared associated with colored tissue on human remains in advanced decomposition. To address this aim we employed Illumina DNA sequencing directly from the donors' tissue, without an isolation step on Petri dishes, to identify fungal species or genuses growing on cadavers of approx. 2 years PMI and provide new insights into the fungal communities associated with human decomposition.

2. Material and methods

2.1. Experimental setting

Sample collection was conducted in summer 2023 from donors at the REST[ES] facility. REST[ES] is located in Southeastern Canada, on the south shore of the Saint-Lawrence river in Quebec (N 46.3473, W 72.4179), on land owned by the Industrial Park and Port of Becancour (SPIPB; *Société du Parc industriel et portuaire de Bécancour*). The region is classified as a humid, continental (Dfb) climate with hot summers and cold winters. The hottest month (July) has an average of 25.4 °C (77.7 °F) and an extreme maximum of 36.7 °C (98.1 °F). Freezing is common and occurs for approximately half of the year with the coldest month (January) having an average of −17.1 °C (1.2 °F) and an extreme minimum of −40.0 °C (-40 °F). The site is characterized by a mix of woodland vegetation, primarily featuring red maple (*Acer rubrum* L.) and white spruce (*Picea glauca*) trees. Its soil composition consists of loamy sand A and B horizons, with sandy soil nearer to the surface transitioning into loamy soil at deeper levels. This location was selected for its representation of a typical environment where local law enforcement might conduct searches for and recover human remains [32].

In this study, we analyzed the remains of three adult donors who had contributed to the Université du Québec à Trois-Rivières (UQTR) Body Donation Program. The selection of donors comprised two males and one female all deployed in fall 2021 with ages ranging from 54 to 78 years old and a body mass index of 27.8, 16.3 and 16.5, respectively. Donors were selected for the present study because they exhibited colored patches that were representative of what was observed on all donors on site. All samples were collected when the donors had a PMI of approx. 21–23 months, meaning that the bodies had undergone almost two cycles of seasonal fluctuation in climatic conditions (e.g. temperature, snowfall/rainfall, etc.).

Following refrigeration at 4°C for approximately 24 hours in the UQTR Anatomy Laboratory morgue, the donors' bodies were transferred to the REST[ES] facility after undergoing preparatory procedures. These preparations involved the removal of clothing, cleansing with 70 % ethyl alcohol, and the attachment of plastic identification tags to their toes [9]. Dentures, medical devices, and implants, if present, were retained within the donors, in keeping with the UQTR Body Donation Program's protocol. The undressed bodies were positioned in a supine position on the soil surface within the REST[ES] facility. Wire mesh cages protected the bodies to limit vertebrate scavengers. However, these cages were designed to permit invertebrate activity, recognized as a significant factor in the decomposition process. Further insights into the entomological communities and vertebrate scavengers at the REST [ES] facility are available in previously published studies [10–12].

2.2. Sample collection

Following ethics approval by the Université du Québec à Trois-Rivières Anatomy Laboratory Ethics Sub-committee (CER-09–148–06.05), sampling was conducted on the donors in a minimally invasive manner. Squares of approximately 0.5 cm^2 of desiccated soft tissue were sampled with a scalpel from macroscopically visible discolored areas on all three donors (Fig. 1A). All samples were collected from the right leg of each donor, more specifically on the dry skin (dermis) covering the patella and/or the heel, four per donor for the three donors were collected and stored at −20 °C on UQTR's premises.

2.3. DNA extraction and polymerase chain reaction

DNA extraction was performed using the Qiagen DNeasy PowerMax Soil kit (Qiagen, Montreal, QC, Canada). DNA extraction followed the manufacturer's protocol.

To identify fungal species, the extracted DNA was amplified by

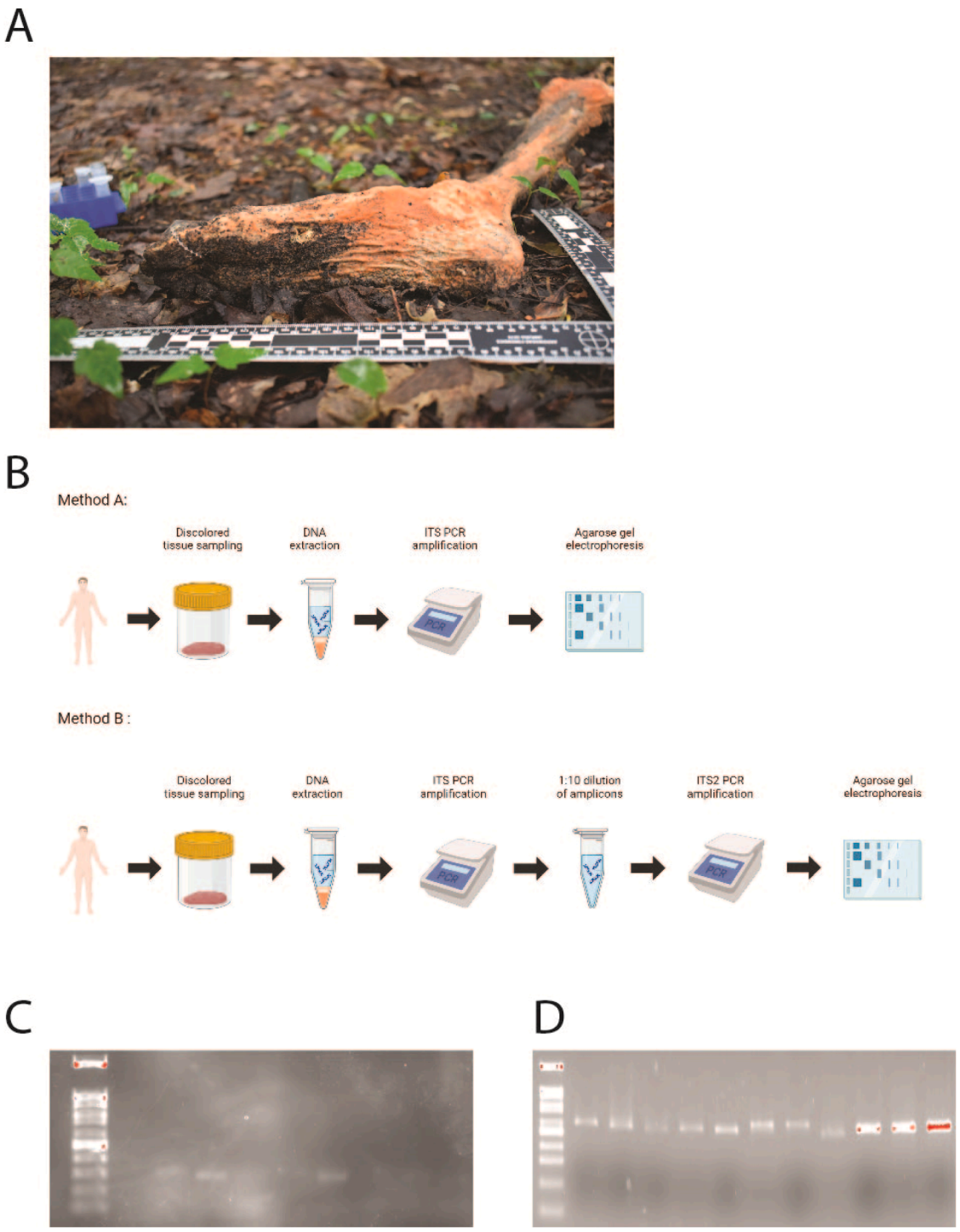

Fig. 1. (A) Sampling of an orange-colored patch observed on desiccated soft tissue in July 2023. (B) Methods A and B utilized and tested for amplification in the present study. (C) Gel electrophoresis results for Method A. (D) Gel electrophoresis results for Method B.

polymerase chain reaction (PCR) targeting the internal transcribed spacer (ITS) region 2. To optimize the PCR reaction, we used a nested reaction composed of two sets of primers. The first PCR reaction, using the ITS1F/ITS4 primers, was followed by verification of DNA presence on a 1 % agarose gel. A second PCR reaction with nBITSF_CS1/n58A2r_CS2 primers (primer sequences are in Table S1), using a 1:10 dilution of the first PCR amplicon was then performed. The cycling conditions for both PCR were an initial 3 minutes denaturation at 95°C followed by 35 cycles of 30 seconds at 95°C, 30 seconds at 52°C, and 30 seconds at 68°C, reactions terminated with a 5 minutes elongation at 68°C before being placed at 4°C. DNA presence was confirmed on a 1 % agarose gel. The 25 µl PCR reaction were constituted of 12.5 µl PCR buffer which already contained the Taq polymerase and nucleotides (NewEngland Biolabs), 400 nM of both forward and reverse primers, 5 µl of extracted DNA, the volume was completed to 25 µl with nuclease free water.

3. DNA sequencing and analysis

Amplicons were sent to Quebec Genome Innovation Center of McGill

University (Montreal, QC, Canada) for library preparation and amplicon sequencing using Illumina MiSeq PE 300 technology. Raw sequences were demultiplexed and adapters and barcodes were removed for all specimens. FASTQ files were uploaded to the Compute Canada servers and quality profiles were plotted and inspected. Primers and adapters were trimmed from the sequences using Cutadapt [33]. Subsequent steps were performed following the DADA2 ITS 1.8 pipeline workflow. Used functions are regrouped in the dada2 R package [34]. Filtering step was performed using the following parameters: maxN = 0, maxEE = c (2, 2), truncQ = 2, minLen = 50. Only sequences longer than 50 bp with a mean number of expected errors below 2 were kept. No trimming was performed at this step as the sequences had already been trimmed with 'cutadapt'. Amplification and sequencing errors were assessed using the 'learnError' function and used for the inference of sample composition in both forward and reverse reads. At this step, ASVs were generated using the dada function [35]. Paired-ends sequences were then merged using the 'mergePairs' function with a minimum overlap of 12 nucleotides and 0 mismatch allowed. Bimeras were removed using the consensus method of the 'removeBimeraDenovo' function. Merged sequences free from bimera were assigned to taxonomy using the UNITE fungal reference database (sh_general_release_dynamic_25.07.2023.fasta) [36] via the 'assign Taxonomy' function implementing the Ribosomal Database Project Naive Bayesian Classifier [37] with kmer size 8 and 100 bootstrap replicates. Taxonomic composition barplots were generated using the R package phyloseq [38]. PCR negative controls (blank) were also sequenced, and species identified within the PCR blanks were substrated from all samples when present.

4. Results

4.1. DNA amplification

Following collection of the colored specimen (Fig. 1A) and DNA extraction, two DNA amplification methods were compared for their efficacy to yield clean PCR products. The first method (herein designated as 'Method A') involved PCR amplification of the entire ITS 2 region. The second method ('Method B') involved a PCR amplification of the entire ITS 2 region, made up of 35 cycles, followed by a 1:10 dilution of the PCR product and a second PCR amplification of the amplicons, comprised of 35 cycles. Both methods are illustrated in Fig. 1B.

To assess the relative performance of the two amplification methods, the amplicons produced by both methods were analyzed using agarose gel electrophoresis. Results showed significant differences in the intensity of bands between samples amplified by both methods; very faint bands can be visualized in Fig. 1C, and some samples could not be amplified. On the contrary, the nested PCR (Method B) provided clear and unique bands for all samples (Fig. 1D). Method B was therefore used for further analysis.

4.2. Identified fungal taxa

A prior assessment of direct PCR sequencing revealed that the sequenced DNA contained traces of multiple species (mixed DNA) and therefore taxa could not be assigned to the sequences using direct amplicon sequencing with Sanger technology. Therefore, all samples were amplified using Method B and sequenced using Illumina sequencing PE300. Following taxon assignment, a total of 12 different species were identified across all samples. Fig. 2 illustrates the relative abundance of fungal taxa identified across the different samples. As expected for samples that had been exposed outdoors for nearly two years, all samples except B11 and O11, were colonized by more than one species of fungi. Despite careful sampling of tissue that visibly displayed the targeted mycelia color, we cannot exclude the possibility that other fungi not visible to the naked eye were present within or beneath the skin. Overall, three species seemed to be dominant: *Fusicolla aquaeductum* (turquoise), *Tausonia pullulans* (pink), and to a lesser extent *Fusicolla septimanfiniscientiae* (blue). The two white samples (B10 and B11) yielded very different profiles making it inconclusive as to which

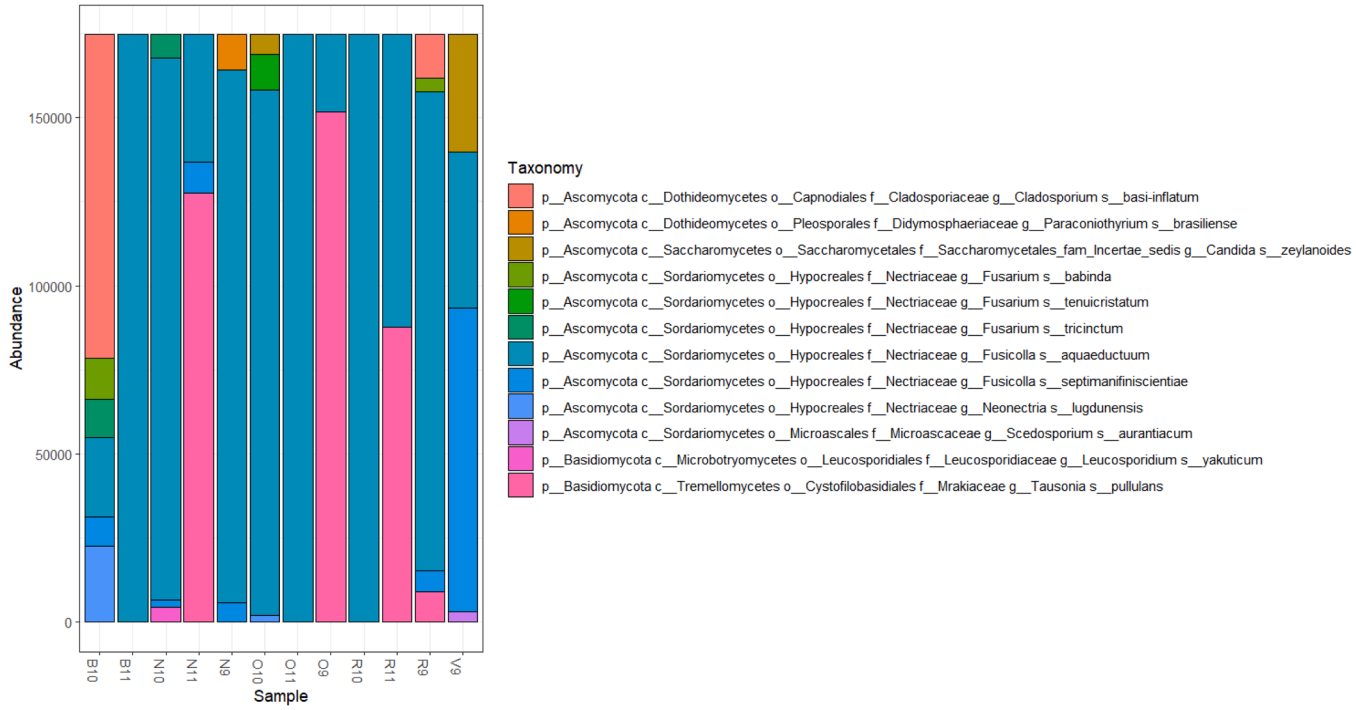

Fig. 2. Relative abundance of fungal taxa in different samples. The taxa are categorized by their taxonomic affiliation, including phylum, class, order, family, genus, and species, as shown in the legend. A color is assigned to each taxon. The samples are displayed on the x-axis, while the abundance is shown on the y-axis. The samples are labeled with codes (e.g., B10, B11, etc.) along the X-axis. B represents a sample taken from a white colored patch. N represents a sample taken from a black colored patch. O represents a sample taken from an orange-colored patch. V represents a sample taken from a green colored patch. The number associated to each sample code stands for the donor the sample was taken from whereas each color represents a species.

species was responsible for the white coloration on the bodies. The three black samples (N9, N10 and N11) also yielded very different profiles with *Fusicolla aquaduectum* being present in all three samples. This species, however, was present in all the different samples, regardless of their color. No other species is common to the black samples, making it impossible to determine which species is causing this coloration. All orange and red samples (O9, O10, O11, R9, R10 and R11) yielded similar profiles. They were dominated by *Fusicolla aquaduectum* and *Tausonia pullulans* with other species being minor contributors. The green sample (V9) was the only one in which the species *Candia zeylanoides* was detected and was a major contributor.

5. Discussion

The aim of this study was to identify fungal taxa that appeared associated with colored tissue on human remains in advanced decomposition. To date, relatively few taphonomic studies have investigated the Fungal kingdom in relation to human remains. The role of fungi as important components of human decomposition seems to have been overlooked in the forensic literature.

Our study compared two DNA amplification methods and used metabarcoding pipelines to putatively attribute species to DNA sequences. We identified 12 fungal species involved in the decomposition process at the advanced decomposition stage at the REST[ES] facility in Quebec using a nested PCR amplification method and Illumina MiSeq PE 300 sequencing. Our results demonstrated that although it can be difficult to assign specific colors to precise fungal species, in other cases such as the orange and green coloration, fungal species can be assigned with more confidence.

We compared the performance of two amplification protocols to yield clean and abundant PCR products. The superior results obtained with Method B likely resulted from an increased sensitivity with the nested PCR technique. This approach effectively improved the yield of the target ITS2 sequences, making it more suitable for the identification of the fungal species in the analyzed samples. While Method B showed higher efficacy in our study, it is more labor intensive and time-consuming compared to Method A. For large scale or time sensitive forensic analyses, the added steps required for nested PCR may pose practical challenges in the context of forensic investigations where time and resources available can be limited.

A diverse array of fungal taxa was observed in association with decomposing human remains, including several notable species known for their 'unique' characteristics and ecological roles. All identified species had been previously observed in soil and plants [39–42]. Among these, *Leucosporidium yakuticum* and *Tausania pullulans* stand out for their cold tolerance [43,44] which aligns with their potential to thrive in environments like our study site. Neonectria and Heliotales species like the ones identified here have previously been shown to be implicated in decomposition of organic matters [45,46].

Fusarium and Candida species have been observed and identified to the genus in a previous study [18]. *Scedosporium aurantiacum* is a known human opportunistic pathogen mostly present in cystic fibrosis patients [47]. To the authors' knowledge, none of the other species identified in the present study have previously been identified on human remains. Species within the genus Fusicolla are recognized for their ability to produce distinctive orange layers on substrates, a feature observed in our samples from discolored patches [48]. *Fusarium tricinctum*, known as a plant pathogen producing a characteristic red pigment, was also detected among our fungal taxa [49]. *Fusarium tenuicristatum* and *Fusarium babinda*, known for their pale red to orange coloration, were identified in our samples [50,51]. *Candida zeylanoides*, with its distinctive blue-green coloration [52], and *Paraconiothyrium brasiliense,* known for its dark brown to black coloration [53], were also among the taxa identified. These species can contribute to the discoloration of desiccated soft tissues observed on the donors, which underscores the complexity of fungal communities in human decomposition. Further investigation into the fungi species present at various stages of decomposition could provide valuable insights into their role in the decomposition process. By understanding how these species develop and interact with human remains over time, researchers can evaluate their potential to serve as reliable biomarkers for estimating the postmortem interval (PMI). Understanding their role in decomposition dynamics and establishing reliable methods to link fungal presence or growth patterns with specific timeframes could significantly enhance their utility for PMI estimation in forensic investigations.

The experimental approach developed in this study is minimally invasive and does not require the use of microbiological media and is, therefore, not biased toward species that can be grown in a laboratory. Some limitations should be noted, such as the identification pipeline only matching sequences to the closest ones in the database, meaning no match is possible if a species' sequence isn't available. Moreover, as is the case for any environmental sample, the presence of spores brought by wind or precipitation may result in a large number of reads and may not reflect the discolorations observed on the remains caused by a vegetatively growing fungus. It should also be noted that while our approach does not require growing the fungi on microbiological media, amplicons have to be processed and indexed in a library which also requires time. Nevertheless, our approach provides a framework for taxonomical assignment of color-causing fungi on human remains, and it is hoped that it will open avenues for further experimental research in the growing field of forensic mycology.

6. Conclusion

The molecular identification of fungi sampled from human cadavers decomposing in an outdoor environment demonstrated a range of species. Notable species included *Leucosporidium yakuticum* and *Tausania pullulans*, known for their cold tolerance; *Neonectria* and *Heliotales* species, implicated in the decomposition of organic matter; *Fusarium* and *Candida* species, previously observed on human remains; and *Scedosporium aurantiacum*, a known human opportunistic pathogen. Species within the genus *Fusicolla* produce distinctive orange layers; *Fusarium tricinctum* is known for its characteristic red pigment; *Fusarium tenuicristatum* and *Fusarium babinda* are noted for their pale red to orange coloration; *Candida zeylanoides* has a distinctive blue-green coloration; and *Paraconiothyrium brasiliense* is known for its dark brown to black coloration. The data provides new information to the limited knowledge base of mycology as it relates to forensic taphonomy.

Ethical approval

This research was approved by the Université du Québec à Trois-Rivières Anatomy Laboratory Ethics Sub-committee (Sous-comité d'éthique du laboratoire d'enseignement et de recherche en anatomie) (CER-09–148–06.05).

Funding

This research was financially supported by the Canada 150 Research Chair in Forensic Thanatology [C150–2017–12], a NSERC USRA grant to SRB and Discovery grant number RGPIN-2020–04002 to HG.

CRediT authorship contribution statement

Forbes Shari L.: Writing – review & editing, Funding acquisition. **Devèze Theo:** Writing – review & editing, Formal analysis. **Ribéreau-Gayon Agathe:** Writing – review & editing, Formal analysis, Conceptualization. **Beaulieu Steven Richard:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Germain Hugo:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interest

Acknowledgements

The authors are deeply grateful to the donors who generously bequeathed their bodies to the REST[ES] facility in the most personal and unselfish way, and without whom this study—and future ones—would not have been possible.

The authors would also like to extend their sincere gratitude to the members of the REST[ES] team for their invaluable support during the sampling process, as well as to all individuals who contributed to the laboratory work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.forsciint.2025.112451.

References

[1] R.L. Lyman, What taphonomy is, what it isn't, and why taphonomists should care about the difference, J. Taphon. 8 (1) (2010) 1–16.
[2] J. Efremov, Taphonomy: a new branch of paleontology, Pan-Am. Geol. v. 74 (1940).
[3] E.M. Schotsmans, N. Márquez-Grant, S.L. Forbes, Taphonomy of Human Remains: Forensic Analysis of the Dead and the Depositional Environment, John Wiley & Sons, 2017.
[4] A.K. Behrensmeyer, Taphonomic and ecologic information from bone weathering, Paleobiology 4 (2) (1978) 150–162.
[5] D.H. Ubelaker, Taphonomic applications in forensic anthropology. Forensic Taphonomy: The Postmortem Fate of Human Remains, 1997. 1.
[6] M.H. Sorg, W.D. Haglund, Forensic Taphonomy: The Postmortem Fate of Human Remains, Crc Press, 1996.
[7] M. Lee Goff, Early post-mortem changes and stages of decomposition in exposed cadavers, Exp. Appl. Acarol. 49 (2009) 21–36.
[8] C. Nienaber, et al., Forensic Taphonomy, Elsevier: The Netherlands, 2023, pp. 700–711.
[9] A. Ribéreau-Gayon, D.O. Carter, S. Forbes, Developing a new scoring method to evaluate human decomposition in a humid, continental (Dfb) climate in Quebec, J. Forensic Sci. 68 (2) (2023) 536–548.
[10] J.-É . Maisonhaute, S.L. Forbes, Decomposition and insect succession on human cadavers in a humid, continental (Dfb) climate (Quebec, Canada), Int. J. Leg. Med. 137 (2) (2023) 493–509.
[11] J.-É . Maisonhaute, S.L. Forbes, Decomposition process and arthropod succession on pig carcasses in Quebec (Canada), Can. Soc. Forensic Sci. J. 54 (1) (2021) 1–26.
[12] K. Séguin, et al., The taphonomic impact of scavenger guilds in southern Quebec during summer and fall in two distinct habitats, J. Forensic Sci. 67 (2) (2022) 460–470.
[13] K. Verma, Role of diatoms in the world of forensic science, J. Forensic Res. 4 (2) (2013).
[14] J.L. Pechal, et al., The potential use of bacterial community succession in forensics as described by high throughput metagenomic sequencing, Int. J. Leg. Med. 128 (2014) 193–205.
[15] J.L. Metcalf, et al., A microbial clock provides an accurate estimate of the postmortem interval in a mouse model system, eLife 2 (2013) e01104.
[16] K. Ishii, et al., Analysis of fungi detected in human cadavers, Leg. Med. 8 (3) (2006) 188–190.
[17] M. Hitosugi, et al., Fungi can be a useful forensic tool, Leg. Med. 8 (4) (2006) 240–242.
[18] P. Schwarz, et al., Molecular identification of fungi found on decomposed human bodies in forensic autopsy cases, Int. J. Leg. Med. 129 (2015) 785–791.
[19] M. Tibbett, D.O. Carter, Mushrooms and taphonomy: the fungi that mark woodland graves, Mycologist 17 (1) (2003) 20–24.
[20] D.O. Carter, M. Tibbett, Taphonomic mycota: fungi with forensic potential, J. Forensic Sci. 48 (1) (2003) JFS2002169.
[21] M.C. Tranchida, S.A. Pelizza, L.A. Eliades, The use of fungi in forensic science, a brief overview, Can. Soc. Forensic Sci. J. 54 (1) (2021) 35–48.
[22] M.C. Tranchida, N.D. Centeno, M.N. Cabello, Soil fungi: their potential use as a forensic tool, J. Forensic Sci. 59 (3) (2014) 785–789.
[23] D.L. Hawksworth, P.E. Wiltshire, Forensic mycology: the use of fungi in criminal investigations, Forensic Sci. Int. 206 (1-3) (2011) 1–11.
[24] N. Sagara, Association of ectomycorrhizal fungi with decomposed animal wastes in forest habitats: a cleaning symbiosis? Can. J. Bot. 73 (S1) (1995) 1423–1433.
[25] X. Fu, et al., Fungal succession during mammalian cadaver decomposition and potential forensic implications, Sci. Rep. 9 (1) (2019).
[26] D.L. Hawksworth, P.E. Wiltshire, Forensic mycology: current perspectives, Res. Rep. Forensic Med. Sci. (2015) 75–83.
[27] M. Blackwell, The Fungi: 1, 2, 3… 5.1 million species? Am. J. Bot. 98 (3) (2011) 426–438.
[28] H. Van de Voorde, P.Van Dijck, Determination of the time of death by fungal growth, Z. F. üR. Rechtsmed. 89 (1982) 75–80.
[29] M.C. Becktell, et al., Identification of fungi found on desiccated human remains in an arid outdoor environment, J. Forensic Sci. 67 (5) (2022) 2048–2054.
[30] H. Kato, et al., Cadavers found outdoor in whom fungal growth was observed on the body surface: consideration of the role of mycology in forensic medicine, Leg. Med. 65 (2023) 102301.
[31] R.L. Barnard, C.A. Osborne, M.K. Firestone, Responses of soil bacterial and fungal communities to extreme desiccation and rewetting, ISME J. 7 (11) (2013) 2229–2241.
[32] E.L. Pecsi, et al., Perspectives on the establishment of a canadian human taphonomic facility: the experience of REST [ES], Forensic Sci. Int. Synerg. 2 (2020) 287–292.
[33] M. Martin, Cutadapt removes adapter sequences from high-throughput sequencing reads, EMBnet. J. 17 (1) (2011) 10–12.
[34] Callahan, B.J.M., Paul J.; Holmes, Susan P. DADA2: High-resolution sample inference from Illumina amplicon data. 2023 [cited 2023; Available from: ⟨https://github.com/benjjneb/dada2⟩.
[35] B.J. Callahan, et al., DADA2: High-resolution sample inference from Illumina amplicon data, Nat. Methods 13 (7) (2016) 581–583.
[36] Abarenkov, K.Z., Allan; Piirmann, Timo; Pöhönen, Raivo; Ivanov, Filipp; Nilsson, R. Henrik; Kõljalg, Urmas, UNITE QIIME release for Fungi 2, U. Community, Editor, 2023.
[37] Q. Wang, et al., Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy, Appl. Environ. Microbiol. 73 (16) (2007) 5261–5267.
[38] P.J. McMurdie, S. Holmes, phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data, PloS One 8 (4) (2013) e61217.
[39] W. Lee, et al., Diversity of Cladosporium (Cladosporiales, Cladosporiaceae) species in marine environments and report on five new species, MycoKeys 98 (2023) 87.
[40] R. Tofalo, et al., The life and times of yeasts in traditional food fermentations, Crit. Rev. Food Sci. Nutr. 60 (18) (2020) 3103–3132.
[41] G.J. Verkley, et al., Paraconiothyrium, a new genus to accommodate the mycoparasite Coniothyrium minitans, anamorphs of Paraphaeosphaeria, and four new species, Stud. Mycol. 50 (2004) 323–335.
[42] A.K. Gupta, R. Baran, R.C. Summerbell, Fusarium infections of the skin, Curr. Opin. Infect. Dis. 13 (2) (2000) 121–128.
[43] A. Trochine, et al., Genomic and proteomic analysis of Tausonia pullulans reveals a key role for a GH15 glucoamylase in starch hydrolysis, Appl. Microbiol. Biotechnol. 106 (12) (2022) 4655–4667.
[44] V. de García, et al., Sex in the cold: taxonomic reorganization of psychrotolerant yeasts in the order Leucosporidiales, FEMS Yeast Res. 15 (4) (2015) fov019.
[45] P. Chaverri, et al., Delimitation of Neonectria and Cylindrocarpon (Nectriaceae, Hypocreales, Ascomycota) and related genera with Cylindrocarpon-like anamorphs, Stud. Mycol. 68 (1) (2011) 57–78.
[46] T. Hosoya, Systematics, ecology, and application of Helotiales: recent progress and future perspectives for research with special emphasis on activities within Japan, Mycoscience 62 (1) (2021) 1–9.
[47] J. Kaur, et al., Phenotypic profiling of Scedosporium aurantiacum, an opportunistic pathogen colonizing human lungs, PLoS One 10 (3) (2015) e0122354.
[48] T. Gräfenhan, et al., An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in Cosmospora, Acremonium, Fusarium, Stilbella, and Volutella, Stud. Mycol. 68 (1) (2011) 79–113.
[49] Y. Wang, R. Wang, Y. Sha, Distribution, pathogenicity and disease control of Fusarium tricinctum, Front. Microbiol. 13 (2022) 939927.
[50] S. Udagawa, Y. Horie, P. Cannon, Two new species of Neocosmospora from Japan, with a key to the currently accepted species, Sydowia 41 (1989) 349–359.
[51] B. Summerell, C. Rugg, L. Burgess, Characterization of Fusarium babinda sp. nov, Mycol. Res. 99 (11) (1995) 1345–1348.
[52] M. Casal, et al., Appearance of colonies of Prototheca on CHROMagar Candida medium, Mycopathologia 137 (1997) 79–82.
[53] D.S. Tennakoon, et al., A taxonomic assessment of novel and remarkable fungal species in Didymosphaeriaceae (Pleosporales, Dothideomycetes) from plant litter, Front. Microbiol. 13 (2022) 1016285.