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Title	Comparative genomics sheds new light on the microbiology of the whiskey fungus Baudoinia
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Publication date	2026-08-05
Original Citation	Perez-Llano, Y, Jackson, S A, Batista Garcia, R A & Dobson, A 2026, 'Comparative genomics sheds new light on the microbiology of the whiskey fungus Baudoinia', Fungal Biology Reviews, vol. 58, 100505, pp. 1-10. https://doi.org/10.1016/j.fbr.2026.100505
Type of publication	Review
Link to publisher's version	https://www.scopus.com/pages/publications/105046499349 - 10.1016/j.fbr.2026.100505
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Download date	2026-11-06 07:14:00
Item downloaded from	https://hdl.handle.net/10468/19177

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Fungal Biology Reviews 58 (2026) 100505

Contents lists available at ScienceDirect

Fungal Biology Reviews

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

Comparative genomics sheds new light on the microbiology of the whiskey fungus *Baudoinia*

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ARTICLE INFO

Keywords:
Baudoinia
Distillery
Extreme
Genomics
Metabolism
Warehouse staining

ABSTRACT

Baudoinia compniacensis is a melanized saprobic fungus that causes blackening of surfaces in the vicinity of spirit maturation warehouses, commercial bakeries, or distilleries that are exposed to low levels of ethanol vapour; with the fungus growing on the ethanol in the vapour. The surfaces that are most affected are those that are highly exposed and undergo extreme diurnal temperature fluctuations. This review focuses on the currently available physiological and genomic data to facilitate a comparative analysis of *Baudoinia compniacensis* with the genomes of a panel of fungi representing a broad spectrum of lifestyles, stress-tolerance strategies, ecological specializations and convergent adaptations that parallel those of *Baudoinia*, together with fungi with ethanol tolerance. By anchoring *Baudoinia* within this rationally selected comparative framework, this review attempts to differentiate traits that are widely shared among melanized and extremotolerant fungi from those that are unique in helping to enable the fungus colonize ethanol-rich, anthropogenic surfaces. The review also provides insights into a number of potential adaptive genetic traits that are likely to underpin the ecological success of *Baudoinia*, including genes involved in carbon and pentose phosphate metabolism, carbohydrate-active enzymes, genes involved in peroxisome and mitochondrial fatty-acid metabolism, together with calcium signalling and in melanin biosynthesis. We place these traits in comparative perspective, noting that many are shared across the broader oligotrophic, melanized black-fungal guild and that ethanol appears to act as a multifunctional, concentration-dependent input — germination cue, carbon source and stressor — rather than as a uniquely defining resource, with wood- and plant-derived carbohydrates likely to supplement ethanol as carbon sources. We also identify priority avenues for future work, including the sequencing of confirmed *B. compniacensis*, systematic survey of natural (non-industrial) reservoirs, and experimental separation of the signalling and nutritional roles of ethanol, together with direct characterisation of carbon metabolism on lignocellulosic (wood-cask) substrates.

2,3-BPG	2,3-bisphosphoglycerate	iPGM	2,3-bisphosphoglycerate-independent phosphoglycerate mutase
AA	Auxiliary Activity	ITS	Internal Transcribed Spacer
ACAA1	Acetyl-CoA Acyltransferase 1	KGDHC	ketoglutarate dehydrogenase
ACC	acetyl CoA carboxylase	LPMO	Lytic Polysaccharide Monooxygenase

(*continued on next column*)

(*continued*)

ACOX	acyl-CoA oxidase	MCU	mitochondrial Ca^{2+} uniporter
ACP	acyl carrier protein	MECR	mitochondrial trans-2-enoyl-ACP reductase
ACSF	acyl-CoA synthetase family	MLA	Modified Leonian's agar
ACSL	long-chain acyl-CoA synthetase	MLB	Modified Leonian's broth

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https://doi.org/10.1016/j.fbr.2026.100505
Received 5 June 2026; Received in revised form 30 July 2026; Accepted 31 July 2026
Available online 5 August 2026
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AGT	alanine-glyoxylate aminotransferase	mtFAS	mitochondrial fatty acid synthesis
ALDH	aldehyde dehydrogenase	NADPH	Nicotinamide Adenine Dinucleotide Phosphate
AMACR	α-methylacyl-CoA racemase	nucITS	nuclear Internal Transcribed Spacer
AMD	acid mine drainage	nucLSU	Nuclear Large Subunit
BPM	*Baudoinia* physiological medium	PAOX	polyamine oxidase
CALM	Calmodulin	PCA	Principal Component Analysis
CAT	catalase	PDCR	Peroxisomal 2,4-Dienoyl-CoA Reductase
CAZymes	carbohydrate-active enzymes	PDH	pyruvate dehydrogenase
CBM	carbohydrate-binding modules	PEX	peroxin
CE	carbohydrate esterases	PHYH	phytanoyl-CoA hydroxylase
DAG	diacylglycerol	PIPOX	L-pipecolic acid oxidase
DAO	D-amino acid oxidase	PKA	Protein kinase A
DERA	deoxyribose-phosphate aldolase	PLC	Phospholipase C
DHN	dihydroxynaphthalene	PRDX5	peroxiredoxin 5
L-DOPA	L-3,4-dihydroxyphenylalanine	PTS	Peroxisomal Targeting Signal
dPGM	cofactor-dependent phosphoglycerate mutase	ROS	reactive oxygen species
ECH	Enoyl-CoA hydratase	SCPX	sterol-carrier protein
EBM	Ewaze's semi-selective *Baudoinia* medium	SERCA	Sarco/Endoplasmic Reticulum Calcium ATPase
EPHX2	epoxide hydrolase	SOD	superoxide dismutase
FAS	fatty acid synthase	SPHK	Sphingosine kinase
FAST	Fusion-Associated Small Transmembrane	SSU rDNA	small subunit ribosomal DNA
GAG	group-specific antigen	TAG	triacylglycerol
GBIF	Global Biodiversity Information Facility	TCA	tricarboxylic acid
GCV	glyoxylate cycle	TEF1	elongation factor 1-alpha
GH	glycoside hydrolases	TUB	beta-tubulin
GMC	glucose–methanol–choline	uFA	unsaturated fatty-acid
GT	glycosyl transferases	VAO	vanillyl-alcohol oxidase
HAO	hydroxylamine oxidoreductase	VDAC	Voltage-dependent anion-selective channel
HTD	hydroxyacyl-ACP dehydratase	XDH	xanthine dehydrogenase
HMGCL	3-hydroxy-methylglutaryl -CoA lyase		
hTAG	hydroxy-triacylglycerol		
IDH	isocitrate dehydrogenase		

1. Introduction

Baudoinia compniacensis is the fungus that is the principal agent of fouling known as “warehouse staining”, which results in the occurrence of the blackening or darkening of buildings, fixtures, and vegetation in the immediate vicinity of spirit maturation warehouses, commercial bakeries, or distilleries and other areas that are exposed to low levels of ethanol vapour. This blackening results from the growth of the fungus, which can use the ethanol present in the vapour emissions from these warehouses and also from bakeries. In addition to ethanol, it requires high relative humidity at least during some parts of the year to support colonization. The surfaces most affected are typically highly exposed and undergo extreme diurnal temperature fluctuations (Ewaze et al., 2007; Scott et al., 2016; Scott and Summerbell, 2016b). Pronounced blackening often extends over significant distances, documented on the order of hundreds of metres, and in transect surveys up to roughly a kilometre or more, from the ethanol emission source (Craig et al., 2023). As a result, the fungus randomly colonizes a variety of exposed surfaces, encompassing both structural and inorganic substrates (masonry, concrete, painted wood, metal railings, glass and roof tiles) and organic substrates (tree bark, foliage and the oak of maturation casks). Scott and co-workers reported the absence of conidia that were morphologically similar to *B. compniacensis* in air samples from regions where significant levels of fungal colonization of building exteriors had been reported (Scott et al., 2007). This suggests that the conidia are unlikely to be dispersed by bioaerosols — a pattern that may reflect the comparatively large, thick-walled, melanized conidia of *Baudoinia*, which arise by disarticulation of the hyphae and, being denser and more adhesive than the small, dry, hydrophobic spores typical of wind-dispersed fungi, are correspondingly less readily lofted and held in suspension. A more likely mechanism of dispersal may include rain or invertebrates such as terrestrial gastropods. Another, and potentially more likely, means of transfer is via whiskey barrels, which can provide sufficient inoculum to initiate colonization of different habitats (Scott et al., 2016b). In this respect, a study on oak barrels used in the bourbon whiskey industry found that the outer layer of barrel staves was composed of 30% cellulose, which could be available to *Baudoinia* to grow on the exterior of the barrels and subsequently in the vicinity of bourbon rickhouses (Gollihue et al., 2018). Indirect genetic support for barrel-mediated dispersal comes from the geographically structured, continental-scale speciation pattern recovered by multilocus phylogenetics (Scott et al., 2016), which is consistent with the historical redistribution of colonised cooperage; direct genetic evidence — for example population-genomic connectivity analyses, or *Baudoinia*-specific qPCR of barrel surfaces along trade routes — has not yet been reported and is a possible target for future work.

Baudoinia was originally described by the French pharmacist Antonin Baudoin in 1872 as a black sooty growth found on the walls and roof tiles of buildings located near distilleries in the Cognac region of France (Roumeguere, 1881). The causative agent at that time was reported to be the fungus *Torula compniacensis* (Richon and Petit, 1881), which upon re-examination in 2007 was subsequently reassigned to the genus *Baudoinia* (Scott et al., 2007). Based on small subunit ribosomal DNA (SSU rDNA) analysis, it was then reported that *B. compniacensis* belonged to the order Capnodiales (Scott et al., 2007). A multilocus DNA sequencing study, which examined 19 *Baudoinia* strains from a variety of different environmental samples taken near distillery warehouses in various geographical regions including, North America, South America, Europe, the Caribbean, and the Far East, confirmed that *Baudoinia* is a monophyletic lineage within the Teratosphaeriaceae (Capnodiales). Subsequent multilocus phylogenetic analysis of nucITS rRNA (ITS1-5.8S-ITS2) and partial nucLSU rRNA, beta-tubulin (TUB), and elongation factor 1-alpha (TEF1) gene sequences indicated that *Baudoinia* consists of five geographically patterned lineages inclusive of four new species namely *Baudoinia antilliensis*, *Baudoinia caledoniensis*, *Baudoinia orientalis* and *Baudoinia panamericana* (Scott et al., 2016). Each new species was named from the Latin name of the type locality with *B. antilliensis* being from samples originating in the island archipelago bordering the Caribbean sea; *B. caledoniensis* being from Scottish samples; *B. orientalis* being from oriental samples (Korea); *B. panamericana* being from the continental Americas (Argentina, USA), while *B. compniacensis* was the species name given to samples from the Cognac region. Interestingly, this report suggested that international trade in used aging whiskey barrels, which were colonized by these fungi, may be a means of promoting their redistribution to these different geographical locations (Scott et al., 2016).

The most recent Global Biodiversity Information Facility, (GBIF) snapshot of the international distribution of *Baudoinia* occurrences indexed in aggregating records attributed to *B. compniacensis* and congeneric species across Europe (United Kingdom, Germany, Denmark), North America (USA, Canada), Central America (Panamá), and Australia, totals 337 records ([https://www.gbif.org/es/search?q=Baudoinia], accessed in January 2026) (Supplementary Fig. 1). Of these 337 records, 211 are from Australia and 56 from the United Kingdom, a distribution that is likely to reflect data-mobilization asymmetries rather than potentially reflecting true biogeographical

differences; for example the strong national digitization pipelines of the Atlas of Living Australia (ALA) and the UK's NBN Atlas, together with differences in the collection of environmental observation datasets, and the post-2007 reconciliation of names (e.g., legacy records under *Torula compniacensis*).To build the map, GBIF was queried at the genus level and for the five currently accepted species, retained only georeferenced occurrences, and performed basic de-duplication (occurrenceID/date/locality) while flagging low-precision coordinates. It should be noted that additional occurrences do appear in the literature but are not as yet indexed by GBIF, and that historical names (e.g., *Torula compniacensis*) are in some instances inconsistently cross-referenced. Taken together, the GBIF layer and literature overview support the broad, multi-regional presence of *Baudoinia* associated with ethanol-emitting facilities, while bearing in mind that spatial patterns should be interpreted cautiously due to the aforementioned reporting biases and variable georeferencing quality. These curated GBIF species pages provide the taxonomic backbone and occurrence indexing used to build the map in Supplementary Fig. 1.

2. Generalized growth cycle

Baudoinia is likely to experience daily fluctuations in both temperature and moisture when growing on ethanol-exposed surfaces in the outdoors, such as walls and materials in the proximity of whiskey, bourbon, and cognac warehouses. In this context, a generalized growth cycle for *Baudoinia* has been proposed, whereby during the early and late evening, the surfaces on which the dormant fungus had been growing cool down, leading to condensation overnight. Given the greater affinity that ethanol has for the liquid phase rather than the vapour phase, the airborne ethanol is adsorbed into the dew on the cold surfaces. This is estimated to result in a 10-fold greater concentration of ethanol in the dew drops than in the surrounding air (Scott and Summerbell, 2016b). It is useful to make these concentrations explicit, because vapour-phase and liquid-phase ethanol operate over very different ranges: germination of dormant cells is stimulated by ethanol vapour at approximately 10 ppm (≈9.5–19 mg m^{-3} at 25°C), whereas continuous mycelial growth on ethanol as a carbon source is optimal only in the low tens-of-millimolar range in the liquid phase (≈43 mM; Ewaze et al., 2007, 2008). Ambient atmospheric concentrations around maturation warehouses therefore act principally as a germination and stress-priming cue that is subsequently enriched in surface dew, rather than themselves constituting a carbon source at the concentrations found in air — a distinction that matters whenever ambient vapour measurements are interpreted in relation to fungal biomass production. The ethanol then stimulates germination of the dormant fungal cells, on the cold surfaces, where it acts not only as a nutrient source but also in initiating cellular stress responses that help protect the fungus. During the day, the surfaces then heat up when they are exposed to sunlight, resulting in the evaporation of the dew; the dehydration of the fungal cells and the reestablishment of dormancy and the growth cycle (Scott and Summerbell, 2016b). Interestingly, the ability of *Baudoinia* to respond to ethanol has raised the possibility of the use of this fungal species as an environmental bioindicator of ethanol production and emissions, together with a potential indicator of temperature variations (Warnasuriya et al., 2023). *B. panamericana* has also recently been reported to be present together with *Exophiala* species and various other black yeast species, including *Zasmidium cellare*, as members of the microbiome of plasticised fabrics that have been experimentally exposed to harsh tropical environmental conditions to explore the role of these microbial communities in the biodegradation of plastic fibres (Radwan et al., 2020). *Baudoinia* has also been detected in the microbial community of fermented grain during the Chinese strong-flavour Baijiu production process using metatranscriptomics (Hu et al., 2020) and in DNA extracted from leaves and twigs from deciduous trees such as Chinese chestnut, walnut, and American elm, suggesting that they may be endophytes or epiphytes of some tree species (LaBonte et al., 2018).

3. Physiology

B. compniacensis is characterized by thick-walled, rugulose, darkly-pigmented hyphae—melanized cells, that separate to form irregularly spherical to barrel-shaped conidia. The fungus can be grown on general-purpose cultivation medium such as ML agar (MLA) on Modified Leonian's broth (MLB), on Ewaze's semi-selective *Baudoinia* medium (EBM) (Ewaze et al., 2008b) or on *Baudoinia* physiological medium (BPM) (Ewaze et al., 2008a; Scott et al., 2007). When grown on MLA, colonies are typically dark brown to black in colour, very slow growing, and reach a diameter of <10 mm following growth at 26°C after 28 days. Similarly, when grown on EBM agar for 8 weeks, colonies are deep-black, both on the surface (Fig. 1A) and on the reverse side (Fig. 1B), circular but irregular-edged, rough, dry, and brittle, ~10 mm in diameter, and umbonate with exaggerated elevation (~8 mm) (Fig. 1C). When stained on wet mount with lactofuschin, conidia are barrel-shaped, thick-walled, and form branching hyphae (Fig. 1D).

With respect to the ability of the fungus to utilize different carbon sources, Ewaze and co-workers have reported that *B. compniacensis* can metabolize a range of various carbon sources such as glucose, acetate and ethanol, with glucose being optimally used in the 1-10 mM, acetate 1 mM, and ethanol in the 40-50 mM range. Growth on ethanol in this range has been reported to occur in a variety of different inorganic nitrogen sources, such as ammonium nitrate, ammonium chloride, sodium nitrate, potassium nitrate, together with organic nitrogen sources such as asparagine, alanine, glutamine, glutamate, and casamino acids. Either very poor growth of *B. compniacensis* or no growth at all was observed when other simple alcohols were used as a carbon source (Ewaze et al., 2007). Notably, biomass yields on glucose (optimally 1–10 mM) and on acetate were comparable to, or exceeded, those obtained at optimal ethanol concentrations, and growth was supported across a broad range of inorganic and organic nitrogen sources; on the basis of these data Ewaze et al. (2007) concluded that, although ethanol is likely to be ecologically important, it is not physiologically essential for the fungus. With respect to atmospheric ethanol concentrations required to sustain growth of *B. compniacensis*, optimal growth has been reported at atmospheric ethanol concentrations of 5000 to 10,000 mg/m^3 (Craig et al., 2023). Such breadth of carbon- and nitrogen-source utilisation is characteristic of oligotrophic, surface-dwelling fungi and is consistent with viewing Baudoinia as a melanized oligotroph for which ethanol acts as a multifunctional, concentration-dependent input rather than as an obligate ethanol specialist.

4. Comparative genomic analysis

A panel of fungi representing a broad spectrum of lifestyles, stress-tolerance strategies, and ecological specializations was assembled to facilitate the genomic analysis of *B. compniacensis* within a coherent and testable comparative framework (Supplementary Table 1). This selection was guided by four traits directly relevant to the biology of *Baudoinia*: (i) lifestyle: given that *Baudoinia* is a melanized saprobe that colonizes outdoor surfaces exposed to evaporating ethanol; (ii) ethanol tolerance: which is central to its survival in ethanol-rich microhabitats; (iii) melanin pigmentation: a recurrent feature in black fungi linked to stress resistance; and (iv) extremotolerance: encompassing the ability to withstand hostile physicochemical conditions, including extremes of pH, temperature, UV radiation, and/or osmotic stress. By contrasting species that span these axes, the supplementary table provides a rational basis for identifying whether *Baudoinia*'s genomic repertoire reflects general attributes of melanized, extremotolerant fungi or unique adaptations to an ethanol-saturated niche.

Several extremotolerant fungi were included as they exemplify convergent adaptations that may parallel those of *Baudoinia*. *Acidomyces richmondensis*, an acidophilic black fungus that thrives in acid mine drainage, represents a model for understanding tolerance to hostile chemical environments (Rosienski et al., 2018; Li et al., 2023). Similarly,

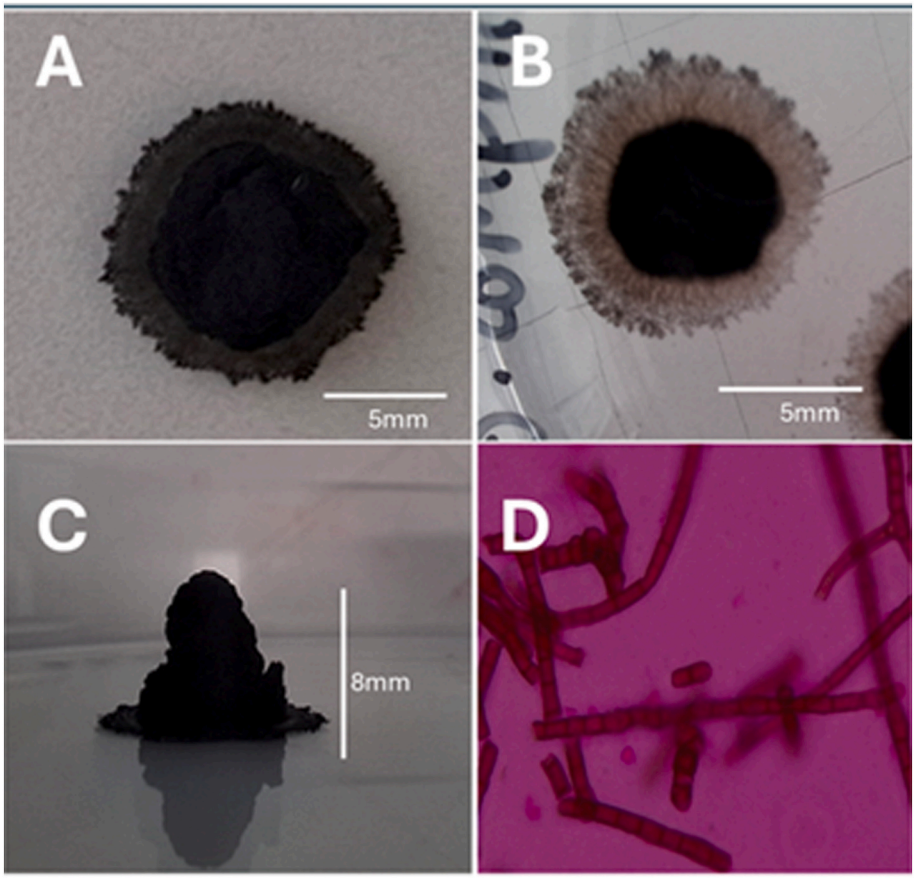


Fig. 1. Colony and conidia morphology of *Baudoinia compniacensis* CBS 123031 grown on EBM agar for 8 weeks (A-C) or stained in wet mount with lactofuchsin (D). (A) colony surface, (B) colony reverse side (C) colony side-view (D) conidia stained with lactofuchsin and viewed under a light microscope (Leica DM750) at 400x magnification.

Aureobasidium pullulans and its relatives (*A. namibiensis*, *A. subglaciale*), *Cryomyces antarticus*, and *Knufia obscura* are well-known polymorphic black yeasts that tolerate desiccation, UV radiation, and in some cases, low temperatures; making them informative comparators for stress-resistance characteristics (Gostinčar et al., 2014, 2019; Gomez-Gutierrrez et al., 2024; Isola et al., 2022). *Exophiala dermatitidis*, a classical opportunistic and polyextremotolerant black yeast, was included as its genome encodes an extensive array of stress-protective systems, including those involved in melanisation and osmolyte regulation, highlighting parallels with other black fungi that thrive under extreme or anthropogenic conditions (de León et al., 2025). Likewise, *Hortaea werneckii*, one of the most halotolerant fungi known, provides an extreme case of osmoadaptation, offering insights into how stress-response genes may be amplified or repurposed in fungi with highly specialized niches (Gunde-Cimerman and Plemenitaš, 2006).

The dataset also incorporates fungi with particular relevance to ethanol tolerance. For instance, *Debaryomyces hansenii* is moderately tolerant to ethanol and osmotic stress respectively, making it relevant for identifying whether *Baudoinia*'s ethanol tolerance is rooted in shared yeast-like pathways or potentially in lineage-specific mechanisms (Sánchez et al., 2006; Prista et al., 2005). Notably, *Zygosaccharomyces rouxii*, a yeast renowned for its exceptional osmotolerance and moderate ethanol tolerance, serves as a positive control for the analysis, since its genome exemplifies how fermentative fungi have evolved mechanisms for survival in both sugar- and ethanol-rich niches (Groleau et al., 1995). In contrast, *Saccharomyces cerevisiae*, the best-studied model yeast, functions as a baseline control given that it exhibits efficient ethanol fermentation but only limited stress tolerance, thus allowing us to potentially distinguish common fermentative pathways from the more specialized adaptations found in black yeasts.

Finally, broadly distributed saprobic filamentous fungi such as *Aspergillus niger* were included to provide generalist reference points. While *A. niger* is not an extremophile, its genome encodes for robust secondary metabolism characteristics and melanized conidia, making it a useful contrast to the highly stress-tolerant black yeasts (Baker, 2006). Together, this combination of extremophiles, ethanol-tolerant yeasts, melanized fungi, and generalist saprobes provides a robust comparative context to potentially provide further important insights on the genomic basis for *Baudoinia*'s survival strategies.

By anchoring *Baudoinia* within this diverse yet rationally selected comparative framework, we are attempting to differentiate traits that are widely shared among melanized and extremotolerant fungi from those that are unique in helping to enable colonization of ethanol-rich, anthropogenic surfaces. For each taxon a single representative genome was selected for orthology inference analysis using Orthofinder on the predicted proteomes. The *Baudoinia* genome used throughout is that of strain UAMH 10762, originally sequenced under the name *B. compniacensis* (Ohm et al., 2012) and later designated the holotype of *B. panamericana* in the multilocus revision of the genus (Scott et al., 2016). All genome-level statements below therefore describe *B. panamericana* specifically. Because no other *Baudoinia* genome is presently available, intraspecific variation and cross-species conservation within the genus could not be evaluated, and standardisation across the comparator panel was necessarily at the level of one genome per species. This design aims to ensure that our genomic comparisons will allow us to potentially identify the adaptive genetic repertoire that is likely to underpin the ecological success of *B. compniacensis*.

A Principal Component Analysis (PCA) computed on the resulting

orthogroup abundance matrix across 26 genomes including *B. panamericana* (Supplementary Table 1), together with the aforementioned melanized fungi, extremotolerant yeasts, and classical fermentative models, revealed that *B. panamericana* occupies a distinct position, separated from both polyextremotolerant black yeasts such as *Aureobasidium* spp. and *Exophiala xenobiotica*, and from fermentative yeasts such as *Saccharomyces cerevisiae*, *Kluyveromyces marxianus*, and *Z. rouxii* (Fig. 2A). Functional enrichment of divergent orthogroups was assessed with Fisher's exact test with Benjamini-Hochberg (BH) multiple-testing correction.

This suggests that *Baudoinia*'s genomic architecture reflects a lineage-specific adaptive strategy shaped by its ethanol-enriched ecological niche. Orthogroup comparisons confirmed this distinction given that of the 17,082 total orthogroups detected, *B. panamericana* shared only 8636 with other fungi but displayed significant differences in 3924 orthogroups, indicating that nearly a quarter of its genomic repertoire diverges in abundance or presence/absence relative to other fungi (Fig. 2B). Functional enrichment analysis of these divergent orthogroups underscored overrepresentation of categories linked to stress adaptation and metabolic flexibility, including cell wall organization, amino acid transport, lipid and organic acid catabolism, and carbohydrate and polyol metabolism. Also overrepresented were orthogroups responding to oxidative stress, nutrient limitation, alcohol exposure, and extracellular stimuli (Fig. 2C). Further insights emerged from domain-based analyses with Pfam families that are significantly expanded in *Baudoinia*. These families included ribosomal proteins, alpha-kinase domains, and polysaccharide biosynthesis proteins (Fig. 2D). The expansion indicates potential enhanced translational efficiency, signalling capacity, and cell wall remodelling (Fig. 2E), features that align with survival under fluctuating and challenging environmental conditions (Coleine et al., 2024; Gostinčar et al., 2019). In addition, *Baudoinia* exhibited enrichment in transposon- and virus-associated protein families, including retroviral GAG polyproteins, viral fusion proteins, and FAST fusion proteins (Fig. 2E) (Teixeira et al., 2017), indicating that genome plasticity mediated by mobile elements may have helped to contribute to adaptive innovation and may have contributed to its ability to colonize and persist in anthropogenic microhabitats saturated with evaporating ethanol (Craig et al., 2023). Taken together, these comparative analyses reveal that *B. panamericana* combines general traits of melanized extremotolerant fungi with potentially unique genomic innovations that appear to underpin its ecological specialization.

Two caveats should temper the interpretation of these single-genome comparisons. First, because orthogroup ordinations across phylogenetically heterogeneous genomes are shaped by taxonomic distance, genome size and annotation depth as well as by ecological adaptation, the position of *B. panamericana* in the PCA, and the apparent enrichment or expansion of particular gene families, are best treated as hypotheses to be confirmed with phylogenetically corrected comparative methods rather than as established adaptive signals. Second, the only class-level phylogenomic analysis to include an alcohol-exposed comparator pair — *B. panamericana* together with the wine-cellar fungus *Zasmidium cellare* — reported a statistically significant (>30%) expansion of major-facilitator-superfamily (MFS) transporters relative to other Dothideomycetes but did not identify any unique genes or gene families associated with ethanol use (Haridas et al., 2020). Read alongside the placement of *Baudoinia* within an ancestrally saprotrophic Dothideomycete lineage (Haridas et al., 2020) and an oligotrophic black-fungal radiation (Coleine et al., 2024), this indicates that much of the repertoire highlighted here reflects a broadly shared extremotolerant, oligotrophic toolkit deployed on an ethanol-rich substrate, with the truly *Baudoinia*-specific, ethanol-linked innovations remaining to be delimited by broader within-genus and phylogenetically controlled sampling.

5. Carbon metabolism survival under fluctuating and challenging environmental conditions

It is well established that *Baudoinia* catabolizes ethanol via alcohol dehydrogenase and acetaldehyde, so that ethanol is assimilated into the tricarboxylic acid (TCA) cycle via acetaldehyde and acetate (Ewaze et al., 2008). This ability to utilize ethanol as a carbon source has also been reported in a number of fungi in addition to *Baudoinia*. For example, the filamentous fungus *Z. cellare*, which is known as the wine cellar mould, forms thick mats of mycelia in wine cellars at high levels of humidity when ethanol vapour is present (Magyar et al., 2018; Cailhol et al., 2020). This fungus can metabolize and grow on vapours of ethanol, esters, and formaldehyde, with colonies of *Z. cellare* being observed in wine cellars near ethanol sources, such as on wine bottle corks (Goodwin et al., 2016). An *A. niger* strain has also been reported to grow on 1% ethanol (Dantigny et al., 2005), while another *A. niger* strain isolated from spoiled pastry products has been reported to be able to grow on potato dextrose agar containing 3% ethanol (*w/w*) (O'Connell and Kelly, 1988). The ethanol utilisation pathway has been well established in both *Aspergillus nidulans* and in *A. niger* (Felenbok et al., 2001). Like *Baudoinia* in *A. nidulans*, ethanol is oxidized to acetaldehyde by alcohol dehydrogenase I, which is further oxidized by aldehyde dehydrogenase (ALDH) to yield acetate, which is then converted to acetyl-CoA by acetyl-CoA synthetase. Acetyl-CoA can then enter a number of metabolic pathways, including primary pathways such as the TCA cycle and lipid synthesis, where acetyl-CoA is carboxylated to malonyl-CoA, which then couples with acetyl-CoA to form acyl-CoA. Acyl-CoA can then act as a substrate for the production of fatty acids, phospholipids and glycerolipids. A similar pathway is likely to operate in *A. niger* ES4 an ethanol-tolerant strain isolated near an ethanol tank of a petroleum company, and which is capable of growing in 5% (*v/v*) ethanol. It is believed that to survive on the wall of the ethanol tank, the *A. niger* strain metabolizes ethanol as a nutrient source to reduce its toxicity (Vinayavekhin et al., 2020). In addition, *A. niger* ES4 also responds to the ethanol stress to which it is exposed by upregulating the production of glycerolipids such as diacylglycerol (DAG), triacylglycerol (TAG), and hydroxy-triacylglycerol (hTAG).

Ethanol also plays an important role in the initiation of cell germination as well as growth in *Baudoinia*, with enhanced levels of germination being observed upon exposure to low ethanol concentrations (10 ppm or 9.5-19 mg/m^3 at 25°C) in a vapour form and 5 mM in liquid form (Ewaze et al., 2008). Ethanol also stimulates cellular stress responses, such as the expression of heat-protective proteins that confer heat resistance, with heat resistance induced by brief sublethal temperature exposure (Scott et al., 2007).

When the carbon metabolic pathways from six filamentous fungal and yeast species, namely *B. panamericana*, *S. cerevisiae*, *A. niger*, *Pichia kudriavzevii*, *Ogataea polymorpha*, and *Scheffersomyces stipitis*, were analysed, a high level of conservation in the glycolytic pathway backbone was apparent (Fig. 3). However, one noticeable difference was that both *Baudoinia* and *A. niger* uniquely possess the enzyme 2,3-bisphosphoglycerate-independent phosphoglycerate mutase (iPGM) (EC 5.4.2.12), which catalyzes the interconversion of 3-phosphoglycerate to 2-phosphoglycerate (Graña et al., 1995), ultimately leading to the production of pyruvate from phosphoenolpyruvate and also resulting in the production of respiratory, fermentation and lipid precursors. Unlike the canonical cofactor-dependent phosphoglycerate mutase dPGM (EC 5.4.2.1), which requires 2,3-BPG for activation, iPGM operates via a metal-dependent phosphoserine mechanism, maintaining flux when 2, 3-BPG pools are low or perturbed by solvent, heat, or oxidative stress (Fig. 3). This redundancy makes glycolysis/gluconeogenesis more robust to environmental fluctuations, a logical advantage for *Baudoinia*'s surface-colonizing, ethanol-exposed lifestyle, allowing pentose/deoxyribose salvage (and intermittent carbohydrate inputs) to be effectively channelled through iPGM even under episodic wetting, temperature swings, and ethanol pulses, while sustaining the supply of pyruvate,

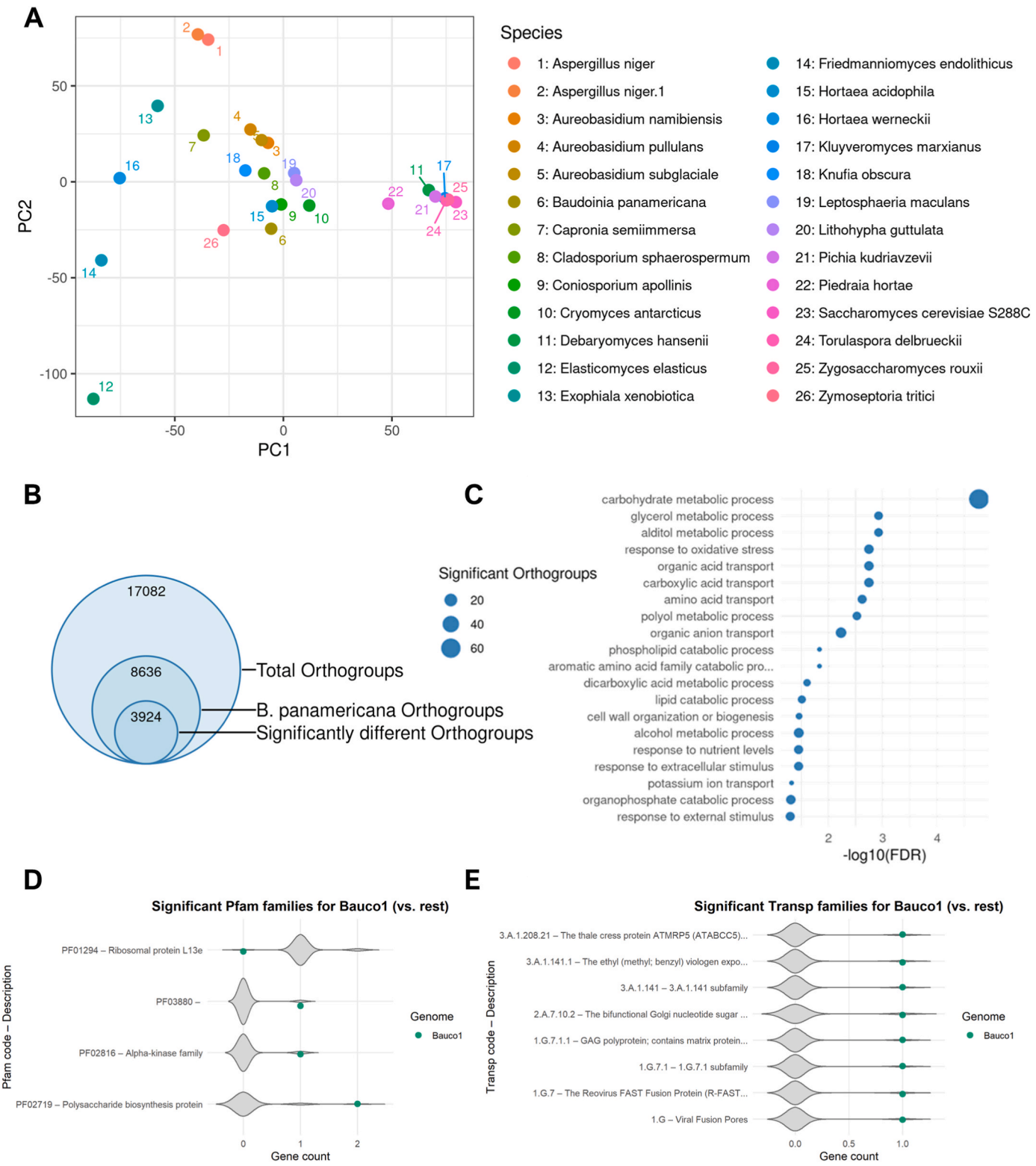


Fig. 2. Comparative genomics of *Baudoinia panamericana* (strain UAMH 10762). Orthologous gene groups (orthogroups) were inferred with OrthoFinder from the predicted proteomes of 26 fungal genomes (Supplementary Table 1) and used as the common input to all panels. (A) Principal Component Analysis (PCA) of the orthogroup presence/absence and copy-number matrix, showing the genomic distinctiveness of *B. panamericana* relative to polyextremotolerant black yeasts and to fermentative yeasts. (B) Orthogroup comparison identifying 3924 groups significantly divergent in presence/absence or copy number in *B. panamericana* relative to the panel. (C) Functional enrichment of the divergent orthogroups (Fisher's exact test with BH multiple-testing correction), highlighting stress- and metabolism-related categories. (D) Pfam domain families significantly expanded in *B. panamericana*, including ribosomal-protein, alpha-kinase and polysaccharide-biosynthesis domains. (E) Enriched transposon- and virus-associated protein families, consistent with a role for mobile-element–mediated genome plasticity. A single representative genome was analysed per species; because only one *Baudoinia* genome is currently available — UAMH 10762, sequenced by Ohm et al. (2012) under the name *B. compniacensis* and reassigned to *B. panamericana* by Scott et al. (2016) — intraspecific variation within the genus, and conservation across the five recognised species, could not be assessed, and the comparisons should be read at the level of this single sequenced strain.

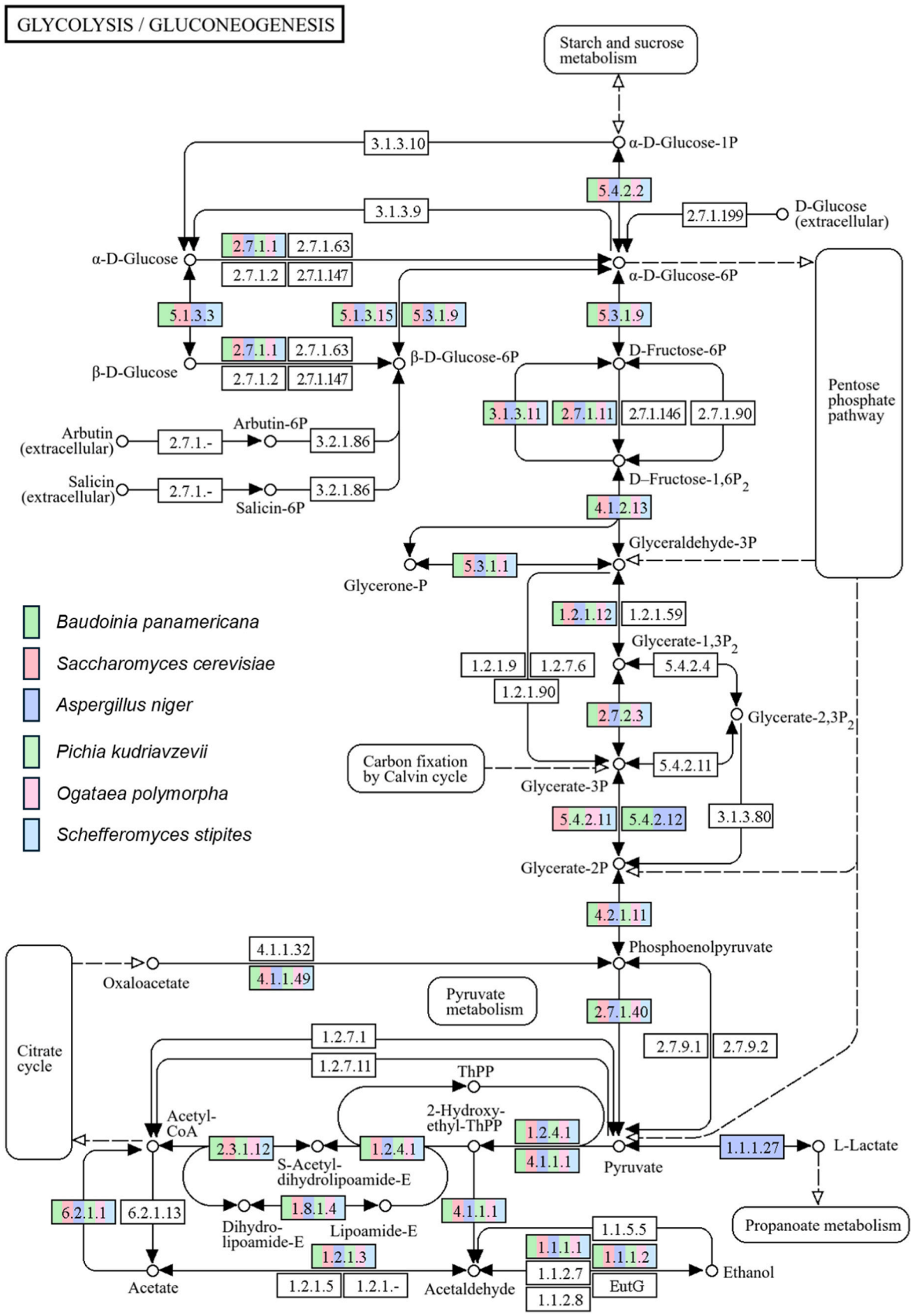


Fig. 3. Comparison of glycolysis and gluconeogenesis pathways of central carbon metabolism across six fungal and yeast models including *Baudoinia panamericana* where only *Baudoinia* and *A. niger* possess the enzyme 2,3-bisphosphoglycerate-independent phosphoglycerate mutase (iPGM) (EC 5.4.2.12), which catalyzes the interconversion of 3-phosphoglycerate to 2-phosphoglycerate.

thereby supporting ATP generation and acetyl-CoA–derived lipid remodelling which is essential for solvent/thermal tolerance and growth on exterior substrates. Direct enzymological testing — comparative specific activities of iPGM and of the cofactor-dependent dPGM in cell extracts under controlled solvent, thermal and oxidative challenge — would be required to confirm that this redundancy translates into a measurable flux advantage under the conditions *Baudoinia* experiences.

In parallel, the canonical TCA enzymes are broadly conserved in all the six filamentous fungal and yeast species, apart from the two C–C bond–forming acyltransferases 2-methylcitrate synthase (EC 2.3.3.5) and ATP-citrate lyase/synthase (EC 2.3.3.8) at the citrate/propionate node, which are significantly enriched in *Baudoinia* and *A. niger* (Fig. 4). EC 2.3.3.5 condenses propionyl-CoA with oxaloacetate to form 2-methylcitrate, thereby initiating the methylcitrate cycle that detoxifies the toxic metabolite propionyl-CoA, by converting it into pyruvate and succinate, preventing its accumulation that could potentially inhibit key cellular processes (Huang et al., 2023). This detoxification of propionate-CoA channels C3 units into central metabolism—supporting growth when odd-chain fatty acids, branched amino acids, or fusel alcohol–derived aldehydes are present. The ATP-citrate lyase/synthase (EC 2.3.3.8) enzyme catalyzes the ATP-coupled interconversion of citrate and acetyl-CoA + oxaloacetate, supplying cytosolic acetyl-CoA for fatty-acid/lipid biosynthesis and acetylation reactions, and enabling rapid shuttling of ethanol-derived acetyl units between mitochondrion and cytosol (Hynes and Murray, 2010).

Thus, these enrichments in the metabolic enzymes iPGM together with acyltransferases 2-methylcitrate synthase and ATP-citrate lyase/synthase are in keeping with the ethanol-based lifestyle of *Baudoinia*, involving growth on periodically wet, sun-exposed surfaces, with ethanol oxidation yielding acetyl-CoA that can be efficiently partitioned toward membrane remodelling and storage lipids to help offset stresses related to solvents or heat. Thus, it is likely that the methylcitrate entry point broadens the carbon flexibility and detoxification capacity in mixed volatile environments around distilleries and bakeries, ultimately reinforcing the ability of *Baudoinia* to establish and persist on a range of diverse substrates.

6. Pentose-phosphate metabolism

Like the glycolytic backbone, the pentose-phosphate enzyme pathway repertoire was also largely conserved across the same six fungi (Supplementary Fig. 2). However, both *Baudoinia* and *A. niger* displayed a significant enrichment in two aldehyde-lyases, namely deoxyribose-phosphate aldolase (DERA) (EC 4.1.2.4) and phosphoketolase (EC 4.1.2.9). The former catalyzes the reversible conversion of 2-deoxy-D-ribose-5-phosphate to glyceraldehyde-3-phosphate and acetaldehyde, providing a route for the degradation of DNA directly into glycolysis while releasing acetaldehyde (Huan et al., 2016). The latter phosphoketolase which is thiamine-diphosphate dependent, converts D-xylulose-5-phosphate and P_i to acetyl-phosphate, glyceraldehyde-3-phosphate and H_2O (Suzuki et al., 2010). This potentially allows the conversion of hemicellulose-derived pentoses such as xylose and xylulose from wood barrels and plant detritus into glyceraldehyde-3-phosphate for energy, and acetyl units via acetyl-phosphate and acetate yielding acetyl-CoA

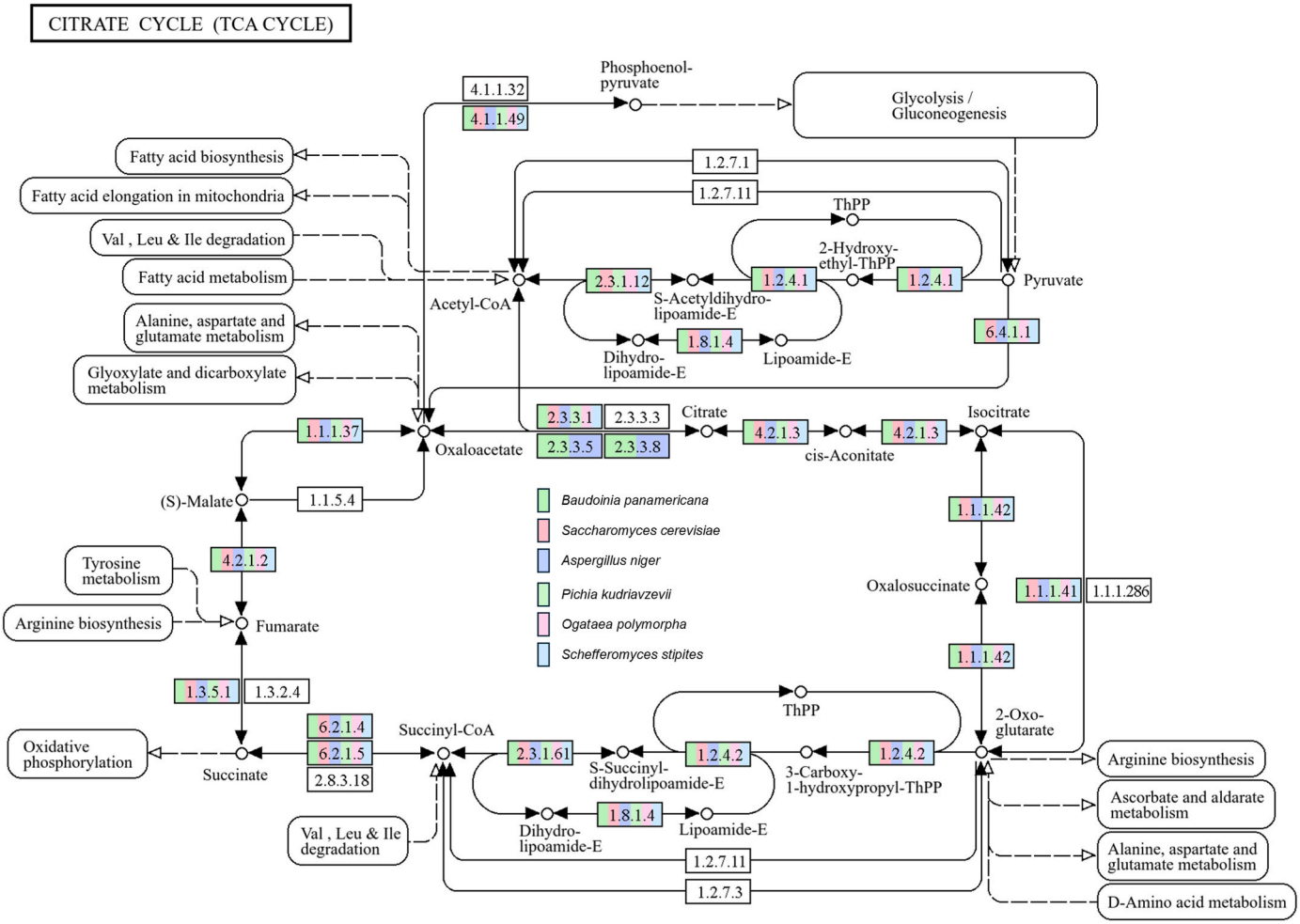


Fig. 4. Comparison of the citrate cycle pathway of central carbon metabolism across six fungal and yeast models including *Baudoinia panamericana* where only *Baudoinia* and *A. niger* possess the 2-methylcitrate synthase (EC 2.3.3.5) and ATP-citrate lyase/synthase (EC 2.3.3.8) at the citrate/propionate node.

for lipid biosynthesis and acetylation. The extent to which this pentose-salvage capacity is actually engaged on wood-derived hemicellulose, rather than remaining a latent metabolic option, remains to be tested directly — for example by growth and 13C-labelling experiments on defined xylose and on hemicellulose hydrolysates prepared from barrel oak and other lignocellulosic substrates.

7. Carbohydrate-active enzymes

A relatively recent comparative genomics study of *Acidiella bohemica*, an acid mine drainage (AMD) fungal isolate, involving five closely related species, was previously undertaken to gain a fuller understanding of the mechanisms of adaptation to AMD environments in the fungus (Ou et al., 2021). The study involved the fungal plant pathogen *Passalora fulva* that causes tomato leaf mould; the extremophilic fungal species found in warm, acidic, and metal-rich environments, *A. richmondensis*; the fungicide-resistant wheat plant pathogen that causes septoria leaf blotch *Zymoseptoria tritici*; the pine tree blight fungal pathogen *Dothistroma septosporum*, and *B. panamericana*. Interestingly, phylogenetic and homologous gene analyses indicated that *A. bohemica* was most closely related to *B. panamericana*, with both having the same functional genes involved in resistance to acid environments and heavy metal stress. While both fungi inhabit quite different environmental niches, these niches do involve exposure to extreme environmental stresses, which may be reflected in the similarity of their genotypes (Ou et al., 2021). In addition to the fact that *A. bohemica* and *B. panamericana* are both saprotrophs which is reflected in the fact that they have similar stress response genes, interestingly both displayed a very high level of similarity with respect to their carbohydrate-active enzymes (CAZymes) genes, involved in carbohydrate degradation. *B. panamericana*, like *A. bohemica*, contains a high number of genes in the following classes: glycoside hydrolases (GH), glycosyl transferases (GT), and carbohydrate esterases (CE), containing approximately 180, 80, and 80 gene copies, respectively (Ou et al., 2021). Thus, while it is clear that *Baudoinia* can assimilate alcohol, it is likely that the fungus relies on other organic materials, including carbohydrates, to supplement its carbon nutrition.

To investigate a possible role for CAZymes in the overall metabolism of *Baudoinia* a comparative analysis of *Baudoinia*'s substrate-resolved CAZyme family repertoire was undertaken (Fig. 5). The distribution of gene counts by substrate suggests that the fungus employs a carbon utilisation strategy that does not include the energetically costly degradation of crystalline cellulose, but instead is more likely to target outer wall plant polymers and anthropogenic deposits to sustain its metabolic activity. The prominent lignin/phenolic signal highlighting AA1 laccases, with support from AA3 glucose–methanol–choline (GMC) oxidoreductases (Fig. 5) (Sützl et al., 2019), indicates the potential capacity to oxidize tannins and lignin fragments from bark and weathered wood, potentially including wooden barrel leachates. Quinones that could be generated by laccases may cross-link with melanin precursors (Land et al., 2004; Solano and García-Borrón, 2006), which could explain the black, resilient patina and increasing resistance to UV and heat that is observed in *Baudoinia*. This oxidative chemistry is also likely to stiffen the extracellular matrix in the fungus, helping to reduce wash-off during rain and dew cycles. Because AA1/AA3 reactions produce reactive species, this profile is likely to be linked with the peroxisomal antioxidant system that will be described later; involving catalase (CAT), peroxiredoxin 5 (PRDX5), and the soluble epoxide hydrolase (EPHX2), suggesting a coordinated oxidization-detoxification approach that is compatible with persistent surface colonization. The presence of the AA4 (vanillyl-alcohol oxidase family) is likely to broaden the aromatic tailoring ability of the fungus by converting the oxidizing phenolic alcohols to aldehydes/quinones (Gygli et al., 2018).

AA7 oxidases (glucooligosaccharide/VAO-like) are likely to act on short neutral oligosaccharides to generate lactones and H_2O_2, providing an auxiliary source of oxidative capacity, potentially reinforcing matrix hardening while creating entry points for carbohydrate metabolism (Savino and Fraaije, 2021). Finally, AA11 LPMOs are a group of copper-dependent enzymes that catalyze the cleavage of glycosidic bonds in recalcitrant polysaccharides such as cellulose, hemicellulose, and chitin by activating molecular oxygen (O2) or hydrogen peroxide (H_2O_2). (Contato and Conte-Junior, 2025), which may offer the fungus the potential to degrade chitinous-containing materials such as insect fragments and fungal debris, with their ROS-linked turnover likely to be coupled to detox/antioxidant capacity of *Baudoinia*. Together, the

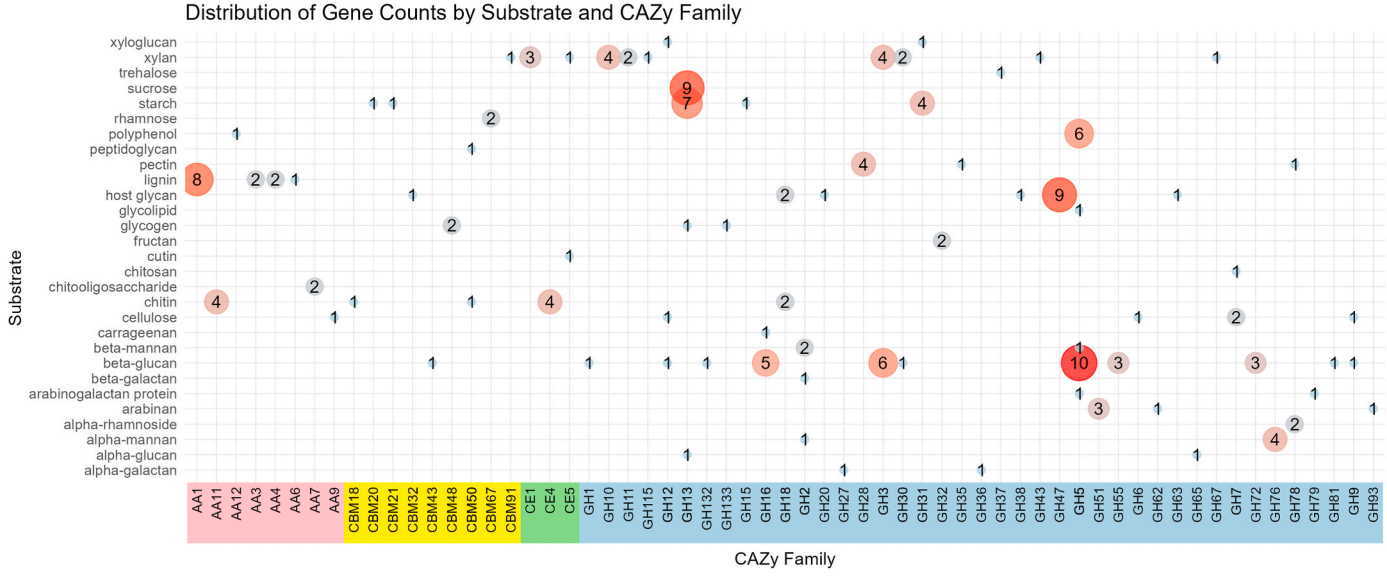


Fig. 5. Substrate-resolved CAZyme repertoire of *Baudoinia* (bubble plot). Rows indicate substrates, columns CAZy families; bubble size and overlaid numbers denote gene counts. CAZy family designations (e.g. GH47, AA1, CE1, CBM48) follow the Carbohydrate-Active enZymes database nomenclature (Drula et al., 2022), in which each numbered family groups enzymes that share sequence, structural fold and catalytic mechanism rather than a single substrate specificity; several families are therefore polyspecific, and a family's row placement reflects the principal substrate class relevant to the *Baudoinia* repertoire discussed in the text. Abbreviations: GH, glycoside hydrolases; GT, glycosyltransferases; CE, carbohydrate esterases; AA, auxiliary (redox) activities; CBM, carbohydrate-binding modules. The bottom colour bar marks CAZy families [Auxiliary Activities (AA) = pink, carbohydrate-binding modules (CBM) = yellow, carbohydrate esterases (CE) = green, glycoside hydrolases (GH) = blue]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

AA4/AA7/AA11 enzyme profile complemented with the AA1–AA3 profile, suggest a phenotype that relies more on light oxidation, cross-linking, and selective substrate cleavage rather than wholesale decay; an approach that would be advantageous for a surface-dwelling fungus such as *Baudoinia* allowing it to thrive on a variety of available carbon containing substrates such as phenolic plant skins, dew-borne oligosaccharides, and ethanol vapours.

Rather than targeting plant cell wall digestion, the substrate-resolved CAZyme repertoire in *Baudoinia* appears to indicate a focus on hemicellulose and pectin debranching (Fig. 5). Enzymes typical of side-chain removal—GH43/51/62/67/78 for arabinan, arabinogalactan, α-rhamnoside and glucuronate decorations on xylan are evident and appear alongside GH28 polygalacturonases and CE1/CE5 (feruloyl esterases and cutinases). From a functionality perspective, this combination of enzymes suggests the cleavage of cuticle and ester cross-links, resulting in increased porosity, and the liberation of carbon in the form of short-chain sugars/oligos and phenolic acids without a strong involvement in broader cellulose degradation; which is suggested by notably weak glycosidase hydrolase GH6/GH7 signatures (Fig. 5). This would make sense from an ecological perspective, as it would allow *Baudoinia* to grow and adhere to exposed surfaces through rapid adhesion and access without the need to produce a range of cellulolytic enzymes to generate metabolizable substrates for energy generation. In addition, the cutinase/feruloyl esterase repertoire of enzymes may help explain the ability of *Baudoinia* to establish on tree leaves and barks, by releasing trace amounts of carbon and co-substrates that synergize with ethanol catabolism from an energy generation perspective. Equally striking is the mannan/N-glycan degrading capability with high gene count numbers for GH47 (α-mannosidase I) and GH76 (α-1,6-mannanase), which together with GH31/GH38 suggest the potential exploitation of glycoprotein-rich aerosols by the fungus (Fig. 5). Given the large number of airborne yeasts and fungi around distilleries, rickhouses, and bakeries, it is likely that many of these yeasts and fungi will ultimately settle and die on hot surfaces and facades and on surrounding foliage, "seeding" these areas with mannan-dense debris pollen. The strong N-glycan/mannan cleavage capacity of *Baudoinia* could therefore potentially supply carbon and nitrogen from this debris, and together with the carbohydrate-binding modules (CBMs) and CBM48/67 in particular (Fig. 5) are likely to improve adhesion to glycan-coated surfaces. Such an approach would complement the ethanol to acetate/acetyl-CoA metabolic route such that when ethanol vapour levels are low or intermittent, glycan metabolism could potentially bridge the gap in terms of energy demand and when ethanol levels increase again, acetyl-CoA units could facilitate lipid remodelling and membrane repair, with mitochondrial fatty acid synthesis (mtFAS) and peroxisomes supplying lipoate. An additional capacity to assimilate different carbohydrate sources is evident in the gene count numbers for GH13/15 (amylases/glucoamylases), GH32 (invertases/inulinases), GH37 (trehalases), which together with CBM20/48 (starch/glycogen binders) indicate an ability to mobilize sucrose, fructans, and starch potentially from plant exudates and weathered wood.

Thus taken together, the observed highest-abundance CAZy families GH47, GH13, GH5, and GH3 may define the overall carbon assimilation strategy of *Baudoinia* (Fig. 4). The aforementioned GH47 (α-mannosidase I) potentially metabolizing N-glycan/mannan in the glycoprotein-rich aerosols from airborne yeasts, fungi, and pollen; providing a source of both carbon and nitrogen for the fungus growing in the vicinity of bakeries or distilleries. The GH13 (α-amylase family) targets starch/glycogen/dextrins, enabling the uptake of plant/exudate carbohydrates, while GH5 a broad modular group that includes endo-β-1,4-glucanases and β-mannanases, are likely to support the assimilation of amorphous cellulose/hemicellulose rather than broader cellulose degradation and working in synergy with CE1/CE5 esterases and AA oxidases to increase the porosity of the matrix to efficiently sequester carbon. Then GH3 (β-glucosidases/β-xylosidases/N-acetyl-β-glucosaminidases) can potentially initiate oligosaccharide hydrolysis, converting released fragments into transportable monomers that could feed glycolysis and the ethanol through the acetate/acetyl-CoA metabolic pathway.

8. Peroxisome metabolism

Peroxisomes are highly dynamic, oxidative organelles that play an important role in lipid metabolism in fungi (Steinberg, 2016) and are implicated in the homeostasis of reactive oxygen species (ROS) (Stehlik et al., 2014). When the peroxisomal systems in the six filamentous fungal and yeast species were analysed, all six were found to contain the core peroxins for matrix import (PEX1, PEX3, PEX5, PEX6) (Judy et al., 2022), with only *Baudoinia* and *A. niger* also possessing PEX16, a hallmark of endoplasmic reticulum (ER)-derived peroxisomal membrane biogenesis (Fig. 6). The presence of the PEX3/PEX16 route implies fast assembly and remodelling of peroxisomal membranes, which would be advantageous for the fungus when growing on exterior substrates where thermal/UV together with ethanol fluctuations would necessitate repeated lipid turnover, redox readjustment, and organelle proliferation. In this context, peroxisomes become dynamic hubs for lipid editing and ROS management, buffering stress while feeding mitochondria with β-oxidation products (Kumar et al., 2024). Thus, an ER with a PEX16-enabled pathway could allow Baudoinia to generate new peroxisomes when ethanol availability increases such as for example during dew events when volatiles are trapped on surfaces and to reduce or recycle these peroxisomes by pexophagy (Wu et al., 2022) during scarcity, thereby minimizing maintenance costs on nutrient-poor facades. Because peroxisomal β-oxidation generates H_2O_2 at the acyl-CoA oxidase (ACOX) step, the ability to expand peroxisomal volume and antioxidant capacity transiently would be a direct fitness gain for the fungus under a regimen of short periods of intense metabolic activity. This plasticity also underpins membrane renovation cycles such as the import/activation of long and branched acyls and the export of acetyl units, that could be central to withstanding solvent stress from ethanol and thermal stress on sun-exposed materials.

In all six genomes studied, when gene activity corresponding to potential nitrogen and redox shunts was investigatedwithin peroxisomes, alanine-glyoxylate aminotransferase (AGT) which catalyzes the conversion of alanine and glyoxylate into pyruvate and glycine, was found. Also present were D-amino acid oxidase (DAO) which allows the metabolism of D-amino acids for energy and growth; isocitrate dehydrogenase (IDH) which catalyzes the oxidative decarboxylation of isocitrate to alpha-ketoglutarate in the TCA cycle, and L-pipecolic acid oxidase (PIPOX) which oxidises L-pipecolate and L-proline (Fig. 6). In addition however, both *Baudoinia* and *A. niger* were found to possess 3-hydroxy-methylglutaryl -CoA lyase (HMGCL) an enzyme that catalyzes the breakdown of leucine, cleaving HMG-CoA into acetyl-CoA and acetoacetate. They also possessed and an ortholog gene closely related to hydroxylamine oxidoreductase (HAO), an enzyme that is involved in nitrogen metabolism, converting hydroxylamine (NH_2OH) into nitrite (NO_2^-) during nitrification, and subsequently releasing electrons that can be used for cellular energy production (Cedervall et al., 2013). To our knowledge the presence of HAO in fungi has not been previously reported, so the function of this ortholog should be further analysed. In addition *Baudoinia* uniquely encodes a polyamine oxidase (PAOX); indicating the potential ability for *Baudoinia* to utilize additional routes to assimilate C_2 units and ketoacids, and the generation of NAD(P)H. The suite of antioxidant enzymes that generally serve to protect fungal cells from damage from reactive oxygen species (ROS) are together likely to play an important role in offsetting the highH_2O_2 flux which is inherent in ACOX-driven β-oxidation (Fig. 6). These antioxidants include catalase (CAT), which degrades hydrogen peroxide (H2O2) into water and oxygen, superoxide dismutase (SOD) which converts superoxide radicals (O2-) into less-reactive hydrogen peroxide and oxygen, and finally peroxiredoxin 5 (PRDX5), which also neutralizes reactive oxygen species. *Baudoinia* and *A. niger* also share the soluble epoxide

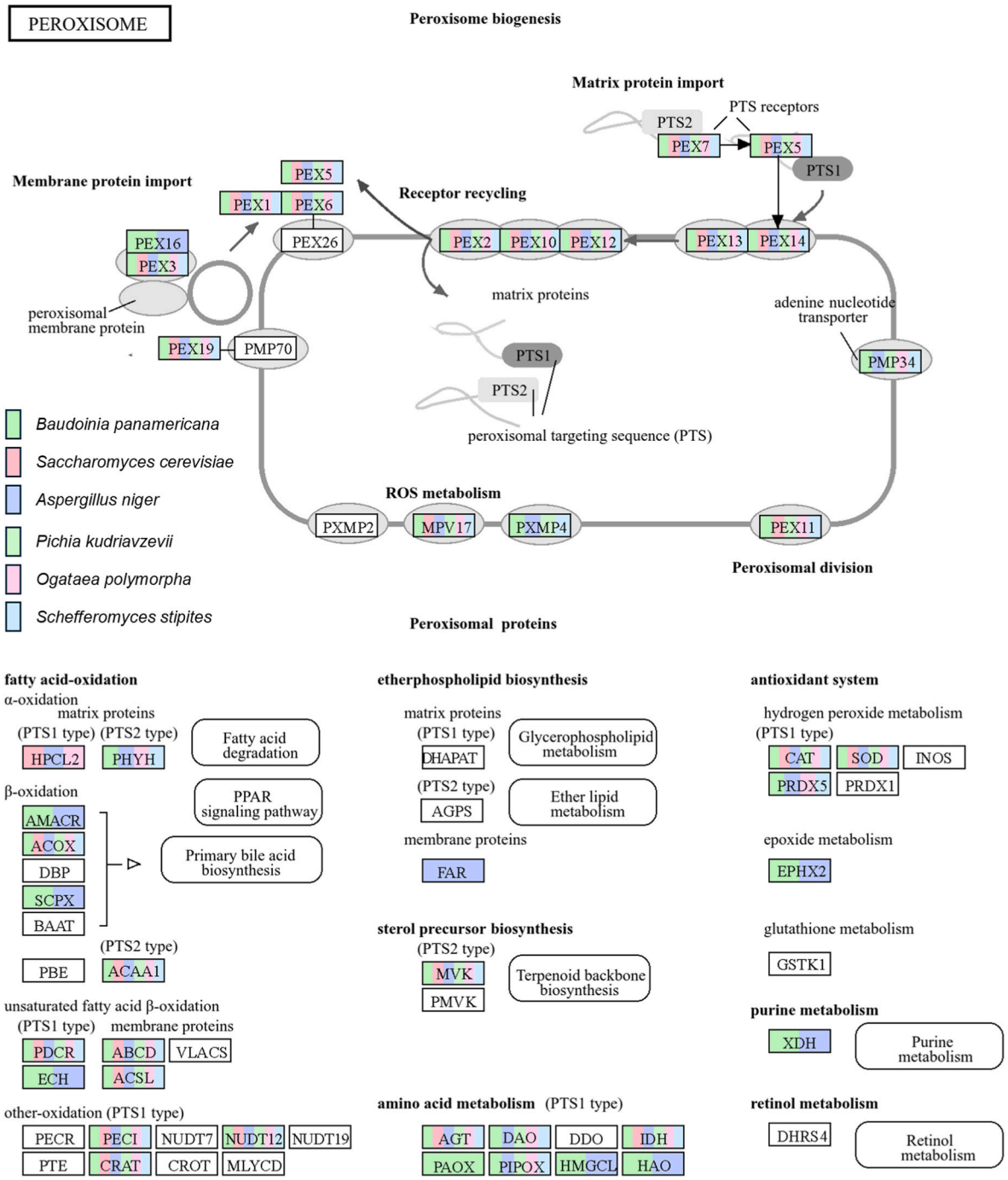


Fig. 6. Peroxisome biogenesis, import, and metabolism across six studied fungi. Figure summarizes peroxins, β-oxidation/uFA enzymes, transport/activation, amino-acid/purine branches, and antioxidant/epoxide-detox modules. All species encode PEX1/3/5/6; only *Baudoinia panamericana* and *Aspergillus niger* carry PEX16 (ER-linked membrane biogenesis). In β-oxidation, *Baudoinia/A. niger* uniquely encode AMACR and SCPX; the core cargo of *Baudoinia* is PTS2-biased (PHYH, ACAA1) with ACOX present. For uFA pathways, *Baudoinia* has PDCR (PTS1) and ECH (PTS1; shared only with *A. niger*), plus ABCD and ACSL in the membrane. Amino-acid/purine modules include AGT, DAO, IDH, PIPOX (common), HMGCL/HAO (shared with *A. niger*), and PAOX (unique to *Baudoinia*). Antioxidant endpoints include CAT, SOD, PRDX5, with EPHX2 shared by *Baudoinia/A. niger*.

hydrolase (EPHX2), which may play a role in safeguarding against epoxide stress from oxidized volatiles and lipid peroxidation products. Finally, XDH (xanthine dehydrogenase) which is present in both species, links purine catabolism to peroxisomal redox chemistry; further integrating carbon and electron flow with ROS control. Thus taken together, the peroxisomal system in *Baudoinia* is likely to allow the fungus to detoxify and shorten complex lipids, export acetyl units to the mitochondria and cytosol, quench oxidants produced as a by-product of β-oxidation, and prime membrane renovation cycles. The system is complete and appears to have a high level of plasticity that is tightly aligned with the fungus's ethanol-exposed, surface-colonizing lifestyle. Fig. 6 also outlines the fatty acid-oxidation repertoire in the six filamentous fungal and yeast species. The β-oxidation repertoire in *Baudoinia* includes acyl-CoA oxidase (ACOX), which catalyzes the first step in β-oxidation of fatty acids. Together with *A. niger*, Baudoinia is distinctive in showing the presence of α-methylacyl-CoA racemase (AMACR) together with thiolase/sterol-carrier protein (SCPX). AMACR converts R-to S-α-methylacyl-CoAs, ensuring the catabolism of branched

and odd-chain substrates, the chemistry that the fungus might encounter from weathered plant waxes, barrel-derived lipids, and fusel-alcohol derived acyls. SCPX for its part is likely to be involved in β-thiolysis of complex intermediates, associated with these different types of carbon substrates. Notably, the core β-oxidation repertoire in *Baudoinia* is PTS2-biased, as shown by the presence of phytanoyl-CoA hydroxylase (PHYH) and peroxisomal thiolase (ACAA1) as peroxisomal targeting signal 2 (PTS2) enzymes (Sibirny, 2016), suggesting the involvement of the PEX7 mediated peroxisomal matrix protein import system (Shin et al., 2021), which is consistent with a niche rich in branched-chain inputs. This apparent PTS2 bias coupled with the PEX7-mediated import, should ensure that bulky or unusual substrates, such as phytanate or branched-chain fatty acids, are targeted directly into the peroxisomal lumen rather than diffusing through the cytosol, a path that would increase potential oxidative risk. By pairing AMACR with SCPX, *Baudoinia* may gain the capacity to process substrates with varied chirality, and to efficiently metabolize long chain fatty acid and liberate acetyl-CoA units for subsequent metabolism even when the available carbon supply is chemically varied. With respect to unsaturated fatty-acid (uFA) catabolism, *Baudoinia* contains the PTS1 type enzymes 2,4-dienoyl-CoA reductase (PDCR) and enoyl-CoA hydratase (ECH). The former catalyzes the NADPH-dependent reduction of the double bonds in 2,4-dienoyl-CoA (Gurvitz et al., 2001), while the latter catalyzes the reversible hydration of unsaturated fatty acyl-CoAs to form beta-hydroxyacyl-CoA. ECHis shared only with *A. niger*, and provides the auxiliary reactions required to fully degrade uFAs (Fig. 6). The presence of the peroxisomal ABC transporter (ABCD) together with the very-long-chain acyl-CoA synthetase (ACSL) suggests the presence of an import–activation gate at the peroxisomal membrane, matching substrate entry with intraluminal capacity thereby ensuring that long/uFA substrates are imported and efficiently used by the fungus (Roche et al., 2013; Theodoulou et al., 2016).

9. Mitochondrial fatty acid metabolism

Across the six fungi analysed, the mitochondrial fatty acid synthesis (mtFAS) biosynthetic system is broadly conserved. It features ACP/ACP synthase, malonyl transfer to ACP, a β-ketoacyl condensation–reduction–dehydration–reduction, and export to lipoate production and to membrane lipids (Fig. 7). What sets *B. panamericana* apart is the unique occurrence of EC 6.2.1.76, a malonate–CoA ligase/malonyl-CoA synthetase acyl-CoA synthetase family 3 like (ACSF) that directly converts malonate to malonyl-CoA within the mitochondria. This capability is likely to decouple mtFAS from exclusive dependence on cytosolic acetyl CoA carboxylase (ACC)-derived malonyl-CoA and provide an autonomous, alternative supply of malonyl for fatty acid biosynthesis which would be beneficial for *Baudoinia* during growth periods when it is metabolizing ethanol through the acetyl-CoA/Acetyl-CoA carboxylase pathway involving the conversion of acetyl-CoA to malonyl-CoA and when carbon resources are scarce. Consistent with a fully functional elongation cycle, *Baudoinia* encodes a mitochondrial trans-2-enoyl-ACP reductase (MECR) which catalyzes the reduction of trans-2-enoyl thioesters, the final step in mitochondrial fatty acid synthesis (Miinalainen et al., 2003) (Fig. 7); and as previously stated retains the full set of ancillary mtFAS components (Fig. 7). However, *Baudoinia* lacks the canonical 3-hydroxyacyl-ACP dehydratase (HTD2), but this

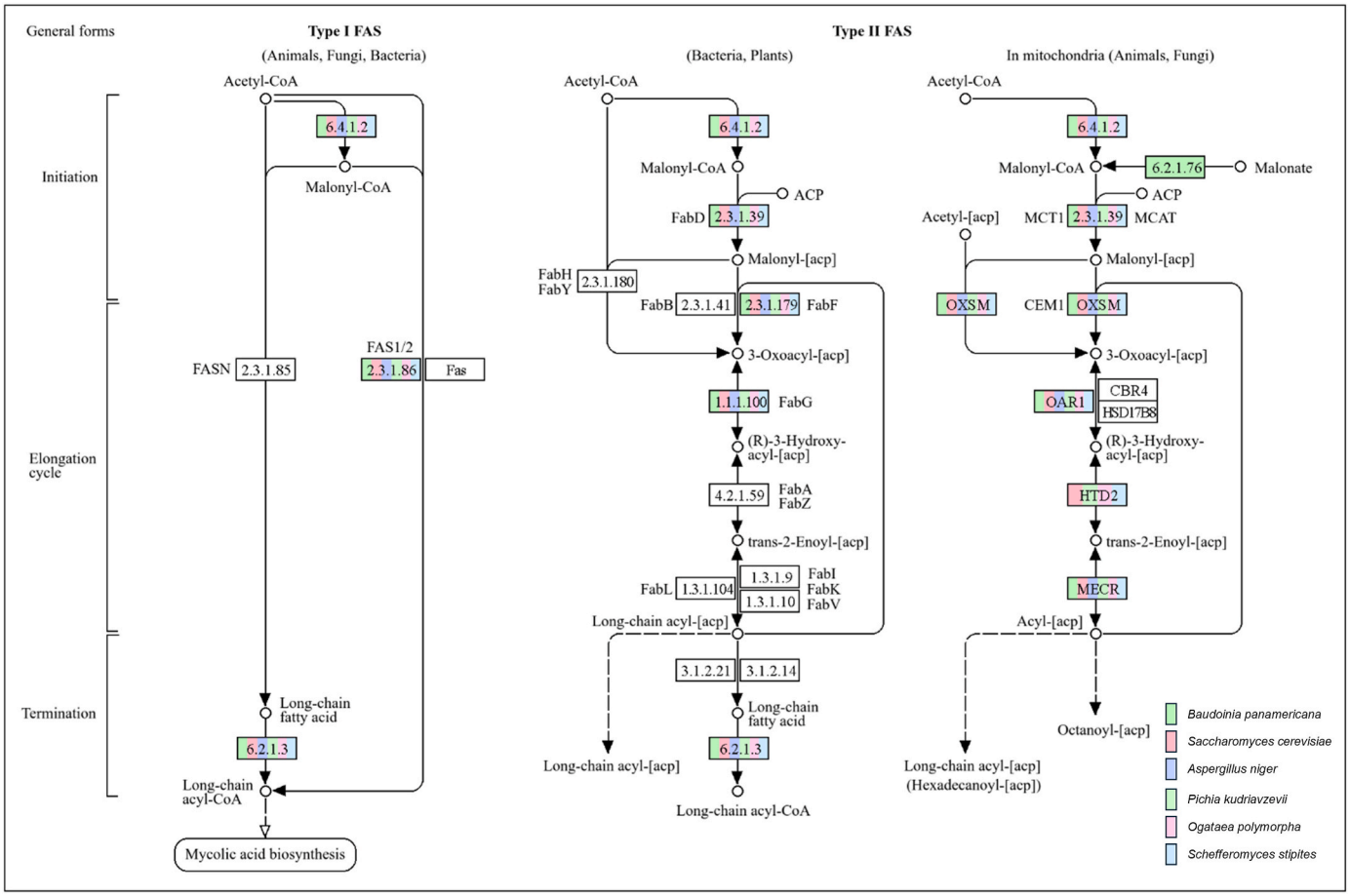


Fig. 7. Type I and type-II fatty-acid synthesis (mtFAS) gene repertoire across six fungi. Only *Baudoinia panamericana* encodes EC 6.2.1.76 (malonate–CoA ligase/malonyl-CoA synthetase), providing intramitochondrial malonyl-CoA. Baudoinia lacks HTD2 but carries MECR and retains the remaining mtFAS components; FAS1 (cytosolic FAS-I α) is present.

may be functionally compensated for by a FabG/Z-like dehydratase or a "moonlighting" dehydratase assortment of organelle localization, a phenomenon which has previously been described in other eukaryotic mtFAS systems (Guan et al., 2020). It should be noted that this dehydration step is not likely to be rate-limiting given the observed completeness of the pathway and the presence of trans-2-enoyl-ACP reductase (MECR) downstream in the pathway. Moreover, *Baudoinia* also contains FAS1 which encodes the beta subunit of the cytosolic fatty acid synthase (FAS) complex which is responsible for the synthesis of fatty acids of up to C18 in length. This suggests a dual approach to lipid metabolism in the fungus with mtFAS potentially supplying lipoic acid for pyruvate dehydrogenase (PDH), alpha-ketoglutarate dehydrogenase (KGDHC)/glyoxylate cycle (GCV) complexes and short acyl chains that sustain the TCA cycle throughput and preserving cellular redox homeostasis, while cytosolic FAS-I supports bulk membrane remodelling.

Thus, in an environment where *Baudoinia* is intermittently exposed to ethanol together with shifts in temperature, there are recurrent demands for membrane fluidity and protein lipoylation, as well as for periodic rapid increases in respiratory metabolism. There is potential adaptive advantage here to the fungus in its combination of an ACSF3-like (EC 6.2.1.76) system that ensures malonyl autonomy, in combination with MECR and a complete mtFAS system. This organization confers appropriate lipoate biogenesis for core dehydrogenases, plus reliable ATP production and acetyl-unit production during periods of ethanol oxidation, and a reliable and rapid response for repairing or rewiring lipid bilayers in a way that is not constrained by cytosolic acetyl CoA carboxylase fluxes or carbon transporter availability.

10. Calcium signalling

Calcium signalling is known to regulate multiple cellular functions in fungi, includinggrowth, development, fertility, virulence and stress tolerance. The calcium signalling pathway gene repertoire in the six fungal species shows the presence of a conserved signalling core present in all six. It includes Protein kinase A (PKA), Phospholipase C (PLC), Sphingosine kinase (SPHK), Calmodulin (CALM) and a commonly seen type of mitochondrial interface including the Voltage-dependent anion-selective channel (VDAC) and adenine nucleotide translocase (ANT) proteins (Suppl. Fig. 3). However only *B. panamericana* and *A. niger* possess the genes encoding the ER Calcium-ATPase (SERCA) which is important in maintaining calcium homeostasis and the mitochondrial Ca^{2+} uniporter (MCU) (Lang and Peiter, 2020; Roy et al., 2020). SERCA is likely to function in *Baudoinia* by actively transporting calcium ions (Ca^{2+}) into the ER and by helping to maintain low cytosolic calcium levels as well as by producing subcellular Ca^{2+} microdomains. MCU may facilitate the entry of Ca^{2+} into the mitochondria at ER mitochondrial contact sites, thereby linking Ca^{2+} signalling and mitochondrial metabolism. This is likely to facilitate activation of Ca^{2+} responsive dehydrogenases such as pyruvate dehydrogenase via dephosphorylation cascades, as well as isocitrate and α-ketoglutarate dehydrogenases. This enhanced ER mitochondria Ca^{2+} system in *Baudoinia* resulting from the presence of SERCA and MCU is likely to provide help in stress buffering, by limiting Ca^{2+} spikes in the cytosol, by supporting redox balance, and by stabilizing Ca^{2+}-dependent processes involved in germination and growth under fluctuating conditions, such as those present in the ecological niches in which Baudoinia grows.

11. Melanin biosynthesis genes

Melanisation is a defining and constitutive trait in many black fungi and is one of the central adaptive features underlying their success in colonising both anthropogenic and natural extreme environments. In fungi, melanins are not a single chemical entity but a family of heterogeneous, high-molecular-weight phenolic polymers produced through distinct yet partially overlapping biosynthetic routes (Chhoker et al., 2025). In Ascomycota, three major melanogenic pathways have been described namely a) the 1,8-dihydroxynaphthalene (DHN) melanin pathway, b) the L-DOPA melanin pathway, and c) the tyrosine catabolism–derived pyomelanin pathway (Teixeira et al., 2017). Comparative genomic studies across Chaetothyriales and other melanized fungi have demonstrated that these pathways frequently coexist within the same genome, indicating that melanisation functions as a modular and flexible adaptive system rather than as a single linear biosynthetic process (Teixeira et al., 2017; Jia et al., 2021; Hennessy et al., 2025; Carr et al., 2023).

Comparative genomic analysis was conducted on *B. panamericana* and on the opportunistic human pathogen *Aspergillus fumigatus* which is known to produce both melanin-dihydroxynaphthalene melanin (DHN-melanin) and pyomelanin. Both molecules are considered to play important roles in stress resistance (Perez-Cuesta et al., 2020). The genome of *B. panamericana* was found to encode a comprehensive repertoire of genes homologous to those involved in DHN-melanin synthesis in *A. fumigatus*, including a non-reducing polyketide synthase homologous to Alb1/PksP, together with downstream enzymes such as Ayg1, Arp1, Arp2, Abr1, and Abr2 (Supplementary Table 2).

In *A. fumigatus*, this pathway is responsible for conidial pigmentation and relies on a tightly regulated sequence of reductive and oxidative steps that culminate in polymerisation of DHN intermediates and their deposition within the cell wall (Perez-Cuesta et al., 2020; Pihet et al., 2009; Youngchim et al., 2004). The presence of these conserved core components in *B. panamericana* strongly supports DHN-melanin as a major contributor to its characteristic black pigmentation.

An important feature that is apparent from this genomic analysis of *B. panamericana* is the multiplicity of oxidoreductases associated with melanin synthesis, particularly multicopper oxidases and laccase-like enzymes (Supplementary Table 2). Homologues of Abr1 and Abr2, which catalyze late oxidative steps in DHN-melanin formation in *A. fumigatus*, are present alongside numerous additional potential laccase-encoding genes. Similar expansions of multicopper oxidases have been reported in other black fungi, including *Exophiala viscosa*, *E. dermatitidis*, and *Exophiala lecanii-corni* and related chaetothyrialean taxa, where they have been interpreted as adaptations enhancing oxidative polymerisation, cross-linking of melanin with cell-wall polymers, and long-term pigment stability under fluctuating environmental stress (Teixeira et al., 2017; Jia et al., 2021; Hennessy et al., 2025; Carr et al., 2023; Romsdahl et al., 2021). Such redundancy is likely to confer functional robustness, allowing melanin synthesis to proceed efficiently under diverse physicochemical conditions (Carr et al., 2023; Teixeira et al., 2017).

In addition to the DHN pathway, the genome of *B. panamericana* also encodes several tyrosinase and tyrosinase-like proteins with homology to enzymes associated with L-DOPA melanin synthesis in other fungi (Teixeira et al., 2017). Although L-DOPA melanin has traditionally been considered less prominent in Chaetothyriales, comparative genomic surveys increasingly indicate that black fungi frequently harbour multiple copper-dependent oxidases capable of oxidizing L-tyrosine or L-DOPA into quinone intermediates (Teixeira et al., 2017; Chhoker et al., 2025). In *A. fumigatus*, tyrosinase-related enzymes are not the primary drivers of conidial melanisation but have been implicated in redox balance and mitigation of oxidative stress. The presence of multiple tyrosinases in *B. panamericana* therefore raises the possibility that DOPA-derived melanins contribute to pigmentation and stress protection in the fungus under specific ecological conditions, such as elevated oxidative stress or increased availability of aromatic amino acids (Jia et al., 2021; Hennessy et al., 2025).

Genomic analysis further indicates that *B. panamericana* possesses a complete tyrosine degradation pathway leading to homogentisic acid formation, supporting the potential for pyomelanin synthesis. Genes encoding tyrosine aminotransferase, 4-hydroxyphenylpyruvate dioxygenase, and homogentisate-processing enzymes are conserved to their counterparts in *A. fumigatus*, where pyomelanin production has been linked to oxidative stress resistance, iron homeostasis, and extracellular

antioxidant capacity (Jia et al., 2021; Teixeira et al., 2017; Chhoker et al., 2025; Carr et al., 2023). In black fungi inhabiting oligotrophic, chemically harsh, or irradiated environments, pyomelanin has been proposed to function as a diffusible protective pigment that complements the structurally integrated, cell-wall-bound DHN melanin. The coexistence of these pathways in *B. panamericana* suggests a layered melanisation strategy that enhances ecological resilience (Hennessy et al., 2025; Teixeira et al., 2017). It should be stressed, however, that because *Baudoinia* produces a black, cell-wall-associated, insoluble pigment rather than the brown, water-soluble polymer characteristic of pyomelanin, and because homogentisic acid has not been reported in its culture supernatants, any contribution of pyomelanin — and, a fortiori, of the phylogenetically uncommon L-DOPA/tyrosinase route, which is rare among Dothideomycetes — should be regarded as hypothetical and probably minor relative to DHN-melanin until directly demonstrated.

All melanin-related genes identified in *B. panamericana* were initially detected by homology to annotated *A. fumigatus* genes, providing a robust comparative approach. In *A. fumigatus*, melanin synthesis is tightly coupled to asexual development and regulated by specific transcription factors, with clear separation between early and late biosynthetic steps. By contrast, comparative genomic analyses of Chaetothyriales appears to reveal frequent gene duplication, diversification and regulatory rewiring of melanin-associated genes, reflecting selection pressures imposed by extreme and often toxic environments rather than developmental specialization.

From an ecological and evolutionary perspective, the rich melanin gene repertoire of *B. panamericana* is consistent with its lifestyle on exposed surfaces subjected to intense solar radiation, desiccation, temperature fluctuations, and chronic exposure to volatile organic compounds such as ethanol. Thus, melanin is likely to not only provide physical shielding against ultraviolet radiation but also contribute to increased cell-wall rigidity, reduced permeability, and mitigation of oxidative stress, all of which are advantageous in such habitats. The apparent redundancy and diversity of melanogenic enzymes in *B. panamericana* is also likely to reflect a strong selective pressure to maintain melanisation capacity, which would be advantageous under a wide range of environmental scenarios (Hennessy et al., 2025; Teixeira et al., 2017).

Future functional studies will be required to uncover the specific contributions of the different melanins in *B. panamericana*. In this context, the gene inventory summarised in Supplementary Table 2 provides a good starting point for hypothesis-driven experimentation. The presence of single-copy versus multiple homologues for key enzymes, such as the DHN-pathway polyketide synthase, reductases, and terminal oxidases, suggests that pathway regulation is likely to be exerted at specific enzymatic nodes rather than uniformly across the pathway. Integrating transcriptomic analyses will be essential to determine which of these genes are preferentially expressed under melanin-inducing conditions and how differential expression patterns contribute to pathway activation, modulation and/or prioritization. In parallel, the relatively high number of tyrosinase- and laccase-like genes identified highlights the need to move beyond presence–absence assessments to determine which of these enzymes are actively engaged in melanin synthesis under defined environmental conditions.

12. Summary

Thus this comparative genomic analysis of *B. panamericana* and the other five filamentous fungi and yeasts provides valuable insights into some of the potential unique adaptive traits that the fungus may be employing and which are likely to underpin its ecological specialization, particularly with respect to ethanol utilisation. The genomic repertoire of *Baudoinia* depicts a surface-dwelling fungus that has the capacity to assimilate intermittently available ethanol vapours and trace levels of carbon to support its growth. To achieve this, the fungus potentially couples the stress-robust, 2,3-bisphosphoglycerate-independent phosphoglycerate mutase with ATP-citrate lyase to divert ethanol-derived acetyl-CoA into cytosolic acetyl units when ethanol vapour levels increase. When the vapours contain C3 volatiles and odd/branched chain hydrocarbons, the enrichment of 2-methylcitrate synthase in *Baudoinia* implies a detoxification response that channels propionate and fusel derivatives into central metabolism. In the periods in between the availability of ethanol, the presence of deoxyribose-phosphate aldolase and phosphoketolase suggests an alternative metabolic route in which DNA fragments and pentoses provide glyceraldehyde-3-phosphate and acetyl units, supporting basal energy generation and carbon recycling during ethanol scarcity.

The substrate-resolved CAZyme analysis suggests that *Baudoinia* employs GH47/13/5/3/43/62/67/78, GH28, and CE1/CE5 to debranch hemicellulose and cleaves cuticle and ester cross-links, thereby potentially increasing porosity and assimilating carbon and enhancing adhesion while leaving crystalline cellulose largely intact. The “dark veneer” of the fungus itself is likely due to oxidative tailoring, in which AA1/AA3 together with AA4/AA7 and AA11 generate quinones and targeted oxidative nicks in cell wall polymers that stiffen the matrix and result in increased UV tolerance, while peroxisomal antioxidants buffer the reactive oxygen species produced by these reactions. The presence of PEX16 suggests organelle plasticity, involving periods of active peroxisome biogenesis during ethanol availability followed by pexophagy when levels decrease. Assimilation of other carbon sources at the wall-air interface is likely due to the presence of AMACR and SCPX with PDCR/ECH auxiliaries for unsaturated fatty acids, preventing the accumulation of phytanyl and double-bonded intermediates. Given that the oxidation of volatiles and lipids will generate epoxides, the epoxide hydrolase (EPHX2) can be expected to play an important role under this epoxide challenge, suggesting a coordinated oxidization detoxification approach that is compatible with persistent surface colonization.

The unique pairing of ER-Ca^{2+}-ATPase and the mitochondrial Ca^{2+} uniporter in *Baudoinia* suggests a coordinated ER-mitochondria Ca^{2+} coupling and the rapid activation of Ca^{2+} -responsive dehydrogenases in response to oscillations in ethanol levels. In parallel, mitochondrial type-II fatty-acid synthesis appears to possess a *Baudoinia*-specific malonate to malonyl-CoA route (EC 6.2.1.76) which is likely to ensure mtFAS and lipoate biosynthesis from PDH/KGDH/GCV under cytosolic ACC stress, with malonate being incorporated into lipoate and maintained respiration under ACC inhibition; with MECR downstream securing the final reduction step, with a compensatory dehydratase which likely substitutes for the canonical HTD2. These mitochondrial advantages, together with peroxisomal β-oxidation, suggest bioenergetic events that result in membrane repair and growth whenever ethanol and humidity co-occur.

The presence of a large number of genes encoding DHN-melanin synthesis in *B. panamericana* suggests that DHN-melanin is a major contributor to the characteristic black pigmentation in the fungus. In addition, the large number of oxidoreductases associated with melanin synthesis particularly multicopper oxidases and laccase-like enzymes, indicates a potentially high level of functional robustness in the fungus, enabling melanin synthesis under a variety of physicochemical conditions. The fungus also possesses several tyrosinase and tyrosinase-like proteins with homology to enzymes associated with L-DOPA melanin synthesis in other fungi, suggesting that DOPA-derived melanins may contribute to both pigmentation and to stress protection in the fungus under specific ecological conditions. The presence of a genes encoding a complete tyrosine degradation pathway leading to homogentisic acid indicates the potential for pyomelanin synthesis in *B. panamericana* which, taken together with the potential to produce DHN-melanin and DOPA-derived melanins; suggests a layered melanisation strategy that is likely to enhance the fungus’ ecological resilience.

13. Future perspectives

The genus *Baudoinia*, and in particular *B. compniacensis*, represents

an interesting example of how fungi can adapt and thrive in environments enriched with ethanol vapours, such as previously mentioned, including those surrounding whisky distilleries, ethanol storage facilities, printing presses, and other industrial sites. Understanding the resilience mechanisms and ecological strategies of fungi such as *Baudoinia* is important, not only for mitigating their potential negative impacts on man-made structures but also to explore their broader environmental and biotechnological potential. *Baudoinia* species, as cosmopolitan black fungi colonizing different surfaces, raise essential questions about how their widespread distribution and adaptability can inform studies on fungal resilience and evolution under rapidly changing environmental conditions. This phenomenon is particularly relevant under conditions of climate change, where changes in temperature, humidity, and human industrial activity may alter not only the distribution of these fungi but also their ecological role.

The cosmopolitan ability of *Baudoinia* species to colonize diverse surfaces, especially in ethanol-rich environments, underscores the importance of characterizing the underlying molecular mechanisms that facilitate their adherence, persistence, and proliferation. As previously outlined, ethanol appears to act not only as a carbon source but also as a stimulant for spore germination and hyphal growth. However, the precise cellular and molecular pathways involved in ethanol recognition, signalling, and metabolic reprogramming remain largely unexplored. This is a critical gap in our knowledge and further studies need to focus on gaining a fuller understanding of the metabolic and physiological processes that have allowed *Baudoinia* to adapt and survive in such specialized ecological niches, by allowing it to maintain its structural and functional integrity. In addition, examining co-metabolism on lignocellulolytic surfaces—such as wood or other organic materials frequently colonized by *Baudoinia* may help elucidate how CAZymes contribute to the fungus' ecological success in diverse habitats.

Melanin production in *Baudoinia* is particularly intriguing, as it is likely to contribute to resistance against ethanol toxicity, thermal stress, and potentially UV radiation, all of which are prevalent in outdoor colonization scenarios. Because the *Baudoinia* melanin polymer has not yet been characterised chemically, confirmatory experiments — tricyclazole inhibition of pigmentation, targeted disruption of the candidate polyketide-synthase and laccase orthologues, and chemical degradation of the polymer with permanganate followed by HPLC quantification of pyrrole-2,3-dicarboxylic and pyrrole-2,3,4-tricarboxylic acid markers, complemented by solid-state 13C NMR and FTIR — will be required to move from the current homology-based inference of a DHN-dominant pathway to a demonstrated pathway assignment, and to establish the relative contributions of DHN-, pyomelanin- and any DOPA-derived components under defined melanin-inducing conditions. The involvement of melanin in enhancing structural integrity and environmental resilience also requires further investigation, especially considering how temperature fluctuations in outdoor environments challenge both fungal persistence and proliferation. Additionally, the biosynthesis and regulation of melanin in response to ethanol exposure and other environmental stressors could reveal important adaptive mechanisms that confer resilience to this genus. Thus the potential role of melanin in conferring resilience to *Baudoinia* in diverse and fluctuating environments should be thoroughly examined, particularly in the context of its association with urban polyextremotolerant fungi.

Biogeography studies on *Baudoinia* remain limited, although the genus is now known to be distributed worldwide, particularly near ethanol-rich environments. However, it is unclear whether this distribution reflects genuine cosmopolitanism or represents localized evolution driven by industrial or agricultural practices. In this respect, the relationship between the fact that *Baudoinia* colonization typically occurring on exposed outdoor surfaces and the concept of urban polyextremotolerance is particularly relevant. Like *Exophiala* species, which have demonstrated resilience in urban-industrial settings (de León et al., 2025), *Baudoinia* may represent an interesting model organism to study how industrialization shapes fungal ecology and evolution. Comparative genomics, phylogenetic analyses, and population genetics could provide valuable information on how *Baudoinia* has spread and adapted to new environments, especially with respect to anthropogenic activities. Several specific and tractable priorities follow from this synthesis. First, all of the genomic inferences discussed above derive from a single sequenced strain, UAMH 10762, which was sequenced under the name *B. compniacensis* (Ohm et al., 2012) but subsequently designated the holotype of *B. panamericana* (Scott et al., 2016); no genome is yet available for *B. compniacensis* sensu stricto from the Cognac type locality. Sequencing additional isolates spanning the five recognised species, would define the limits within which any cross-species inference about the *Baudoinia* genome can legitimately be drawn and would allow intraspecific variation to be assessed directly. Second, the natural, non-anthropogenic reservoirs of the genus remain essentially unmapped; targeted amplicon and qPCR surveys of bark, sap-flux exudates, fermenting fruit, decaying heartwood and insect-associated fermentative galleries, at the sensitivity routinely achieved at distillery-proximate sites, are required before the extent of any natural niche can be established. Third, the dual role of ethanol as a germination cue and as a carbon source could be separated experimentally through transcriptomic time-series at defined vapour and liquid concentrations and through 13C-ethanol metabolic-flux analysis, which would also quantify the fraction of realised fungal carbon derived from ethanol as opposed to co-metabolised organic deposits. In addition future research strategies should focus on integrating ecological, biochemical, and evolutionary approaches, enabling an improved understanding of the complex mechanisms underlying *Baudoinia*'s adaptation to ethanol-enriched environments. This approach is expected to provide valuable new insights into universal fungal adaptation strategies.

Author contributions

Conceptualization: YP-L, RAB-G and AD. Methodology: YP-L and RAB-G. Formal analysis: YP-L, RAB-G AND SJ. Data curation: YP-L and RAB-G. Writing: YP-L, RAB-G, and A.D. Writing – review and editing: YP-L, RAB-G, SJ and A.D. Visualization: YP-L and RAB-G. Data Curation: YP-L and RAB-G. Funding acquisition: RAB-G and AD. All authors read and approved the final manuscript.

Declaration of competing interest

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Acknowledgments and Funding

This work was supported by RYC2022-037554-Iproject funded by MCIN/AEI/10.13039/501100011033 and FSE+ (RAB-G, YP-L). RAB-G received a Sabbatical fellowship (CVU: 389616) from the National Council of Science and Technology (CONACyT), Government of Mexico. ADWD and SAJ acknowledge funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 101000392626 (MARBLES).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fbr.2026.100505.

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