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Review

They too serve who tolerate and survive: the need to study halotolerant fungi to appreciate their role in saline ecosystems



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ABSTRACT

Saline habitats support both halophilic fungi (having an obligate requirement for salt for their growth) and halotolerant fungi (not needing salt for growth but capable of growth in the presence of salt). Halophilic fungi are exceptional since they are restricted to hypersaline habitats and there is not enough information about these fungi of various types of saline environments. However, due to their co-occurrence with halophilic microorganisms and their wide range of salt tolerance, the ecosystem services provided by halotolerant fungi in saline environments require attention. The fact that halotolerant fungi do not exist as mere inactive resting structures and that they tolerate different strengths of external salt stress are indicative of their sustained ecological roles in saline environments as well as in normal environments experiencing extreme salinity conditions with some regularity. Here, we underscore the need to study halotolerant fungi with more zeal to understand their ecological roles in saline ecosystems.

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1. Introduction

Hypersaline environments which are thalassohaline (formed from seawater in which sodium chloride is the most abundant salt), like any other extreme environment, are highly selective and support only microbes adapted to grow in high salinity. Though fungi have evolved to tolerate different abiotic stressors including high salinity (Coleine *et al.*, 2022), it is the prokaryotes, particularly the archaea, of extreme environments which have been studied more intensely (Zhu *et al.*, 2020; Coleine *et al.*, 2022; Zheng *et al.*, 2022; Hu *et al.*, 2023). It is only recently that halophilic fungi which have an obligate requirement for salt for growth (Kis-Papo *et al.*, 2014;

Plemenitaš *et al.*, 2014) and halotolerant fungi which are adapted to survive in normal as well as high salt environments (Zajc *et al.*, 2012; Azpiazu-Muniozgueren *et al.*, 2021) have been studied in more detail. The halotolerant fungi do not exist as mere inactive resting structures in hypersaline habitats and are adapted to tolerate different strengths of external salt stress. This indicates their heightened ecological fitness and sustained ecological roles in saline environments as well as in normal environments experiencing extreme salinity conditions with some regularity. With reference to marine fungi, generally two ecological types are recognised: the obligate marine fungi which grow and sporulate exclusively in marine habitat, and the facultative marine fungi

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occur which in freshwater habitats but could be isolated from different marine habitats (Kohlmeyer and Kohlmeyer, 1979). Although this definition or its variations (Overy et al., 2014) are used to broadly classify the marine fungi ecologically, studies are needed to confirm if all 'obligate' marine fungi are strictly so. For instance, the black yeast *Hortaea werneckii* which is found in natural hypersaline environments and seawater, can grow in NaCl concentrations ranging from 0 to 30% (Zalar et al., 2019). Thus, it is necessary to investigate more intensely the halotolerant fungi to appreciate their role in saline ecosystems.

2. Halotolerant fungi in hypersaline habitats

It is generally assumed that hypersaline habitat is comparatively simpler (Shu and Huang, 2022) due to its depauperate microbial species diversity. However, investigations on halophilic archaea and bacteria reveal that hypersaline habitats are more complex than expected (Oren, 2002). Solar salterns formed by the evaporation of sea water are among the hypersaline habitats whose microbial diversity has been studied in greater detail (Gunde-Cimerman et al., 2004). Salinity is usually expressed as ppt or as PSU (practical salinity unit) which is based on water temperature and conductivity measurements (Fofonoff, 1985). The average salinity of seawater is 34–35 PSU; evaporation of sea water leads precipitation of the salts (mainly NaCl) thus increasing its salinity which could be as high as 300 PSU (Gostinčar et al., 2009). It is well known that archaea and bacteria survive in salterns (Chung et al., 2019); it is only recently recognised that fungi too survive in solar salterns and there is little information on their roles in such hypersaline ecosystems (Gunde-Cimerman et al., 2004; Ali et al., 2013; Chung et al., 2019). Interestingly, many of the fungi of hypersaline environments including salt lakes, solar salterns, and mangrove ecosystem are halotolerant rather than halophilic (Plemenitaš et al., 2014). Thirunavkkarasu et al. (2017) showed that halotolerant fungi of solar salterns of southern India do not have an obligate requirement for salt for their growth and could grow in the highest salt concentration tried in this study (20% NaCl). These fungi also occur as parasites (Soler-Hurtado et al., 2016) or non-pathogenic endosymbionts of marine organisms including sponges (Thirunavkkarasu et al., 2012), and endophytes of sea grasses (Venkatachalam et al., 2015) and seaweeds (Govinda Rajulu et al., 2022). In terrestrial plants, association with endophytic fungal partners increases the host plant's performance by enhancing its resistance/tolerance to abiotic (Suryanarayanan and Uma Shaanker, 2021) and biotic (Estrada et al., 2013) stress. Some endophytes of terrestrial plants are potential pathogens and could initiate disease in their host plants under conditions favouring pathogenesis (Collinge et al., 2022). No such information is available on the role of halotolerant fungal endosymbionts of marine organisms with respect to their contribution to their hosts' ecological fitness.

3. Halotolerant fungi of mangrove ecosystem

Mangroves are salt tolerant ecotones between terrestrial and marine ecosystems. Tropical mangrove soil is an environment

experiencing high variability in salinity due to tidal variations (Tomlinson, 1994) and vagaries of precipitations and cyclones. Fungi are associated with mangrove roots (both as endophytes and surface fungi), decaying leaves, roots, and wood; they are also associated with drift wood, intertidal grasses, algae, crustaceans, corals, mollusc shells, sediments and soils of mangrove ecosystem (Jones et al., 2009; Kumaresan et al., 2021). Paranetharan et al. (2022) report that fungal endophytes of mangrove roots do not require salt for their growth and could grow in medium with 4.5% NaCl concentration which is more than that of the seawater. Fungal endophytes of the aerial parts of mangroves such as those of the leaves, though not in direct contact with the seawater, are halotolerant. Mangrove leaves accumulate salt to high levels (Cram et al., 2002). Popp et al. (1984) found that the salt levels in the leaves of 23 mangrove species were similar to that of seawater. Hence, mangrove leaf fungal endophytes should be adapted to tolerate salt stress. Kumaresan et al. (2002) confirmed this by showing that mangrove foliar fungal endophytes are halotolerant and could grow in a medium containing twice the amount of salt as that of seawater.

4. Strategies of halotolerant fungi to survive in saline habitats

Halotolerant fungi possess a wide range of survival strategies to adapt to the osmotic stress resulting due to the low water availability in saline environment. Due to the high external ionic concentration in thalassohaline environments, Na⁺ enters the cell leading to the impairment of cell membranes (Plemenitaš et al., 2014). To counter ion entry, halotolerant fungi synthesise and accumulate polyols such as glycerol, erythritol, arabitol and mannitol which do not interfere with the normal cell metabolism (Gunde-Cimerman et al., 2018). Termed compatible solutes, such low-molecular-weight organic compounds aid in maintaining a positive turgor pressure at high external salt concentrations. In several halotolerant fungi, the activity polyol metabolism enzymes (Ravishankar and Suryanarayanan, 1998) and compatible solute concentration increases with increasing external salinity (Plemenitaš et al., 2014). Using halotolerant black yeast *Hortaea werneckii* and halophilic fungus *Wallemia ichthyophaga*, Plemenitaš (2021) showed that though both the fungi use the high-osmolarity glycerol (HOG) signal transduction pathway for adapting to the external salinity, the mechanism of activation of this pathway differs between them. Even though the synthesis of compatible solutes to maintain turgor is metabolically expensive than accumulating Na⁺ in vacuoles as halophilic vascular plants do, this method is not seen in fungi possibly owing to the reduced vacuole size characteristic of mycelial fungi (Clipson and Jennings, 1992). Melanin deposition on the cell wall to increase its strength to counter osmotic shock experienced by fungal hyphae exposed to constantly changing external salinity is another strategy developed by halotolerant fungi (Elsayis et al., 2022). The black yeast *Hortaea werneckii* deposits melanin in its cell wall as an adaptation to survive in hypersaline environments (Kejžar et al., 2013). Ravishankar et al. (1995) observed that the hyphae of *Cirrenalia pygmaea*, a halotolerant, saprotrophic mangrove root fungus,

owing to melanised cell walls could withstand sudden external osmotic changes; however, upon inhibition of melanin synthesis, the hyphae exploded at their tips when subjected to osmotic shock. Furthermore, melanin deposition on hyphae increases with the increase in external salinity (Ravishankar et al., 1995). In this fungus, the unsaturation index of fatty acids decreases with increasing external salinity implying that the membranes become more rigid to retain the internal compatible solutes (Hosono, 1992; Ravishankar et al., 1994). Furthermore, it appears that different genes of halotolerant fungi get activated under different salt stress strengths. We observed that a *Talaromyces stipitatus* isolate (a mangrove endophyte) produced different isoforms of chitin modifying enzymes under different external salt concentrations (Paranetharan et al., 2018); besides, a *Trichoderma harzianum* endophytic in the brown seaweed *Sargassum wightii*, is capable of growing in 1.2 M NaCl and secretes more xylanase and xylosidase enzymes in NaCl-amended growth media than when cultured without the salt (Thirunavukkarasu et al., 2015). These results and that the physiological responses of halophilic fungi differ greatly with reference to external salinity and are not mere quantitative alteration of metabolites (Pérez-Llano et al., 2020) indirectly inform salt-induced gene activation. Hence, direct studies as done with *Bacillus* sp (SX4) where more than 100 genes are up and down regulated as a response to different levels of salt stress (Zhang et al., 2021) are needed to understand the physiological response of fungi to salt stress. Although the described adaptations partially explain the success of halotolerant fungi in occupying niches varying from very low to high salt concentrations, detailed molecular studies including the use of deletion mutants of genes coding for stress tolerance would provide critical insights into the survival strategies of these fungi.

The most common, and usually dominant halotolerant fungi of salterns (Cantrell et al., 2006; Evans et al., 2013), endophytes of brown, green and red seaweeds (Suryanarayanan et al., 2010; Govinda Rajulu et al., 2022) and seagrasses (Venkatachalam et al., 2015), as well as endosymbionts of marine sponges (Thirunavukkarasu et al., 2012) include species *Cladosporium*, *Aspergillus*, and *Penicillium*. A monthly screening of saltern from southern India for ten months revealed that species of *Aspergillus* persist irrespective of the season (Suryanarayanan et al., 1996). Generally, many extremotolerant fungi including halotolerant ones are anamorphic forms reproducing only asexually and hence, it is possible that the random process of genetic drift could establish alleles in individuals enhancing their phenotypic plasticity thus aiding in the adaptation of mesophilic fungi to survive in extreme habitats (Gostinčar et al., 2009). Interestingly, the cellular responses and molecular mechanisms to combat salinity stress vary between the halophilic and halotolerant fungi. Genome and transcriptome analysis showed that the number of genes activated by salinity and the physiological response to salinity in halophilic and halotolerant *Aspergillus* species differ widely (Tafer et al., 2019). The halotolerant ones possess extraordinary genetic redundancy and a comparatively recent whole genome duplication attesting to their heightened adaptability (Plemenitaš et al., 2014). Such a panoply of difference at the gene level partly explains the metabolic and the

consequent ecological flexibility of the halotolerant fungi. This also suggests that the metabolic patterns (Vaupotic et al., 2008) of halotolerant and halophilic fungi may not overlap to a great extent such that the former are not redundant with reference to their ecological functions in saline habitats.

5. Ecological role of halotolerant fungi

The adaptability of halotolerant fungi to occupy normal and extreme environments reflects their heightened ecological fitness and phenotypic plasticity. Their constant presence and ability to grow in different external salt concentrations lend evidence to the fact that halotolerant fungi contribute to the functions of saline ecosystem. In mangrove ecosystem where soil and water salinity are widely fluctuating, the halotolerant fungi which possess a wide spectrum of salt tolerance ability are most suited to survive. Though it is known that fungi play a key role in lignocellulose mineralization in mangrove ecosystem (Thatoi et al., 2013), the specific role of halotolerant fungi in this process is not known. Recent studies show that salt alters the composition and activity of secreted lignocellulolytic enzymes of halotolerant fungi of mangroves. Mangrove root endophytes elaborate salt induced and salt tolerant cellulase, β -glucosidase, and laccase enzymes (Paranetharan et al., 2022). In the halotolerant mangrove fungus *Pestalotiopsis* sp., the presence of salt increases the secretion of xylanases and cellulases and reduces the production of oxidases (Arfi et al., 2013). Halotolerant fungi associated with deep sea sponges elaborate halotolerant xylanases and peroxidase/phenol oxidases (Batista-García et al., 2017). With such a broad arsenal of salt tolerant biomass destructuring enzymes (Arfi et al., 2013), it is conceivable that these fungi contribute to nutrient recycling in the dynamic tropical mangrove soil habitat (Paranetharan et al., 2022). Apart from the mangrove soil fungi and root endophytes, the halotolerant fungal endophytes of mangrove leaf also appear to play role in nutrient recycling. Some of these foliar endophytes switch to a saprotrophic mode and grow faster on senesced mangrove leaves (Kumaresan and Suryanarayanan, 2002), and produce an array of biomass degrading enzymes including cellulase, laccase, pectate transeliminase, and tyrosinase (Kumaresan et al., 2002, 2021) indicating their participation in nutrient recycling in the mangrove ecosystem. Similarly, in *Trichoderma harzianum*, a halotolerant endophyte of the brown alga *Sargassum wightii*, different salt concentrations induced a three-fold increase in the secretion of biomass degrading enzymes xylanase and xylosidase (Thirunavukkarasu et al., 2015).

Interestingly, not only the microbes and their enzymes, but their secondary metabolite production may also be influenced by salt concentration. Some of the salt tolerant fungi of solar salterns produce antifungal and antibacterial compounds (Panchal et al., 2022; Wingfield et al., 2023) suggesting that they may have a role in influencing the microbial composition of saline environments. Sepcic et al. (2010) showed that external stress including salinity induces halophilic fungi to produce specific bioactive metabolites. In the absence of any direct proof, such basic findings lead to a syllogistic conclusion that halotolerant fungi contribute to the microbial composition and nutrient status of saline habitats.

6. Conclusion

Many questions regarding halotolerant fungi remain unanswered. Their diversity (Zalar et al., 2007, 2008; Fryar et al., 2019), range and mechanism of salt tolerance, and trait alterations under different degrees of salt stress have to be addressed to appreciate their ecological roles. Although their degree of halotolerance varies, the universal presence of species of *Aspergillus* and *Penicillium* in saline environments (Frisvad, 2005), as endophytes of seagrasses (Venkatachalam et al., 2015) and seaweeds (Suryanarayanan et al., 2010) and as endosymbionts of marine sponges (Thirunavukkarasu et al., 2012) indicates their wide ecological amplitude. Although the same species of these fungi could exist in these ecological niches, it is not clear if there is trait difference between them as a consequence of their interaction between cooccurring microbes which are bound to differ with these niches. Marine isolates of *Aspergillus sydowii* cause disease in corals while the terrestrial isolates are not pathogenic indicating the existence of different ecotypes of this fungus (Alker et al., 2001). To summarise, halotolerant fungi necessarily have evolved the ability to survive under different levels of salt stress. Although it is not clear if selection pressure guided the evolution of phenotypic plasticity of these fungi or whether such fungi are ecophenes, it is possible that such flexibility goes with alterations in the expression of different tolerance related genes. With such trait versatility expressed by halotolerant fungi, information on the ecology of saline environments is bound to be incomplete sans studies on these fungi. Apart from culture dependant investigations, multiple omics studies are needed to unravel the biodiversity and functional variations of halotolerant fungi to understand their role in the ecological process of saline environments (Li et al., 2021).

Conflict of interest

None declared.

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REFERENCES

- Ali, I., Kanhayuwa, L., Rachdawong, S., Rakshit, S.K., 2013. Identification, phylogenetic analysis and characterization of obligate halophilic fungi isolated from a man-made solar saltern in Phetchaburi province, Thailand. *Ann. Microbiol.* 63, 887–895. <https://doi.org/10.1007/s13213-012-0540-6>.
- Alker, A.P., Smith, G.W., Kim, K., 2001. Characterization of *Aspergillus sydowii* (Thom et Church), a fungal pathogen of Caribbean sea fan corals. *Hydrobiologia* 460, 105–111. <https://doi.org/10.1023/A:1013145524136>.
- Arfi, Y., Chevret, D., Henrissat, B., Berrin, J.-G., Levasseur, A., Record, E., 2013. Characterization of salt-adapted secreted lignocellulolytic enzymes from the mangrove fungus *Pestalotiopsis* sp. *Nat. Commun.* 4, 1810. <https://doi.org/10.1038/ncomms2850>.
- Azpiazu-Muniozguren, M., Perza, A., Rementeria, A., Martinez-Malaxetxebarria, I., Alonso, R., Laorden, L., Gamboa, J., Bikandi, J., Garaizar, J., Martinez-Ballesteros, I., 2021. Fungal diversity and composition of the continental solar saltern in Añana Salt Valley (Spain). *J. Fungi* 7, 1074. <https://doi.org/10.3390/jof7121074>.
- Batista-García, R.A., Sutton, T., Jackson, S.A., Tovar-Herrera, O.E., Balcázar-López, E., Sánchez-Carbente, M.R., Sánchez-Reyes, A., Dobson, A.D.W., Folch-Mallol, J.L., 2017. Characterization of lignocellulolytic activities from fungi isolated from the deep-sea sponge *Stelletta normani*. *PLoS One*. <https://doi.org/10.1371/journal.pone.0173750>.
- Cantrell, S.A., Casillas-Martínez, L., Molina, M., 2006. Characterization of fungi from hypersaline environments of solar salterns using morphological and molecular techniques. *Mycol. Res.* 110, 962–970. <https://doi.org/10.1016/j.mycres.2006.06.005>.
- Chung, D., Kim, H., Choi, H.S., 2019. Fungi in salterns. *J. Microbiol.* 57, 717–724.
- Clipson, N.J.W., Jennings, D.H., 1992. *Dendryphiella salina* and *Debaryomyces hansenii*: models for ecophysical adaptation to salinity by fungi that grow in the sea. *Can. J. Bot.* 70, 2097–2105. <https://doi.org/10.1139/b92-260>.
- Coleine, C., Stajich, J.E., Selbmann, L., 2022. Fungi are key players in extreme ecosystem. *Trends Ecol. Evol.* 37, 517–528. <https://doi.org/10.1016/j.tree.2022.02.002>.
- Collinge, D.B., Jensen, B., Jørgensen, H.J.L., 2022. Fungal endophytes in plants and their relationship to plant disease. *Curr. Opin. Microbiol.* 69, 102177. <https://doi.org/10.1016/j.mib.2022.102177>.
- Cram, J.W., Torr, P.G., Rose, D.A., 2002. Salt allocation during leaf development and leaf fall in mangroves. *Trees* 16, 112–119. <https://doi.org/10.1007/s00468-001-0153-3>.
- Elsayis, A., Hassan, S.W.M., Ghanem, K.M., Khairy, H., 2022. Optimization of melanin pigment production from the halotolerant black yeast *Hortaea werneckii* AS1 isolated from solar salter in Alexandria. *BMC Microbiol.* 8, 92. <https://doi.org/10.1186/s12866-022-02505-1>.
- Estrada, C., Wcislo, W.T., Van Bael, S.A., 2013. Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. *New Phytol.* 198, 241–251.
- Evans, S., Hansen, R.W., Schneegurt, M.A., 2013. Isolation and characterization of halotolerant soil fungi from the great salt plains of Oklahoma. *Cryptogam. Mycol.* 34, 329–341.
- Fofonoff, N.P., 1985. Physical properties of seawater: A new salinity scale and equation of state for seawater. *J. Geophys. Res.* 90, 3332–3342.
- Frisvad, J.C., 2005. Halotolerant and halophilic fungi and their extrolite production. In: Gunde-Cimerman, N., Oren, A., Ana Plemenitaš, A. (Eds.), *Adaptation to life at high salt concentrations in Archaea, Bacteria, and Eukarya*. Springer, The Netherlands, pp. 425–440.
- Fryar, S.C., Haelewaters, D., Catcheside, D.E.A., 2019. *Annabella australiensis* gen. & sp. nov. (Helotiales, Cordieritidaceae) from South Australian mangroves. *Mycol. Prog.* 18, 973–981. <https://doi.org/10.1007/s11557-019-01499-x>.
- Gostinčar, C., Grube, M., De Hoog, S., Zalar, P., Gunde-Cimerman, N., 2009. Extremotolerance in fungi: evolution on the edge. *FEMS Microbiol. Ecol.* 71, 2–11. <https://doi.org/10.1111/j.1574-6941.2009.00794.x>.
- Govinda Rajulu, M.B., Rajamani, T., Murali, T.S., Suryanarayanan, T.S., Minj, D., 2022. The fungal endobiome of seaweeds of the Andaman Islands, India. *Curr. Sci.* 123, 1508–1514. <https://doi.org/10.18520/cs/v123/i12/1508-1514>.
- Gunde-Cimerman, N., Zalar, P., Petrovič, U., Turk, M., Kogej, T., de Hoog, G.S., Plemenitaš, A., 2004. Fungi in the salterns. In:

- Ventosa, A. (Ed.), *Halophilic microorganisms*. Springer, Heidelberg, pp. 103–113. https://doi.org/10.1007/978-3-662-07656-9_7.
- Gunde-Cimerman, N., Plemenitaš, A., Oren, A., 2018. Strategies of adaptation of microorganisms of the three domains of life to high salt concentrations. *FEMS Microbiol. Rev.* 42, 353–375. <https://doi.org/10.1093/femsre/fuy009>.
- Hosono, K., 1992. Effect of salt stress on lipid composition and membrane fluidity of the salt-tolerant yeast *Zygosaccharomyces roucii*. *J. Gen. Microbiol.* 138, 91–96. <https://doi.org/10.1515/botm.1994.37.5.479>.
- Hu, Y., Ma, X., Li, X.X., Tan, S., Cheng, M., Hou, J., Cui, H.L., 2023. *Natrinema caseinilyticum* sp. nov., *Natrinema gelatinilyticum* sp. nov., *Natrinema marinum* sp. nov., *Natrinema zhouii* sp. nov., extremely halophilic archaea isolated from marine environments and a salt mine. *Extremophiles* 27, 9. <https://doi.org/10.1007/s00792-023-01294-3>.
- Jones, E.B.G., Sakayaroj, J., Suetrong, S., Somrithipol, S., Pang, K.L., 2009. Classification of marine Ascomycota, anamorphic taxa and Basidiomycota. *Fungal Divers.* 35, 1–187.
- Kejžar, A., Gobec, S., Plemenitaš, A., Lenassi, M., 2013. Melanin is crucial for growth of the black yeast *Hortaea werneckii* in its natural hypersaline environment. *Fungal Biol.* 117, 368–379.
- Kis-Papo, T., Weig, A., Riley, R., Peršoh, D., Salamov, A., Sun, H., Lipzen, A., Wasser, S.P., Rambold, G., Grigoriev, I.V., Nevo, E., 2014. Genomic adaptations of the halophilic Dead Sea filamentous fungus *Eurotium rubrum*. *Nat. Commun.* 5, 3745. <https://doi.org/10.1038/ncomms4745>.
- Kohlmeyer, J., Kohlmeyer, E., 1979. *Marine Mycology: the Higher Fungi*. Elsevier.
- Kumaresan, V., Suryanarayanan, T.S., 2002. Endophyte assemblages in young, mature and senescent leaves of *Rhizophora apiculata*: evidence for the role of endophytes in mangrove litter degradation. *Fungal Divers.* 9, 81–91.
- Kumaresan, V., Suryanarayanan, T.S., Johnson, J.A., 2002. Ecology of mangrove endophytes. In: Hyde, K.D. (Ed.), *Fungi of Marine Environments. Fungal Diversity Research Series 9*. Fungal Diversity Press, Hong Kong, pp. 145–166.
- Kumaresan, V., Thirunavukkarasu, N., Suryanarayanan, T.S., 2021. Endophytes of mangroves: diversity, secondary metabolites and enzymes. In: Satyanarayana, T., Deshmukh, S.K., Deshpande, M.V. (Eds.), *Progress in Mycology*. Springer, Singapore, pp. 277–309. https://doi.org/10.1007/978-981-16-2350-9_10.
- Li, M., Wen, J., 2021. Recent progress in the application of omics technologies in the study of bio-mining microorganisms from extreme environments. *Microb. Cell Factories* 20, 178. <https://doi.org/10.1186/s12934-021-01671-7>.
- Oren, A., 2002. Molecular ecology of extremely halophilic Archaea and Bacteria. *FEMS Microbiol. Ecol.* 39, 1–7. <https://doi.org/10.1111/j.1574-6941.2002.tb00900.x>.
- Overy, D.P., Bayman, P., Kerr, R.G., Bills, G.F., 2014. An assessment of natural product discovery from marine (*sensu strictu*) and marine-derived fungi. *Mycology* 5, 145–167. <https://doi.org/10.1080/21501203.2014.931308>.
- Panchal, S., Murali, T.S., Suryanarayanan, T.S., Sanyal, K., 2022. Hypersaline fungi as a source of potentially active metabolites against pathogenic *Candida* species. *Czech Mycol.* 74, 93–101. <https://doi.org/10.33585/cmy.74107>.
- Paranetharan, M.S., Thirunavukkarasu, N., Rajamani, T., Murali, T.S., Suryanarayanan, T.S., 2018. Salt-tolerant chitin and chitosan modifying enzymes from *Talaromyces stipitatus*, a mangrove endophyte. *Mycosphere* 9, 215–226. <https://doi.org/10.5943/mycosphere/9/2/5>.
- Paranetharan, M.S., Thirunavukkarasu, N., Rajamani, T., Suryanarayanan, T.S., 2022. Biomass destructuring enzymes of fungal endophytes of mangrove roots. *Curr. Res. Environ. Appl. Mycol.* 12, 259–267. <https://doi.org/10.5943/cream/12/1/16>.
- Plemenitaš, A., Lenassi, M., Konte, T., Kejžar, A., Zajc, J., Gostinčar, C., Gunde-Cimerman, N., 2014. Adaptation to high salt concentrations in halotolerant/halophilic fungi: a molecular perspective. *Front. Microbiol.* 5, 199. <https://doi.org/10.3389/fmicb.2014.00199>.
- Plemenitaš, A., 2021. Sensing and Responding to Hypersaline Conditions and the HOG Signal Transduction Pathway in Fungi Isolated from Hypersaline Environments: *Hortaea werneckii* and *Wallemia ichthyophaga*. *J. Fungi* 7, 988. <https://doi.org/10.3390/jof7110988>.
- Popp, M., Larher, F., Weigel, P., 1984. Chemical composition of Australian mangroves III. Free amino acids, total methylated onium compounds and total nitrogen. *Z. Pflanzenphysiol.* 114, 15–25. [https://doi.org/10.1016/S0044-328X\(84\)80074-4](https://doi.org/10.1016/S0044-328X(84)80074-4).
- Ravishankar, J.P., Muruganandam, V., Suryanarayanan, T.S., 1994. Effect of salinity on fatty acid composition of *Cirrenalia pygmea*, an obligate marine fungus. *Bot. Mar.* 37, 479–481. <https://doi.org/10.1515/botm.1994.37.5.479>.
- Ravishankar, J.P., Muruganandam, V., Suryanarayanan, T.S., 1995. Isolation and characterization of melanin from a marine fungus. *Bot. Mar.* 38, 413–416. <https://doi.org/10.1515/botm.1995.38.1-6.413>.
- Ravishankar, J.P., Suryanarayanan, T.S., 1998. Influence of salinity on the activity of polyol metabolism enzymes and peroxidase in the marine fungus *Cirrenalia pygmea* (Hyphomycetes). *Indian J. Mar. Sci.* 27, 237–238.
- Sepcic, K., Zalar, P., Gunde-Cimerman, N., 2010. Low water activity induces the production of bioactive metabolites in halophilic and halotolerant fungi. *Mar. Drugs* 9, 43–58. <https://doi.org/10.3390/md9010043>.
- Shu, W.S., Huang, L.N., 2022. Microbial diversity in extreme environments. *Nat. Rev. Microbiol.* 20, 219–235. <https://doi.org/10.1038/s41579-021-00648-y>.
- Soler-Hurtado, M.M., Sandoval-Sierra, J.V., Machordom, A., Diéguez-Urbeondo, J., 2016. *Aspergillus sydowii* and other potential fungal pathogens in gorgonian octocorals of the Ecuadorian Pacific. *PLoS One* 11e0165992. <https://doi.org/10.1371/journal.pone.0165992>.
- Suryanarayanan, T.S., Muruganandam, V., Rajagopal, K., Girivasan, K.P., 1996. Soil mycoflora of a commercially operated solar saltern. *Kavaka* 24, 11–13.
- Suryanarayanan, T.S., Venkatachalam, A., Thirunavukkarasu, N., Ravishankar, J.P., Doble, M., Geetha, V., 2023. Internal mycobiota characterization of halophilic and halotolerant fungi from man-made solar salterns in Pattani Province, Thailand. *PLoS One* 18e0281623. <https://doi.org/10.1371/journal.pone.0281623>.
- Suryanarayanan, T.S., Uma Shaanker, R., 2021. Can fungal endophytes fast-track plant adaptations to climate change? *Fungal Ecol.* 50, 101039. <https://doi.org/10.1016/j.funeco.2021.101039>.
- Tafer, H., Poyntner, C., Lopandic, K., Sterflinger, K., Piñar, G., 2019. Back to the salt mines: Genome and transcriptome comparisons of the halophilic fungus *Aspergillus salisburgensis* and its halotolerant relative *Aspergillus sclerotialis*. *Genes* 10, 381. <https://doi.org/10.3390/genes10050381>.
- Thatoi, H., Behera, B.C., Mishra, R.R., 2013. Ecological role and biotechnological potential of mangrove fungi: a review. *Mycology* 4, 54–71. <https://doi.org/10.1080/21501203.2013.785448>.
- Thirunavukkarasu, N., Suryanarayanan, T.S., Girivasan, K.P., Venkatachalam, A., Geetha, V., Ravishankar, J.P., Doble, M., 2012. Fungal symbionts of marine sponges from Rameswaram, southern India: species composition and bioactive metabolites. *Fungal Divers.* 55, 37–46. <https://doi.org/10.1007/s13225-011-0137-6>.
- Thirunavukkarasu, N., Jahnes, B., Broadstock, A., Govinda Rajulu, M.B., Murali, T.S., Gopalan, V., Suryanarayanan, T.S.,

2015. Screening marine-derived endophytic fungi for xylan-degrading enzymes. *Curr. Sci.* 109, 112–120. <http://www.jstor.org/stable/24905695>.
- Thirunavukkarasu, N., Suryanarayanan, T.S., Rajamani, T., Govinda Rajulu, M.B., 2017. Diversity and technological potential of fungi from solar salterns of southern India. *Kavaka* 48, 26–32.
- Tomlinson, P.B., 1994. *The Botany of Mangroves*. Cambridge University Press, Cambridge, p. 433.
- Vaupotic, T., Veranic, P., Petrovic, U., Gunde-Cimerman, N., Plemenitas, A., 2008. HMG-CoA reductase is regulated by environmental salinity and its activity is essential for halotolerance in halophilic fungi. *Stud. Mycol.* 61, 61–66. <https://doi.org/10.3114/sim.2008.61.05>.
- Venkatachalam, A., Thirunavukkarasu, N., Suryanarayanan, T.S., 2015. Distribution and diversity of endophytes in seagrasses. *Fungal Ecol.* 13, 60–65. <https://doi.org/10.1016/j.funeco.2014.07.003>.
- Wingfield, L.K., Jitprasitporn, N., Che-alee, N., 2023. Isolation and characterization of halophilic and halotolerant fungi from man-made solar salterns in Pattani Province, Thailand. *PLoS One* 18e0281623. <https://doi.org/10.1371/journal.pone.0281623>.
- Zajc, J., Zalar, P., Plemenitaš, A., Gunde-Cimerman, N., 2012. The mycobiota of the salterns. In: Raghukumar, C. (Ed.), *Biology of Marine Fungi*. Springer –Verlag Berlin Heidelberg, pp. 133–158.
- Zalar, P., De Hoog, G.S., Schroers, H.J., Crous, P.W., Groenewald, J.Z., Gunde-Cimerman, N., 2007. Phylogeny and ecology of the ubiquitous saprobe *Cladosporium sphaerospermum*, with descriptions of seven new species from hypersaline environments. *Stud. Mycol.* 58, 157–183. <https://doi.org/10.3114/sim.2007.58.06>.
- Zalar, P., Frisvad, J.C., Gunde-Cimerman, N., Varga, J., Samson, R.A., 2008. Four new species of *Emericella* from the Mediterranean region of Europe. *Mycologia* 100, 779–795. <https://doi.org/10.3852/08-078>.
- Zalar, P., Zupančič, J., Gostinčar, C., Zajc, J., de Hoog, G.S., De Leo, F., Azua-Bustos, A., Gunde-Cimerman, N., 2019. The extremely halotolerant black yeast *Hortaea werneckii*-a model for intraspecific hybridization in clonal fungi. *IMA Fungus* 10, 1–27. <https://doi.org/10.1186/s43008-019-0007-5>.
- Zhang, J., Xiao, Q., Guo, T., Wang, P., 2021. Effect of sodium chloride on the expression of genes involved in the salt tolerance of *Bacillus* sp. strain “SX4” isolated from salinized greenhouse soil. *Open Chem* 19, 9–22. <https://doi.org/10.1515/chem-2020-0181>.
- Zheng, X.W., Wu, Z.P., Sun, Y.P., Wang, B.B., Hou, J., Cui, H.L., 2022. *Halorussus vallis* sp. nov., *Halorussus aquaticus* sp. nov., *Halorussus gelatinilyticus* sp. nov., *Halorussus limi* sp. nov., *Halorussus salilacus* sp. nov., *Halorussus salinisoli* sp. nov.: six extremely halophilic archaea isolated from solar saltern, salt lake and saline soil. *Extremophiles* 26, 32. <https://doi.org/10.1007/s00792-022-01280-1>.
- Zhu, D., Adebisi, W.A., Ahmad, F., Sethupathy, S., Danso, B., Sun, J., 2020. Recent development of extremophilic bacteria and their application in biorefinery. *Front. Bioeng. Biotechnol.* 8, 483. <https://doi.org/10.3389/fbioe.2020.00483>.