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UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
(MICROBIOLOGIA APLICADA)

DESVENDANDO A ECOLOGIA DE INTERAÇÕES INSETO-LEVEDURAS: CARACTERIZAÇÃO TAXONÔMICA, MOLECULAR E DESCOBRIMENTO DE NOVAS TOXINAS KILLER

RODOLFO BIZARRIA JÚNIOR

Rio Claro – SP
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RODOLFO BIZARRIA JÚNIOR

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Microbiologia Aplicada).

Orientador: Prof. Dr. André Rodrigues

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IMPACTO POTENCIAL DESTA PESQUISA

O presente estudo explorou interações entre leveduras e insetos, apoiando-se em dois modelos: os jardins de fungo de formigas atíneas e besouros associados aos frutos de pau-ferro. Identificamos leveduras presentes nos jardins de fungo que produzem toxinas de natureza antifúngica e que apresentam atividade contra diferentes patógenos humanos de importância clínica. Futuramente, tais toxinas podem ser exploradas como alternativas à moléculas antifúngicas sintéticas no controle de infecções fúngicas, principalmente, em decorrência do surgimento de patógenos humanos resistentes aos medicamentos empregados atualmente. Além disso, apresentamos uma nova interação inseto-levedura, entre uma espécie de *Cyberlindnera* e um besouro que infesta frutos de pau-ferro. Considerando a distribuição dessa árvore em território brasileiro, consideramos que esse pode ser um modelo primordial para estudo dessas interações no Brasil. Foi observado que a levedura produz atrativos voláteis, que futuramente poderão ser estudados em armadilhas entomológicas de insetos de importância econômica, em manejos integrados que mitiguem os danos causados nas lavouras. Em conclusão, o estudo além de elucidar a ecologia e evolução dessas interações, avança em linhas de pesquisa com impacto comercial e de interesse público.

POTENTIAL IMPACT OF THIS RESEARCH

This study explored insect-yeast interactions relying on two models: the fungus gardens of attine ants and beetles associated with "pau-ferro" fruits. We identified that yeasts present in fungus gardens produce antifungal toxins against human pathogens of clinical importance. In the future, such toxins may be explored as alternatives to synthetic antifungal molecules to control fungal infections, an emerging field considering the human pathogens' resistance to the current available drugs. Furthermore, we present a new insect-yeast interaction between a species of *Cyberlindnera* and a beetle that infests "pau-ferro" fruits. Considering the distribution of this tree in the Brazilian territory, we consider that this could be a primordial model for studying these interactions in Brazil. We observed that the yeast produces volatile attractants, which eventually could be studied in entomological traps for economically important insects, in an integrated management to mitigate crop damage. In conclusion, the study elucidates the ecology and evolution of these interactions and advances on research lines with commercial and public interest.

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Rio Claro

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Remember when you were young, you shone like the sun.
Shine on you crazy diamond.
Now there's a look in your eyes, like black holes in the sky."
Pink Floyd
Wish You Were Here (1975)

"Eu medi os céus, agora, as sombras eu meço.

Para o firmamento viaja a mente, na terra descansa o corpo."

Johannes Kepler (1571-1630)

RESUMO

Leveduras estão frequentemente associadas a insetos e seus ambientes. Benefícios mútuos foram observados em interações insetos-leveduras e incluem, dentre outros, o uso das leveduras como fonte de alimento e sua dispersão por insetos atraídos por seus voláteis. Nesse cenário, as interações inseto-levedura são modelos interessantes para entendimento da ecologia e evolução de mutualismos. Formigas atíneas são componentes importantes da fauna do continente americano, pois praticam uma fungicultura de fungos basidiomicetos, desempenhando importantes papéis ecológicos. Leveduras foram reportadas nos jardins de fungo de formigas atíneas, porém, até o momento, pouco foi explorado sobre a diversidade de leveduras em diferentes fungiculturas. Nosso estudo indica que os jardins são ricos em leveduras, entretanto, são dissimilares em relação à composição. Além disso, algumas leveduras do jardim produzem toxinas antifúngicas, com amplo espectro de atividade, incluindo contra patógenos humanos de importância clínica. Nosso estudo identificou elementos codificadores genômicos de uma nova toxina, que futuramente poderão ser empregados no estudo e busca de novas toxinas em leveduras. Além disso, apresentamos uma nova interação inseto-levedura, entre uma espécie de *Cyberlindnera* e um besouro que infesta frutos de pau-ferro, sendo essa, uma árvore nativa e acessível em território brasileiro. Por fim, demonstramos que a levedura *Cyberlindnera* possui rearranjos em genes ribossomais, como a primeira evidência desse fenômeno em leveduras desse clado. Nossa hipótese é que esse fenômeno pode ser um resultado da interação com os besouros. Em conclusão, insetos e seus ambientes apresentam uma grande diversidade de leveduras de interesse biotecnológico, e seu estudo pode elucidar sobre a ecologia e evolução de mutualismos, um campo ainda inexplorado considerando a vasta diversidade de insetos.

Palavras-chave: Mutualismo. Formigas cultivadoras de fungos. Toxinas *killer*. *Cyberlindnera*. *Libidibia ferrea*

ABSTRACT

Yeasts are often associated with insects and their environments. Mutual benefits have been reported in different insect-yeast interactions including, among others, the use of yeasts as nutritional sources and their dispersal by insects attracted to their volatiles. Therefore, insect-yeast interactions are interesting models for understanding the ecology and evolution of mutualisms. Attine ants are key players in the American fauna, performing a fungiculture of basidiomycete fungi with important ecological roles. Yeasts have been reported in fungus gardens of attine ants; to date, the diversity of yeasts in different fungicultures is elusive. Our study indicates that fungus gardens are rich yeast environments, but dissimilar in terms of community composition. In addition, some yeasts from fungus gardens produce antifungal toxins with a broad spectrum of activity, including towards human pathogens of clinical importance. Our study identified a new toxin encoded by genomic elements, which in the future could be used in the study and search for new toxins from yeasts. Furthermore, we present a new insect-yeast interaction, between a species of *Cyberlindnera* and a beetle that infests "pau-ferro" fruits, a native and accessible tree in the Brazilian territory. Finally, we demonstrated that the associated yeast *Cyberlindnera* has rearrangements in ribosomal genes, the first evidence of these characteristics in this clade. We hypothesize that it may be a result of the interaction with the beetles. In conclusion, insects and their environments harbor a diversity of yeasts of biotechnological interest. The study of these yeasts can shed light on the evolution and ecology of mutualisms, which is still an unexplored field considering the vast diversity of insects.

Keywords: Mutualism. Fungus-growing ants. Killer toxins. *Cyberlindnera*. *Libidibia ferrea*

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BREVE CONTEXTO

A natureza é repleta de formas de vida complexas que interagem entre si e competem por recursos importantes em seus habitats, com pressões seletivas que regem os ciclos de vida das espécies e sua ascendência ao longo das gerações. O resultado são adaptações e comportamentos que aumentam em frequência nas populações, uma vez que conferem vantagens na disputa por recursos. Simbiose é uma associação entre organismos distintos que compartilham o mesmo habitat, um importante modo de vida para o surgimento de adaptações e conquista de novos habitats. Alguns insetos sociais ganham destaque pelo uso de fungos como recurso nutritivo, transmitindo-os ao longo de novas gerações e hábitats, em processo similar a agricultura humana, como é o caso do mutualismo das formigas cultivadoras de fungos. Em outros casos, dois organismos distintos podem compartilham o mesmo nicho, porém sem interação física, ou com associação limitada pela geografia, distribuição ou ciclo de vida. Esse é o caso de muitas associações entre leveduras e insetos, que aqui denominamos como mutualismos não simbióticos, uma vez que, benefícios mútuos da associação são evidentes. Usualmente as leveduras contribuem para a nutrição, detoxificação e sinalização de recursos aos insetos, inclusive modulando comportamentos, ao passo que esses, contribuem para sua dispersão e por fornecimento de um ambiente propício para que as leveduras possam interagir, e eventualmente, se reproduzir. Uma série de outros benefícios foi evidenciada em outros modelos, ainda carecendo de maiores esclarecimentos, como proteção no combate de patógenos, por exemplo. A complexidade dessas interações é refletida na diversificação das associações ao longo da história de vida dos insetos, sendo que alguns mantêm associações com predominância de táxons, enquanto outros possuem múltiplas espécies compondo uma complexa comunidade.

Neste estudo, nos dedicamos a investigar duas dessas interações, a primeira entre leveduras associadas a jardins de fungo de formigas cultivadoras, e a segunda, a interação entre leveduras associadas a frutos de pau-ferro e o besouro que os infesta. As formigas cultivadoras de fungos mantêm em seus jardins uma diversa comunidade de leveduras, com poucas assinaturas de especificidade, que potencialmente reflete a diversidade de leveduras nos substratos forrageados pelas formigas e outras fontes, como o solo. Isso caracteriza a comunidade associada de leveduras como um elemento do holobionte das formigas cultivadoras de fungos. Nosso estudo explorou a diversidade de leveduras em jardins de diferentes formigas, que praticam diferentes estilos de fungicultura, sendo o maior esforço amostral realizado nesse ambiente até o momento. Constatamos que os jardins são complexos e que nenhum taxon comum entre todas as amostras foi encontrado, sendo as comunidades diferentes mesmo entre jardins da mesma espécie e localidade.

Apesar das leveduras nos jardins terem sido historicamente exploradas para diversidade taxonômica, alguns estudos fizeram avanços acerca da ecologia de leveduras nesse ambiente. Um desses estudos identificou que leveduras de jardins secretam toxinas antifúngicas que poderiam ter um papel protetivo nesse mutualismo, dessa forma, em um segundo estudo exploramos esse fenótipo denominado '*killer*' em leveduras obtidas desse ambiente. Constatamos que os jardins abrigam tais leveduras, e mesmo em casos de ausência, podem estar associados a outros fatores relacionados aos métodos de expressão do fenótipo. É importante ressaltar, que nosso estudo evidenciou que as toxinas produzidas por essas leveduras possuem ação inibitória contra diferentes leveduras patogênicas humanas, podendo ser futuramente exploradas para descobrimentos de novas drogas de interesse clínico, mitigando infecções fúngicas em humanos e outros organismos. Nosso estudo resultou no descobrimento do que pode ser

uma nova toxina '*killer*', de estrutura e ação semelhante a uma toxina previamente conhecida e mobilizada em elementos citoplasmáticos.

Em um segundo momento, dedicamo-nos ao estudo de uma nova associação entre leveduras, frutos de pau-ferro e besouros que infestam os frutos. Nesse estudo, identificamos que uma nova espécie de levedura, que momentaneamente acomodamos no gênero *Cyberlindnera*, é o componente predominante da comunidade. Tal levedura possui a habilidade de produzir compostos voláteis a partir dos extratos dos frutos, que são atrativos e distinguíveis pelos besouros. Essa levedura, que habita os frutos, têm na atividade de construção de galerias pelos besouros um apoio, potencializando sua densidade no fruto. Uma vez que em alguns casos não encontramos essa levedura associada aos frutos infestados, e a levedura também estar presente nos frutos sadios, mesmo que em baixas quantidades, postulamos essa interação até o momento, como um mutualismo não simbiótico. Demais interações entre o besouro e a levedura são discutidas adiante. Curiosamente, tal levedura também apresenta rearranjos em genes ribossomais, que apesar de normalmente estarem associados a pressões seletivas de purificação, em outros casos podem estar sujeitos a outros eventos e pressões evolutivas, como reticulação, homoplasias e mecanismos de evolução '*birth-and-death*'. Nossos resultados indicaram que a levedura em questão mantém cópias diferentes de regiões ribossomais, resultando em alterações estruturais dessas moléculas de ácido ribonucleico. Nossa hipótese é que a interação com os besouros nos frutos potencializa os rearranjos de genes nessa levedura, devido à atuação de outras pressões seletivas que não as de purificação. Os resultados estimulam a investigação sobre evolução dos genes ribossomais em leveduras e outros organismos.

No geral, o estudo explora dois modelos complexos de interações inseto-levedura, em contexto diferentes, com alta diversidade e ausência de especificidade,

além de predominância de um taxon. As interações foram investigadas sob a ótica de outras interações inseto-levedura e as avaliações deste estudo podem ser futuramente exploradas em outros modelos. A tese central é que as interações mutualísticas com insetos desempenham um papel central na ecologia e evolução de leveduras.

CONCLUSÃO

Nesse estudo, exploramos dois modelos de interações inseto-levedura, os jardins de fungo de formigas atíneas e os besouros associados aos frutos de pau-ferro. Nossos resultados indicam que os jardins de fungo abrigam uma grande diversidade de leveduras oriundas do forrageamento das formigas, e que as comunidades de leveduras são dissimilares mesmo entre colônias da mesma espécie de formiga. Nos jardins de fungo, identificamos que algumas leveduras produzem toxinas antifúngicas, com atividade frente a uma coleção de leveduras sensíveis, que incluem leveduras patogênicas de interesse clínico. Em particular, em um isolado de *Candida sinolaborantium*, identificamos elementos codificadores de uma nova toxina por mineração genômica, que possui similaridade com toxinas codificadas por elementos de dsRNA em *Saccharomyces cerevisiae*. Futuramente, as toxinas poderão ser uma alternativa aos medicamentos empregados no combate de infecções fúngicas, que por vezes são ineficazes frente a patógenos resistentes. Durante a busca por leveduras associadas a insetos, identificamos uma nova interação entre uma espécie endofítica de *Cyberlindnera* e um besouro que infesta os frutos de pau-ferro. Observamos que a levedura produz metabólitos voláteis atrativos e distinguíveis pelos besouros, e que aumentam em densidade no fruto em decorrência da escavação de galerias pelos besouros. Além disso, observamos que a levedura possui rearranjos nos genes ribossomais, e que acreditamos ser resultado da interação com os besouros. De modo geral, expandimos nosso conhecimento sobre a ecologia e evolução de interações inseto-levedura, e os resultados encorajam a investigação de novas interações na prospecção de leveduras de interesse biotecnológico.

REFERÊNCIAS

Abranches, J., Mendonça-Hagler, L. C., Hagler, A. N., Morais, P. B., Rosa, C. A. (1997). The incidence of killer activity and extracellular proteases in tropical yeast communities. **Canadian Journal of Microbiology**, 43(4), 328-336.

Adams, A. S., Six, D. L., Adams, S. M., Holben, W. E. (2008). In vitro interactions between yeasts and bacteria and the fungal symbionts of the mountain pine beetle (*Dendroctonus ponderosae*). **Microbial ecology**, 56, 460-466.

Allen, A., Islamovic, E., Kaur, J., Gold, S., Shah, D., Smith, T. J. (2011). Transgenic maize plants expressing the Totivirus antifungal protein, KP4, are highly resistant to corn smut. **Plant biotechnology journal**, 9(8), 857-864.

Almeida, N. C. O. da S., Furtado, S. da C., Barcellos, J. F. M. (2021). A Narrative Review of Libidibia ferrea: Botanical Aspects, Ethnopharmacological Properties, Phytochemical Characteristics, Toxicity, and Experimental Tests. **European Journal of Medicinal Plants**, 32(12), 16-30.

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., Lipman, D. J. (1990). Basic local alignment search tool. **Journal of molecular biology**, 215(3), 403-410.

Amos, B. A., Hayes, R. A., Leemon, D. M., Furlong, M. J. (2019). Small hive beetle (Coleoptera: Nitidulidae) and the yeast, *Kodamaea ohmeri*: a facultative relationship under laboratory conditions. **Journal of Economic Entomology**, 112(2), 515-524.

Ananthakrishnan, T. N. (1997). Gallic and salicylic acids: sentinels of plant defence against insects. **Current Science**, 73(7), 576-579.

Angelis C de, Serzedello A and De Angelis DF (1983). Yeasts found in gardens of *Atta sexdens rubropilosa* and *Atta laevigata*. **Naturalia**, 8, 149–151.

Arcuri, S. L., Pagnocca, F. C., da Paixão Melo, W. G., Nagamoto, N. S., Komura, D. L., Rodrigues, A. (2014). Yeasts found on an ephemeral reproductive caste of the leaf-cutting ant *Atta sexdens rubropilosa*. **Antonie Van Leeuwenhoek**, 106(3), 475–487.

Arrey, G., Li, G., Murphy, R., Guimaraes, L., Alizadeh, S., Poulsen, M., Regenberg, B. (2021). Isolation, characterization, and genome assembly of *Barnettozyma botsteinii* sp. nov. and novel strains of *Kurtzmaniella quercitrusa* isolated from the intestinal tract of the termite *Macrotermes bellicosus*. **G3**, 11(12), jkab342.

Asplund, J., Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. **Biological Reviews**, 92(3), 1720-1738.

Baig, F., Farnier, K., Piper, A. M., Speight, R., Cunningham, J. P. (2020). Yeasts influence host selection and larval fitness in two frugivorous *Carpophilus beetle* species. **Journal of chemical ecology**, 46, 675-687.

Bankevich, A., et al. (2012). SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. **Journal of computational biology**, 19(5), 455-477.

Bariani, A., Gonçalves, J. F. D. C., Chevreuil, L. R., Cavallazzi, J. R. P., Souza, L. A. G. D., Bentes, J. L. D. S., Pando, S. C. (2012). Purificação parcial de inibidores de tripsina de sementes de *Caesalpinia ferrea* e *Swartzia polyphylla* e o efeito dos extratos protéicos sobre fungos fitopatogênicos. **Summa Phytopathologica**, 38, 131-138.

Becher, P. G., et al. (2012). Yeast, not fruit volatiles mediate *Drosophila melanogaster* attraction, oviposition and development. **Functional Ecology**, 26(4), 822-828.

Bellutti, N., Gallmetzer, A., Innerebner, G., Schmidt, S., Zelger, R., Koschier, E. H. (2018). Dietary yeast affects preference and performance in *Drosophila suzukii*. **Journal of pest science**, 91, 651-660.

Benda, N. D., Boucias, D., Torto, B., Teal, P. (2008). Detection and characterization of *Kodamaea ohmeri* associated with small hive beetle *Aethina tumida* infesting honey bee hives. **Journal of Apicultural Research**, 47(3), 194-201.

Bengtsson-Palme, J., et al. (2013). Improved software detection and extraction of ITS1 and ITS 2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. **Methods in Ecology and Evolution**, 4(10), 914-919.

Bevan, E. A., Herring, A. J., Mitchell, D. J. (1973). Preliminary characterization of two species of dsRNA in yeast and their relationship to the "killer" character. **Nature**, 245(5420), 81-86.

Bevan, E. A., Makower, M. (1963). The inheritance of a killer character in yeast (*Saccharomyces cerevisiae*). In: **Proceedings of the International Congress of Genetics XI**. Oxford: Pergamon Press, 1963. p. 202-203.

Bever, J. D. (2002). Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. **Proceedings of the Royal Society of London. Series B: Biological Sciences**, 269(1509), 2595-2601.

Bizarria Jr, R., de Castro Pietrobon, T., Ferreira, H., Rodrigues, A. (2023b). Polymorphisms of rDNA genes in *Cyberlindnera* yeast suggest birth and death evolution events. **FEMS Yeast Research**, foad032.

Bizarria Jr, R., de Castro Pietrobon, T., Rodrigues, A. (2023a). Uncovering the Yeast Communities in Fungus-Growing Ant Colonies. **Microbial Ecology**, 86(1), 624-635.

Bizarria Jr, R., Pagnocca, F. C., Rodrigues, A. (2022). Yeasts in the attine ant–fungus mutualism: Diversity, functional roles, and putative biotechnological applications. **Yeast**, 39(1-2), 25-39.

Blackman, M. W. (1942). New species of bark beetles (Pityophthorini) from Mexico and tropical America (Coleoptera, Scolytidae). **Proceedings of the United States National Museum**.

Blanton, C. M., Ewel, J. J. (1985). Leaf-cutting ant herbivory in successional and agricultural tropical ecosystems. **Ecology**, 66(3), 861–869.

Bohner, F., Papp, C., Gácser, A. (2022). The effect of antifungal resistance development on the virulence of *Candida* species. **FEMS Yeast Research**, 22(1), foac019.

Bongomin, F., Gago, S., Oladele, R. O., Denning, D. W. (2017). Global and multi-national prevalence of fungal diseases—estimate precision. **Journal of fungi**, 3(4), 57.

Boucher, D. H., James, S., Keeler, K. H. (1982). The ecology of mutualism. **Annual Review of Ecology and Systematics**, 13(1), 315-347.

Boynton, P. J. (2019). The ecology of killer yeasts: Interference competition in natural habitats. **Yeast**, 36(8), 473–485.

Branstetter, M. G., Ješovnik, A., Sosa-Calvo, J., Lloyd, M. W., Faircloth, B. C., Brady, S. G., and Schultz, T. R. (2017). Dry habitats were crucibles of domestication in the evolution of agriculture in ants. **Proceedings of the Royal Society B: Biological Sciences**, 284(1852), 20170095.

Breinig, F., Sendzik, T., Eisfeld, K., Schmitt, M. J. (2006). Dissecting toxin immunity in virus-infected killer yeast uncovers an intrinsic strategy of self-protection. **Proceedings of the National Academy of Sciences**, 103(10), 3810-3815.

Breinig, F., Tipper, D. J., Schmitt, M. J. (2002). Kre1p, the plasma membrane receptor for the yeast K1 viral toxin. **Cell**, 108(3), 395-405.

Briones-Roblero, C. I., Rodríguez-Díaz, R., Santiago-Cruz, J. A., Zúñiga, G., Rivera-Orduña, F. N. (2017). Degradation capacities of bacteria and yeasts isolated from the gut of *Dendroctonus rhizophagus* (Curculionidae: Scolytinae). **Folia microbiologica**, 62, 1-9.

Bruen, T., Bruen, T. (2005). **PhiPack: PHI test and other tests of recombination**. McGill University, Montreal, Quebec.

Brůna, T., Hoff, K. J., Lomsadze, A., Stanke, M., Borodovsky, M. (2021). BRAKER2: automatic eukaryotic genome annotation with GeneMark-EP+ and AUGUSTUS supported by a protein database. **NAR genomics and bioinformatics**, 3(1), lqaa108.

Brysch-Herzberg, M. (2004). Ecology of yeasts in plant–bumblebee mutualism in Central Europe. **FEMS microbiology ecology**, 50(2), 87–100.

Buser, C. C., Jokela, J., Martin, O. Y. (2021). Scent of a killer: How could killer yeast boost its dispersal?. **Ecology and Evolution**, 11(11), 5809-5814.

Buser, C. C., Newcomb, R. D., Gaskett, A. C., Goddard, M. R. (2014). Niche construction initiates the evolution of mutualistic interactions. **Ecology Letters**, 17(10), 1257-1264.

Bussey, H., Vernet, T., Sdicu, A. M. (1988). Mutual antagonism among killer yeasts: Competition between Kl and K2 killers and a novel cDNA-based K1-K2 killer strain of *Saccharomyces cerevisiae*. **Canadian journal of microbiology**, 34(1), 38-44.

Buzzini, P., Lachance, M. A., Yurkov, A. (2017). **Yeasts in natural ecosystems: diversity**. Basel, Switzerland: Springer International Publishing, pp. 499.

Cappelli, A., Ulissi, U., Valzano, M., Damiani, C., Epis, S., Gabrielli, M. G., Conti, S., Polonelli, L., Bandi, C., Favia, G., and Ricci, I. (2014). A *Wickerhamomyces anomalus* killer strain in the malaria vector *Anopheles stephensi*. **PloS One**, 9(5), e95988.

Cappelli, A., Valzano, M., Cecarini, V., Bozic, J., Rossi, P., Mensah, P., Amantini, C., Favia, G., Ricci, I. (2019). Killer yeasts exert anti-plasmodial activities against the malaria parasite *Plasmodium berghei* in the vector mosquito *Anopheles stephensi* and in mice. **Parasites and Vectors**, 12(1), 1–8.

Carranza, S., Giribet, G., Ribera, C., Riutort, M. (1996). Evidence that two types of 18S rDNA coexist in the genome of *Dugesia* (Schmidtea) *mediterranea* (Platyhelminthes, Turbellaria, Tricladida). **Molecular Biology and Evolution**, 13(6), 824-832.

Carreiro, S. C. (2000). P**esquisa de fator killer e análise da degradação de polissacarídeos vegetais por leveduras associadas aos ninhos de Atta sexdens.** PhD thesis, UNESP, Rio Claro, São Paulo, Brasil.

Carreiro, S. C., Pagnocca, F. C., Bacci, M., Bueno, O. C., Hebling, M. J. A., Middelhoven, W. J. (2002). Occurrence of killer yeasts in leaf-cutting ant nests. **Folia Microbiologica**, 47(3), 259–262.

Carreiro, S. C., Pagnocca, F. C., Bueno, O. C., Júnior, M. B., Hebling, M. J. A., and da Silva, O. A. (1997). Yeasts associated with nests of the leaf-cutting ant *Atta sexdens rubropilosa* Forel, 1908. **Antonie van Leeuwenhoek**, 71(3), 243–248.

Carvalho, P. E. R. (2008). **Espécies arbóreas brasileiras**. Embrapa Florestas.

Case, T. J., Gilpin, M. E. (1974). Interference competition and niche theory. **Proceedings of the National Academy of Sciences**, 71(8), 3073–3077.

Castillo, A., Cifuentes, V. (1994). Presence of double-stranded RNA and virus-like particles in *Phaffia rhodozyma*. **Current genetics**, 26, 364-368.

Chakraborty, A., et al. (2022). Yeast and fruit fly mutual niche construction and antagonism against mould. **Functional Ecology**, 36(7), 1639-1654.

Chand Dakal, T., Giudici, P., Solieri, L. (2016). Contrasting patterns of rDNA homogenization within the *Zygosaccharomyces rouxii* species complex. **PloS One**, 11(8), e0160744.

Chang, S. L., Leu, J. Y., Chang, T. H. (2015). A population study of killer viruses reveals different evolutionary histories of two closely related *Saccharomyces* sensu stricto yeasts. **Molecular Ecology**, 24(16), 4312–4322.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sande, E. L., Ma, K. H., Colwell, R. K., Ellison, A. M. (2014). "Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies." **Ecological Monographs**, 84, 45–67.

Chen, S., Zhou, Y., Chen, Y., Gu, J. (2018). fastp: an ultra-fast all-in-one FASTQ preprocessor. **Bioinformatics**, 34(17), i884-i890.

Cho, H., Rohlfs, M. (2023). Transmission of beneficial yeasts accompanies offspring production in *Drosophila*—An initial evolutionary stage of insect maternal care through manipulation of microbial load?. **Ecology and Evolution**, 13(6), e10184.

Chomicki, G., Weber, M., Antonelli, A., Bascompte, J., Kiers, E. T. (2019). The impact of mutualisms on species richness. **Trends in Ecology & Evolution**, 34(8), 698-711.

Coelho, A. R., Tachi, M., Pagnocca, F. C., Nobrega, G. M. A., Hoffmann, F. L., Harada, K. I., Hirooka, E. Y. (2009). Purification of *Candida quilliermondii* and *Pichia ohmeri* killer toxin as an active agent against *Penicillium expansum*. **Food Additives and Contaminants**, 26(1), 73-81.

Coluccio, A. E., Rodriguez, R. K., Kernan, M. J., Neiman, A. M. (2008). The yeast spore wall enables spores to survive passage through the digestive tract of *Drosophila*. **PLoS One**, 3(8), e2873.

Comandolli-Wyrepkowski, C. D., et al. (2017). Antileishmanial activity of extracts from *Libidibia ferrea*: development of in vitro and in vivo tests. **Acta Amazonica**, 47, 331-340.

Corrêa, M. M., Silva, P. S., Wirth, R., Tabarelli, M., Leal, I. R. (2010). How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages. **Oecologia**, 162, 103-115.

Costa Lima, A. (1929). Sobre dois scolytideos. **Memórias do Instituto Oswaldo Cruz**, v. 22, p. 109-112.

Costa Lima, A.M. (1956). **Insetos do Brasil**: Coleópteros. Escola Nacional de Agronomia, v. 10.

Crabtree, A. M., Kizer, E. A., Hunter, S. S., Van Leuven, J. T., New, D. D., Fagnan, M. W., Rowley, P. A. (2019). A rapid method for sequencing double-stranded RNAs purified from yeasts and the identification of a potent K1 killer toxin isolated from *Saccharomyces cerevisiae*. **Viruses**, 11(1), 70.

Craven, S. E., Dix, M. W., Michaels, G. E. (1970). Attine fungus gardens contain yeasts. **Science**, 169(3941), 184–186.

Crispell, J., Balaz, D., Gordon, S. V. (2019). HomoplasyFinder: a simple tool to identify homoplasies on a phylogeny. **Microbial genomics**, 5(1), e000245.

Cristiano, M. P., Cardoso, D. C., Sandoval-Gómez, V. E., Simões-Gomes, F. C. (2020). *Amoimyrmex Cristiano*, Cardoso and Sandoval, gen. nov. (Hymenoptera: Formicidae): a new genus of leaf-cutting ants revealed by multilocus molecular phylogenetic and morphological analyses. **Austral Entomology**, 59(4), 643–676.

da Costa Neto, D. J., de Morais, P. B. (2020). The vectoring of *Starmerella* species and other yeasts by stingless bees in a Neotropical savanna. **Fungal Ecology**, 47, 100973.

Dammann, R., Lucchini, R., Koller, T., Sogo, J. M. (1993). Chromatin structures and transcription of rDNA in yeast *Saccharomyces cerevisiae*. **Nucleic Acids Research**, 21(10), 2331-2338.

Davis, T. S., Hofstetter, R. W., Foster, J. T., Foote, N. E., Keim, P. (2011). Interactions between the yeast *Ogataea pini* and filamentous fungi associated with the western pine beetle. **Microbial ecology**, 61, 626-634.

Davis, T. S., Stewart, J. E., Clark, C., Van Buiten, C. (2022). Nutritional profile and effects on fungal growth of yeast symbionts associated with North American spruce beetle (*Dendroctonus rufipennis*).

de Carvalho Maria, T. R. B., Bomm, B. F. H., Nesi, J., Ho, T. L., Bobrowski, R. (2020). Canopy architecture and morphometry of tree species used in the urban forest. **Floresta**, 50(4), 1892-1901.

de Fine Licht, H. H., Boomsma, J. J. (2010). Forage collection, substrate preparation, and diet composition in fungus-growing ants. **Ecological Entomology**, 35(3), 259–269.

de Moraes, G. J., Berti Filho, E. (1974). **Coleobrocas que ocorrem em essências florestais**.

de Mendiburu, F. (2021). **agricolae: Statistical Procedures for Agricultural Research**. R package version 1.3-6. Available online: https://CRAN.R-project.org/package=agricolae.

Dohet, L., Gregoire, J. C., Berasategui, A., Kaltenpoth, M., Biedermann, P. H. (2016). Bacterial and fungal symbionts of parasitic *Dendroctonus* bark beetles. **FEMS Microbiology Ecology**, 92(9), fiw129.

Dowd, P. F., Shen, S. K. (1990). The contribution of symbiotic yeast to toxin resistance of the cigarette beetle (*Lasioderma serricorne*). **Entomologia Experimentalis et Applicata**, 56(3), 241-248.

Dowd, P. F., Shen, S. K. (1990). The contribution of symbiotic yeast to toxin resistance of the cigarette beetle (*Lasioderma serricorne*). **Entomologia Experimentalis et Applicata**, 56(3), 241-248.

Dusa, A. (2021). venn: Draw Venn Diagrams. R package version 1.10. https://CRAN.R-project.org/package=venn

Farji-brener, A. G., Werenkraut, V. (2015). A meta-analysis of leaf-cutting ant nest effects on soil fertility and plant performance. **Ecological Entomology**, 40(2), 150-158.

Fernando, W. D., Ramarathnam, R., Krishnamoorthy, A. S., Savchuk, S. C. (2005). Identification and use of potential bacterial organic antifungal volatiles in biocontrol. **Soil Biology and Biochemistry**, 37(5), 955-964.

Ferreira, M. R., Fernandes, M. T., da Silva, W. A., Bezerra, I. C., de Souza, T. P., Pimentel, M. F., Soares, L. A. (2016). Chromatographic and spectrophotometric analysis of phenolic compounds from fruits of *Libidibia ferrea* Martius. **Pharmacognosy Magazine**, 12(Suppl 2), S285.

Fisher, M. C., et al. (2022). Tackling the emerging threat of antifungal resistance to human health. **Nature reviews microbiology**, 20(9), 557-571.

Fisher, P. J., Stradling, D. J., Sutton, B. C., Petrini, L. E. (1996). Microfungi in the fungus gardens of the leaf-cutting ant *Atta cephalotes*: a preliminary study. **Mycological Research**, 100(5), 541–546.

Fowell, R. R. (1952). Sodium acetate agar as a sporulation medium for yeast. **Nature**, 170(4327), 578-578.

Fredericks, L. R., et al. (2021a). The species-specific acquisition and diversification of a K1-like family of killer toxins in budding yeasts of the *Saccharomycotina*. **PLoS genetics**, 17(2), e1009341.

Fredericks, L. R., et al. (2021b). Vaginal isolates of *Candida glabrata* are uniquely susceptible to ionophoric killer toxins produced by *Saccharomyces cerevisiae*. **Antimicrobial Agents and Chemotherapy**, 65(7), 10-1128.

French, S. L., Osheim, Y. N., Cioci, F., Nomura, M., Beyer, A. L. (2003). In exponentially growing *Saccharomyces cerevisiae* cells, rRNA synthesis is determined by the summed RNA polymerase I loading rate rather than by the number of active genes. **Molecular and Cellular Biology**, 23(5), 1558-1568.

Fuentefria, A. M., Faganello, J., Pazzini, F., Schrank, A., Valente, P., Vainstein, M. (2007). Typing and patterns of cellular morphological alterations in *Cryptococcus neoformans* and *Cryptococcus gattii* isolates exposed to a panel of killer yeasts. **Medical mycology**, 45(6), 503-512.

Fuentefria, A. M., Franskoviaki, I. M., Mercado, L. W., Ramos, J. P., Vainstein, M. H., Valente, P. (2006). Inhibition of clinical and environmental *Cryptococcus neoformans* isolates by two Brasilian killer yeasts. **Journal of basic microbiology**, 46(2), 87-93.

Fuentefria, A. M., Perez, L. R., Alves d'Azevedo, P., Pazzini, F., Schrank, A., Vainstein, M. H., Valente, P. (2008). Typing of *Staphylococcus epidermidis* clinical strains by a selected panel of Brasilian killer yeasts. **Journal of basic microbiology**, 48(1), 25-30.

Ganley, A. R., Kobayashi, T. (2007). Highly efficient concerted evolution in the ribosomal DNA repeats: total rDNA repeat variation revealed by whole-genome shotgun sequence data. **Genome Research**, 17(2), 184-191.

Ganter, P. F. (1988). The vectoring of cactophilic yeasts by *Drosophila*. **Oecologia**, 75(3), 400–404.

Ganter, P. F., Starmer, W. T. (1992). Killer Factor as a Mechanism of Interference Competition in Yeasts Associated with Cacti: Ecological Archives. **Ecology**, 73(1), 54-67.

Glass, N. L., Donaldson, G. C. (1995). Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. **Applied and environmental microbiology**, 61(4), 1323-1330.

Golubev, V. I. (2015). Action spectrum of *Wickerhamomyces ciferrii* mycocin. **Biotechnology in Russia**, (1), 15-21.

Golubev, W. I. (1998). Mycocins (killer toxins). In **The Yeasts** (pp. 55-62). Elsevier.

Golubev, W. I. (2006). Antagonistic interactions among yeasts. **Biodiversity and ecophysiology of yeasts** (pp. 197-219). Berlin, Heidelberg: Springer Berlin Heidelberg.

Golubev, W. I., Pfeiffer, I., Golubeva, E. (2002). Mycocin production in *Trichosporon pullulans* populations colonizing tree exudates in the spring. **FEMS microbiology ecology**, 40(2), 151-157.

Gordon, J. L., Wolfe, K. H. (2008). Recent allopolyploid origin of *Zygosaccharomyces rouxii* strain ATCC 42981. **Yeast**, 25(6), 449-456.

Goto, K., Iwatuki, Y., Kitano, K., Obata, T., Hara, S. (1990). Cloning and nucleotide sequence of the KHR killer gene of *Saccharomyces cerevisiae*. **Agricultural and biological chemistry**, 54(4), 979-984.

Greig, D., Travisano, M. (2008). Density-dependent effects on allelopathic interactions in yeast. **Evolution**, 62(3), 521-527.

Guamán-Burneo, M. C., et al. (2015). Xylitol production by yeasts isolated from rotting wood in the Galápagos Islands, Ecuador, and description of *Cyberlindnera galapagoensis* fa, sp. nov. **Antonie Van Leeuwenhoek**, 108, 919-931.

Gurevich, A., Saveliev, V., Vyahhi, N., Tesler, G. (2013). QUAST: quality assessment tool for genome assemblies. **Bioinformatics**, 29(8), 1072-1075.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. **Nucleic Acids. Symposium Series** 41:95-98.

Hershkovitz, M. A., Zimmer, E. A. (1996). Conservation patterns in angiosperm rDNA ITS2 sequences. **Nucleic acids research**, 24(15), 2857-2867.

Hilber-Bodmer, M., Schmid, M., Ahrens, C. H., Freimoser, F. M. (2017). Competition assays and physiological experiments of soil and phyllosphere yeasts identify Candida subhashii as a novel antagonist of filamentous fungi. **BMC microbiology**, 17, 1-15.

Hillis, D. M., Dixon, M. T. (1991). Ribosomal DNA: molecular evolution and phylogenetic inference. **The Quarterly Review of Biology**, 66(4), 411-453.

Hillis, D. M., Moritz, C., Porter, C. A., Baker, R. J. (1991). Evidence for biased gene conversion in concerted evolution of ribosomal DNA. **Science**, 251(4991), 308-310.

Howe, H. F. (1984). Constraints on the evolution of mutualisms. **The American Naturalist**, 123(6), 764-777.

Hsieh, T. C, Ma, K. H, Chao, A. (2020). iNEXT: Interpolation and Extrapolation for Species Diversity. **R package version 2.0.20**, http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Hua, M. X., Chi, Z., Liu, G. L., Buzdar, M. A., Chi, Z. M. (2010). Production of a novel and cold-active killer toxin by *Mrakia frigida* 2E00797 isolated from sea sediment in Antarctica. **Extremophiles**, 14, 515-521.

Hunt, D. W. A., Borden, J. H. (1990). Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). **Journal of Chemical Ecology**, 16(4), 1385-1397.

Huson, D. H., Bryant, D. (2006). Application of phylogenetic networks in evolutionary studies. **Molecular Biology and Evolution**, 23(2), 254-267.

Isaeva, O. V., Glushakova, A. M., Yurkov, A. M., Chernov, I. Y. (2009). The yeast *Candida railenensis* in the fruits of English oak (*Quercus robur* L.). **Microbiology**, 78(3), 355–359.

Ivannikova, Y. V., Naumova, E. S., Naumov, G. I. (2006). Detection of viral dsRNA in the yeast *Saccharomyces bayanus*. **Doklady Biological Sciences** (Vol. 406, pp. 100-102). New York: Consultants Bureau, c1965-1992.

Ivannikova, Y. V., Naumova, E. S., Naumov, G. I. (2007). Viral dsRNA in the wine yeast *Saccharomyces bayanus* var. *uvarum*. **Research in microbiology**, 158(8-9), 638-643.

Jumper, J., et al. (2021). Highly accurate protein structure prediction with AlphaFold. **Nature**, 596(7873), 583-589.

Kabir, M. E., Karim, N., Krishnaswamy, S., Selvakumar, D., Miyamoto, M., Furuichi, Y., Komiyama, T. (2011). Peptide derived from anti-idiotypic single-chain antibody is a potent antifungal agent compared to its parent fungicide HM-1 killer toxin peptide. **Applied microbiology and biotechnology**, 92, 1151-1160.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., Von Haeseler, A., and Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. **Nature methods**, 14(6), 587–589. DOI: 10.1038/nmeth.4285.

Kast, A., Klassen, R., Meinhardt, F. (2014). rRNA fragmentation induced by a yeast killer toxin. **Molecular Microbiology**, 91(3), 606-617.

Katoh, K., Rozewicki, J., Yamada, K. D. (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. **Briefings in Bioinformatics**, 20(4), 1160-1166.

Keeler, K. H. (1981). A model of selection for facultative nonsymbiotic mutualism. **The American Naturalist**, 118(4), 488-498.

Kindt, R., Coe, R. (2005). Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. **World Agroforestry Centre (ICRAF)**, Nairobi (Kenya). ISBN 92-9059-179-X, http://www.worldagroforestry.org/output/tree-diversity-analysis.

Klassen, R., Meinhardt, F. (2007). Linear protein-primed replicating plasmids in eukaryotic microbes. **Microbial Linear Plasmids** (pp. 187-226). Berlin, Heidelberg: Springer Berlin Heidelberg.

Klassen, R., Schaffrath, R., Buzzini, P., Ganter, P. F. (2017). Antagonistic interactions and killer yeasts. **Yeasts in natural ecosystems**: ecology, 229-275.

Klassen, R., Teichert, S., Meinhardt, F. (2004). Novel yeast killer toxins provoke S-phase arrest and DNA damage checkpoint activation. **Molecular microbiology**, 53(1), 263-273.

Koerte, S., Keesey, I. W., Easson, M. L., Gershenzon, J., Hansson, B. S., Knaden, M. (2020). Variable dependency on associated yeast communities influences host range in *Drosophila species*. **Oikos**, 129(7), 964-982.

Koltin, Y., Day, P. R. (1976). Suppression of the killer phenotype in *Ustilago maydis*. **Genetics**, 82(4), 629-637.

Kozlov, A. M., Darriba, D., Flouri, T., Morel, B., Stamatakis, A. (2019). RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. **Bioinformatics**, 35(21), 4453–4455.

Krassowski, T., et al. (2018). Evolutionary instability of CUG-Leu in the genetic code of budding yeasts. **Nature communications**, 9(1), 1887.

Kriventseva, E. V., Kuznetsov, D., Tegenfeldt, F., Manni, M., Dias, R., Simão, F. A., Zdobnov, E. M. (2019). OrthoDB v10: sampling the diversity of animal, plant, fungal, protist, bacterial and viral genomes for evolutionary and functional annotations of orthologs. **Nucleic acids research**, 47(D1), D807-D811.

Kunishima, N., Kashiwagi, T., Suzuki, C., Nikkuni, S., Tsuchiya, F., Arata, Y., Morikawa, K. (1997). Crystallization and preliminary X-ray diffraction studies of a novel killer toxin from a halotolerant yeast *Pichia farinosa*. **Acta Crystallographica Section D: Biological Crystallography**, 53(1), 112-113.

Kurtzman, C. P. (2008). Cletus P. Kurtzman, Jack W. Fell, Teun Boekhout. **The Yeasts** (Fifth Edition), Elsevier, 2011, Chapter 42, p. 521-543.

Kurtzman, C. P. (2011a). *Lindnera* Kurtzman, Robnett Basehoar-Powers (2008). **The Yeasts** (pp. 521-543). Elsevier.

Kurtzman, C. P. (2011b). *Wickerhamomyces* Kurtzman, Robnett Basehoar-Powers (2008). **The Yeasts** (pp. 899-917). Elsevier.

Kurtzman, C. P., Robnett, C. J. (1998). Identification and phylogeny of ascomycetous yeasts from analysis of nuclear large subunit (26S) ribosomal DNA partial sequences. **Antonie van Leeuwenhoek**, 73(4), 331–371.

Kurtzman, C. P., Robnett, C. J. (2003). Phylogenetic relationships among yeasts of the '*Saccharomyces* complex'determined from multigene sequence analyses. **FEMS yeast research**, 3(4), 417-432.

Lacerda, L. T., Gusmão, L. F., Rodrigues, A. (2018). Diversity of endophytic fungi in *Eucalyptus microcorys* assessed by complementary isolation methods. **Mycological Progress**, *17*, 719–727.

Lachance, M. A., Daniel, H. M., Meyer, W., Prasad, G. S., Gautam, S. P., Boundy-Mills, K. (2003). The D1/D2 domain of the large-subunit rDNA of the yeast species *Clavispora lusitaniae* is unusually polymorphic. **FEMS yeast research**, 4(3), 253-258.

Lachance, M. A., Rosa, C. A., Starmer, W. T., Schlag-Edler, B. I. R. G. I. T., Barker, J. S. F., Bowles, J. M. (1998). *Wickerhamiella australiensis*, *Wickerhamiella cacticola*, *Wickerhamiella occidentalis*, *Candida drosophilae* and *Candida lipophila*, five new related yeast species from flowers and associated insects. **International Journal of Systematic and Evolutionary Microbiology**, 48(4), 1431–1443.

Lachance, M. A., Starmer, W. T., Rosa, C. A., Bowles, J. M., Barker, J. S. F., Janzen, D. H. (2001). Biogeography of the yeasts of ephemeral flowers and their insects. **FEMS yeast research**, 1(1), 1–8.

Laetsch, D. R., Blaxter, M. L. (2017). BlobTools: Interrogation of genome assemblies. **F1000Research**, 6(1287), 1287.

Leal, I. R., Oliveira, P. S. (1998). Interactions between Fungus-Growing Ants (Attini), Fruits and Seeds in Cerrado Vegetation in Southeast Brasil 1. **Biotropica**, 30(2), 170-178.

Leal, I. R., Wirth, R., Tabarelli, M. (2014). The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. **Biotropica**, 46(5), 516-528.

Leal-Dutra, C. A., Griffith, G. W., Neves, M. A., McLaughlin, D. J., McLaughlin, E. G., Clasen, L. A., Dentinger, B. (2020). Reclassification of *Pterulaceae* Corner (Basidiomycota: Agaricales) introducing the ant-associated genus *Myrmecopterula* gen. nov., *Phaeopterula* Henn. and the corticioid *Radulomycetaceae* fam. nov. **IMA fungus**, 11(1), 1-24.

Lee, Y. M., Lee, H., Heo, Y. M., Hong, J. H., Jang, S., Kang, K. Y., Kim, J. J. (2017). Phylogenetic analysis of wood-inhabiting molds and assessment of soft-rot wood deterioration. Part 5. Genus *Aureobasidium*. **Holzforschung**, 71(5), 437–443.

Legendre, P., Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. **Oecologia**, 129(2), 271–280.

Li, H. (2018). Minimap2: pairwise alignment for nucleotide sequences. **Bioinformatics**, 34(18), 3094-3100.

Li, H., et al. (2009). The sequence alignment/map format and SAMtools. **Bioinformatics**, 25(16), 2078-2079.

Li, Y., Jiao, L., Yao, Y. J. (2013). Non-concerted ITS evolution in fungi, as revealed from the important medicinal fungus *Ophiocordyceps sinensis*. **Molecular Phylogenetics and Evolution**, 68(2), 373-379.

Liao, D. (1999). Concerted evolution: molecular mechanism and biological implications. **American Journal of Human Genetics**, 64(1), 24.

Liao, D., Pavelitz, T., Kidd, J. R., Kidd, K. K., Weiner, A. M. (1997). Concerted evolution of the tandemly repeated genes encoding human U2 snRNA (the RNU2 locus) involves rapid intrachromosomal homogenization and rare interchromosomal gene conversion. **The EMBO Journal**, 16(3), 588-598.

Libkind, D., Brizzio, S., Van Broock, M. (2004). *Rhodotorula mucilaginosa*, a carotenoid producing yeast strain from a Patagonian high-altitude lake. **Folia microbiologica**, 49, 19-25.

Ljunggren, J., et al. (2019). Yeast volatomes differentially affect larval feeding in an insect herbivore. **Applied and Environmental Microbiology**, 85(21), e01761-19.

Lomsadze, A., Ter-Hovhannisyan, V., Chernoff, Y. O., Borodovsky, M. (2005). Gene identification in novel eukaryotic genomes by self-training algorithm. **Nucleic acids research**, 33(20), 6494-6506.

Lou, Q. Z., Lu, M., Sun, J. H. (2014). Yeast diversity associated with invasive *Dendroctonus valens* killing *Pinus tabuliformis* in China using culturing and molecular methods. **Microbial ecology**, 68, 397-415.

Louis, V. L., et al. (2012). *Pichia sorbitophila*, an interspecies yeast hybrid, reveals early steps of genome resolution after polyploidization. **G3**, 2(2), 299-311.

Macedo, J. H. P. (1985). **Manual dos Scolytidae nos reflorestamentos brasileiros**. Curitiba: Universidade Federal do Paraná: GTZ, 69 p.

Macêdo, N. S., et al. (2020). *Caesalpinia ferrea* C. Mart.(Fabaceae) phytochemistry, ethnobotany, and bioactivities: a review. **Molecules**, 25(17), 3831.

Madbouly, A. K., Elyousr, K. A. A., Ismail, I. M. (2020). Biocontrol of *Monilinia fructigena*, causal agent of brown rot of apple fruit, by using endophytic yeasts. **Biological control**, 144, 104239.

Madden, A. A., Epps, M. J., Fukami, T., Irwin, R. E., Sheppard, J., Sorger, D. M., Dunn, R. R. (2018). The ecology of insect–yeast relationships and its relevance to human industry. **Proceedings of the Royal Society B: Biological Sciences**, 285(1875), 20172733.

Magliani, W., Conti, S., Gerloni, M., Bertolotti, D., Polonelli, L. (1997). Yeast killer systems. **Clinical microbiology reviews**, 10(3), 369-400.

Makower, M., Bevan, E. A. (1963). The inheritance of a killer character in yeast (*Saccharomyces cerevisiae*). **Proc Int Congr Genet XI**, v. 1, n. 202, 235-244.

Maksimova, I. A., Glushakova, A. M., Kachalkin, A. V., Chernov, I. Y., Panteleeva, S. N., Reznikova, Z. I. (2016). Yeast communities of Formica aquilonia colonies. **Microbiology**, 85, 124-129.

Markmann, M., Tautz, D. (2005). Reverse taxonomy: an approach towards determining the diversity of meiobenthic organisms based on ribosomal RNA signature sequences. **Philosophical Transactions of the Royal Society B: Biological Sciences**, 360(1462), 1917-1924.

Marquina, D., Santos, A., Peinado, J. (2002). Biology of killer yeasts. **International Microbiology**, 5(2), 65–71.

Martinac, B., Zhu, H., Kubalski, A., Zhou, X. L., Culbertson, M., Bussey, H., Kung, C. (1990). Yeast K1 killer toxin forms ion channels in sensitive yeast spheroplasts and in artificial liposomes. **Proceedings of the National Academy of Sciences**, 87(16), 6228-6232.

Martins M, Kluczkovski AM, Souza TP, Pacheco C, Savi GD, Scussel VM (2014). Inhibition of growth and aflatoxin production of *Aspergillus parasiticus* by guaraná (*Paullinia cupana* Kunth) and jucá (*Libidibia ferrea* Mart) extracts. **Afr. J. Biotech**. 13(1):131-137.

Martinson, V. G. (2020). Rediscovering a forgotten system of symbiosis: historical perspective and future potential. **Genes**, 11(9), 1063.

Mathews, D. H. (2006). RNA secondary structure analysis using RNAstructure. **Current protocols in bioinformatics**, 13(1), 12-16.

Mathews, D. H. (2014). Using the RNA structure software package to predict conserved RNA structures. **Current Protocols in Bioinformatics**, 46(1), 12-14.

McBride, R., Greig, D., Travisano, M. (2008). Fungal viral mutualism moderated by ploidy. **Evolution**, 62(9), 2372-2380.

Melo, W. G. P., de Oliveira, T. B., Arcuri, S. L., de Morais, P. B., Pagnocca, F. C. (2021). Yeasts in the nests of the leaf-cutter ant *Acromyrmex balzani* in a Savanna biome: exploitation of community and metabolic diversity. **Antonie van Leeuwenhoek**, 114(6), 751–764.

Mendes, T. D., Rodrigues, A., Dayo-Owoyemi, I., Marson, F. A., Pagnocca, F. C. (2012). Generation of nutrients and detoxification: possible roles of yeasts in leaf-cutting ant nests. **Insects**, 3(1), 228–245.

Mestre, M. C., Rosa, C. A., Fontenla, S. B. (2011). *Lindnera rhizosphaerae* sp. nov., a yeast species isolated from rhizospheric soil. **International journal of systematic and evolutionary microbiology**, 61(4), 985-988.

Meyer, S. T., Leal, I. R., Tabarelli, M., Wirth, R. (2011). Ecosystem engineering by leaf-cutting ants: nests of *Atta cephalotes* drastically alter forest structure and microclimate. **Ecological entomology**, 36(1), 14-24.

Meyer, W., Mitchell, T. G., Freedman, E. Z., Vilgalys, R. (1993). Hybridization probes for conventional DNA fingerprinting used as single primers in the polymerase chain reaction to distinguish strains of *Cryptococcus neoformans*. **Journal of Clinical Microbiology**, 31(9), 2274–2280.

Miller, M.A., Pfeiffer, W., Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. **Proceedings of the Gateway Computing Environments Workshop (GCE)**, 14 Nov. 2010, New Orleans, LA pp 1–8.

Möller, A. (1893). **Die Pilzgärten einiger südamerikanischer Ameisen** (No. 6). G. Fischer.

Morales, L., Dujon, B. (2012). Evolutionary role of interspecies hybridization and genetic exchanges in yeasts. **Microbiology and Molecular Biology Reviews**, 76(4), 721-739.

Mueller, U. G., Rabeling, C. (2008). A breakthrough innovation in animal evolution. **Proceedings of the National Academy of Sciences of The United States of America**, 105(14), 5287–5288.

Mullineux, T., Hausner, G. (2009). Evolution of rDNA ITS1 and ITS2 sequences and RNA secondary structures within members of the fungal genera *Grosmannia* and *Leptographium*. **Fungal Genetics and Biology**, 46(11), 855-867.

Mylvaganam, S., Dennis, P. P. (1992). Sequence heterogeneity between the two genes encoding 16S rRNA from the halophilic archaebacterium *Haloarcula marismortui*. **Genetics**, 130(3), 399-410.

Nakamura, E. S., et al. (2002). Cancer chemopreventive effects of a Brasilian folk medicine, Juca, on in vivo two-stage skin carcinogenesis. **Journal of Ethnopharmacology**, 81(1), 135-137.

Naumov, G. I., IuV, I., Naumova, E. S. (2005). Molecular polymorphism of viral dsRNA of yeast *Saccharomyces paradoxus*. **Molekuliarnaia Genetika, Mikrobiologiia i Virusologiia**, (1), 38-40.

Naumov, G. I., Ivannikova, Y. V., Chernov, I. Y., Naumova, E. S. (2009). Natural polymorphism of the plasmid double-stranded RNA of the *Saccharomyces* yeasts. **Microbiology**, 78, 208-213.

Nei, M., Rooney, A. P. (2005). Concerted and birth-and-death evolution of multigene families. **Annual Review of Genetics**, 39, 121.

Nguyen, L. T., Schmidt, H. A., Von Haeseler, A., Minh, B. Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. **Molecular Biology and Evolution**, 32(1), 268-274.

Nguyen, N. H., Suh, S. O., Blackwell, M. (2007). Five novel *Candida* species in insect-associated yeast clades isolated from Neuroptera and other insects. **Mycologia**, 99(6), 842–858.

Nguyen, N. H., Suh, S. O., Erbil, C. K., Blackwell, M. (2006). *Metschnikowia noctiluminum* sp. nov., *Metschnikowia corniflorae* sp. nov., and *Candida chrysomelidarum* sp. nov., isolated from green lacewings and beetles. **Mycological research**, 110(3), 346-356.

Nomoto, H., Kitano, K., Shimazaki, T., Kodama, K., Hara, S. (1984). Distribution of killer yeasts in the genus *Hansenula*. **Agricultural and biological chemistry**, 48(3), 807-809.

Nundaeng, S., Suwannarach, N., Limtong, S., Khuna, S., Kumla, J., Lumyong, S. (2021). An updated global species diversity and phylogeny in the genus *Wickerhamomyces* with addition of two new species from thailand. **Journal of Fungi**, 7(11), 957.

Nygaard, S., et al. (2016). Reciprocal genomic evolution in the ant–fungus agricultural symbiosis. **Nature Communications**, 7(1), 12233.

O'Donnell, K., Cigelnik, E., Nirenberg, H. I. (1998). Molecular systematics and phylogeography of the *Gibberella fujikuroi* species complex. **Mycologia**, 90(3), 465-493.

Okada, R., Kiyota, E., Moriyama, H., Fukuhara, T., Natsuaki, T. (2015). A simple and rapid method to purify viral dsRNA from plant and fungal tissue. **Journal of General Plant Pathology**, 81, 103-107.

Oksanen, J. F., et al. (2020). vegan: Community Ecology Package. **R package version 2.5-7**. https://CRAN.R-project.org/package=vegan.

Oliveira, F.G., Fernando, E.M.P. ***Libidibia*** **in Flora e Funga do Brasil.** Jardim Botânico do Rio de Janeiro. Disponível online: https://floradobrasil.jbrj.gov.br/FB109828

Pagnocca, F. C., Carreiro, S. C., Bueno, O. C., Hebling, M. J., Da Silva, O. A. (1996). Microbiological changes in the nests of leaf-cutting ants fed on sesame leaves. **Journal of Applied Entomology**, 120(1-5), 317–320.

Pagnocca, F. C., Rodrigues, A., Nagamoto, N. S., Bacci, M. (2008). Yeasts and filamentous fungi carried by the gynes of leaf-cutting ants. **Antonie van Leeuwenhoek**, 94(4), 517–526.

Perez, M. F., Contreras, L., Garnica, N. M., Fernández-Zenoff, M. V., Farías, M. E., Sepulveda, M., Ramallo, J., Dib, J. R. (2016). Native killer yeasts as biocontrol agents of postharvest fungal diseases in lemons. **PloS One**, 11(10), e0165590.

Pfeiffer, I., Golubev, W. I., Farkas, Z., Kucsera, J., Golubev, N. (2004). Mycocin production in *Cryptococcus aquaticus*. **Antonie Van Leeuwenhoek**, 86, 369-375.

Phillisкirk, G., Young, T. W. (1975). The occurrence of killer character in yeasts of various genera. **Antonie van Leeuwenhoek**, 41, 147-151.

Pieczynska, M. D., de Visser, J. A. G., Korona, R. (2013). Incidence of symbiotic dsRNA 'killer' viruses in wild and domesticated yeast. **FEMS Yeast Research**, 13(8), 856–859.

Pieczynska, M. D., Wloch-Salamon, D., Korona, R., de Visser, J. A. G. (2016). Rapid multiple-level coevolution in experimental populations of yeast killer and nonkiller strains. **Evolution**, 70(6), 1342-1353.

Pintar, J., Starmer, W. T. (2003). The costs and benefits of killer toxin production by the yeast *Pichia kluyveri*. **Antonie van Leeuwenhoek**, 83, 89-97.

Polonelli, L., Conti, S., Gerloni, M., Magliani, W., Castagnola, M., Morace, G., Chezzi, C. (1991). 'Antibiobodies': antibiotic-like anti-idiotypic antibodies. Journal of medical and veterinary mycology, 29(4), 235-242.

Polonelli, L., Morace, G. (1986). Reevaluation of the yeast killer phenomenon. **Journal of Clinical Microbiology**, 24(5), 866–869.

R Core Team. (2021). R: A Language and Environment for Statistical Computing.; **R Foundation for Statistical Computing: Vienna, Austria**; Available online: https://www.R-project.org/ (accessed on 20 December 2021).

Rafferty, N. E., CaraDonna, P. J., Bronstein, J. L. (2015). Phenological shifts and the fate of mutualisms. **Oikos**, 124(1), 14-21.

Rambaut, A., 2016. **Figtree v. 1.4.3**. http://tree.bio.ed.ac.uk/software/figtree/2016.

Ramirez, M., Lopez-Pineiro, A., Velazquez, R., Munoz, A., Regodon, J. A. (2020a). Analysing the vineyard soil as a natural reservoir for wine yeasts. **Food Research International**, 129, 108845.

Ramírez, M., Velázquez, R., Maqueda, M., López-Piñeiro, A., Ribas, J. C. (2015). A new wine Torulaspora delbrueckii killer strain with broad antifungal activity and its toxin-encoding double-stranded RNA virus. **Frontiers in microbiology**, 6, 983.

Ramírez, M., Velázquez, R., Maqueda, M., Martínez, A. (2020b). Genome organization of a new double-stranded RNA LA helper virus from wine *Torulaspora delbrueckii* killer yeast as compared with its *Saccharomyces* counterparts. **Frontiers in Microbiology**, 11, 593846.

Reuter, M., Bell, G., Greig, D. (2007). Increased outbreeding in yeast in response to dispersal by an insect vector. **Current Biology**, 17(3), R81-R83.

Rivera, F. N., Gonzalez, E., Gomez, Z., Lopez, N., Hernandez-Rodriguez, C., Berkov, A., Zuniga, G. (2009). Gut-associated yeast in bark beetles of the genus *Dendroctonus* Erichson (Coleoptera: Curculionidae: Scolytinae). **Biological Journal of the Linnean Society**, 98(2), 325-342.

Roberts, D. W. (2019). labdsv: Ordination and Multivariate Analysis for Ecology. **R package version 2.0-1.** https://CRAN.R-project.org/package=labdsv.

Robledo-Leal, E., Elisondo-Zatuche, M., Treviño-Rangel, R. J., González, G. M., Hernández-Luna, C. (2016). Isolation of killer yeasts from ants of the genus *Atta* and their effect on the red tomato's fungal pathogen *Geotrichum candidum*. **Mexican Journal of Phytopathology**, 34, 258–269.

Rodrigues, A., Bacci Jr, M., Mueller, U. G., Ortiz, A., Pagnocca, F. C. (2008). Microfungal "weeds" in the leafcutter ant symbiosis. **Microbial Ecology**, 56, 604-614.

Rodrigues, A., Cable, R. N., Mueller, U. G., Bacci, M., Pagnocca, F. C. (2009). Antagonistic interactions between garden yeasts and microfungal garden pathogens of leaf-cutting ants. **Antonie van Leeuwenhoek**, 96(3), 331–342.

Rodrigues, A., Mueller, U. G., Ishak, H. D., Bacci Jr, M., Pagnocca, F. C. (2011). Ecology of microfungal communities in gardens of fungus-growing ants (Hymenoptera: Formicidae): a year-long survey of three species of attine ants in Central Texas. **FEMS Microbiology Ecology**, 78(2), 244-255.

Rodríguez-Cousiño, N., Gómez, P., Esteban, R. (2017). Variation and distribution of LA helper totiviruses in *Saccharomyces* sensu stricto yeasts producing different killer toxins. **Toxins**, 9(10), 313.

Ronque, M. U. V., Feitosa, R. M., Oliveira, P. S. (2019). Natural history and ecology of fungus-farming ants: a field study in Atlantic rainforest. **Insectes Sociaux**, 66(3), 375–387.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, S.A., Huelsenbeck, J.P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. **Systematic biology**, 61(3), 539–542.

Rooney, A. P. (2004). Mechanisms underlying the evolution and maintenance of functionally heterogeneous 18S rRNA genes in apicomplexans. **Molecular Biology and Evolution**, 21(9), 1704-1711.

Rooney, A. P., Ward, T. J. (2005). Evolution of a large ribosomal RNA multigene family in filamentous fungi: birth and death of a concerted evolution paradigm. **Proceedings of the National Academy of Sciences USA**, 102(14), 5084-5089.

Roscini, L., et al. (2018). Early ongoing speciation of *Ogataea uvarum* sp. nov. within the grape ecosystem revealed by the internal variability among the rDNA operon repeats. **Frontiers in Microbiology**, 9, 1687.

Rowley, P. A. (2017). The frenemies within: viruses, retrotransposons and plasmids that naturally infect *Saccharomyces* yeasts. **Yeast**, 34(7), 279-292.

RStudio Team. (2021). RStudio: Integrated Development Environment for R.; **RStudio**, PBC: Boston, MA, USA; http://www.rstudio.com/.

Sampaio, J. P., Gadanho, M., Santos, S., Duarte, F. L., Pais, C., Fonseca, A., Fell, J. W. (2001). Polyphasic taxonomy of the basidiomycetous yeast genus *Rhodosporidium*: *Rhodosporidium kratochvilovae* and related anamorphic species. **International Journal of Systematic and Evolutionary Microbiology**, 51(2), 687–697.

Sanglard, D., Ischer, F., Calabrese, D., de Micheli, M., Bille, J. (1998). Multiple resistance mechanisms to azole antifungals in yeast clinical isolates. **Drug Resistance Updates**, 1(4), 255-265.

Santos, A. R. D. O., Lee, D. K., Ferreira, A. G., do Carmo, M. C., Rondelli, V. M., Barros, K. O., Hsiang, T., Rosa, C. A., Lachance, M. A. (2020). The yeast community of *Conotelus* sp. (Coleoptera: Nitidulidae) in Brasilian passionfruit flowers (*Passiflora edulis*) and description of *Metschnikowia amazonensis* sp. nov., a large-spored clade yeast. **Yeast**, 37(3), 253–260.

Schaffrath, R., Meinhardt, F., Klassen, R. (2018). Yeast killer toxins: Fundamentals and applications. **Physiology and Genetics: Selected Basic and Applied Aspects**, 87-118.

Scheidler, N. H., Liu, C., Hamby, K. A., Zalom, F. G., Syed, Z. (2015). Volatile codes: correlation of olfactory signals and reception in *Drosophila*-yeast chemical communication. **Scientific reports**, 5(1), 14059.

Schmitt, M. J., Breinig, F. (2006). Yeast viral killer toxins: lethality and self-protection. **Nature Reviews Microbiology**, 4(3), 212–221.

Schmitt, M. J., Klavehn, P., Wang, J., Schönig, I., Tipper, D. J. (1996). Cell cycle studies on the mode of action of yeast K28 killer toxin. **Microbiology**, 142(9), 2655–2662.

Schmitt, M. J., Neuhausen, F. (1994). Killer toxin-secreting double-stranded RNA mycoviruses in the yeasts *Hanseniaspora uvarum* and *Zygosaccharomyces bailii*. **Journal of virology**, 68(3), 1765-1772.

Schmitt, M. J., Reiter, J. (2008). Viral induced yeast apoptosis. **Biochimica et Biophysica Acta (BBA)-Molecular Cell Research**, 1783(7), 1413–1417.

Schmitt, M., Brendel, M., Schwarz, R., Radler, F. (1989). Inhibition of DNA synthesis in *Saccharomyces cerevisiae* by yeast killer toxin KT28. **Microbiology**, 135(6), 1529–1535.

Schmitt, R. J., Holbrook, S. J. (2003). Mutualism can mediate competition and promote coexistence. **Ecology Letters**, 6(10), 898-902.

Schneider, C. A., Rasband, W. S., Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. **Nature methods**, 9(7), 671-675.

Schoch, C. L., et al. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. **Proceedings of the National Academy of Sciences**, 109(16), 6241-6246.

Schultz, T. R., Brady, S. G. (2008). Major evolutionary transitions in ant agriculture. **Proceedings of the National Academy of Sciences**, 105(14), 5435–5440.

Schultz, T. R., Sosa-Calvo, J., Brady, S. G., Lopes, C. T., Mueller, U. G., Bacci Jr, M., Vasconcelos, H. L. (2015). The most relictual fungus-farming ant species cultivates the most recently evolved and highly domesticated fungal symbiont species. **The American Naturalist**, 185(5), 693–703.

Seike, T., Sakata, N., Matsuda, F., Furusawa, C. (2021). Elevated sporulation efficiency in fission yeast *Schizosaccharomyces japonicus* strains isolated from *Drosophila*. **Journal of Fungi**, 7, 350.

Sena, L. M., Morais, C. G., Lopes, M. R., Santos, R. O., Uetanabaro, A., Morais, P. B., Vital, M. J. S., Morais, M. A. Jr., Lachance, M. A., Rosa, C. A. (2017). d-Xylose fermentation, xylitol production and xylanase activities by seven new species of *Sugiyamaella*. **Antonie van Leeuwenhoek**, 110(1), 53–67.

Seppey, M., Manni, M., Zdobnov, E. M. (2019). BUSCO: assessing genome assembly and annotation completeness. **Gene prediction: methods and protocols**, 227-245.

Shen, S. K., Dowd, P. F. (1989). Xenobiotic induction of esterases in cultures of the yeast-like symbiont from the cigarette beetle. **Entomologia experimentalis et applicata**, 52(2), 179-184.

Shen, S. K., Dowd, P. F. (1991). Detoxification spectrum of the cigarette beetle symbiont *Symbiotaphrina kochii* in culture. **Entomologia Experimentalis et Applicata**, 60(1), 51-59.

Shi, C. F., Zhang, K. H., Chai, C. Y., Yan, Z. L., Hui, F. L. (2021). Diversity of the genus *Sugiyamaella* and description of two new species from rotting wood in China. **MycoKeys**, 77, 27.

Silva, A., Bacci Jr, M., de Siqueira, C. G., Bueno, O. C., Pagnocca, F. C., Hebling, M. J. A. (2003). Survival of *Atta sexdens* workers on different food sources. **Journal of Insect Physiology**, 49(4), 307-313.

Silva, A., Bacci Jr, M., Pagnocca, F. C., Bueno, O. C., Hebling, M. J. A. (2006). Starch metabolism in *Leucoagaricus gongylophorus*, the symbiotic fungus of leaf-cutting ants. **Microbiological research**, 161(4), 299-303.

Simon, U. K., Weiß, M. (2008). Intragenomic variation of fungal ribosomal genes is higher than previously thought. **Molecular Biology and Evolution**, 25(11), 2251-2254.

Sipiczki, M. (2020). *Metschnikowia pulcherrima* and related pulcherrimin-producing yeasts: Fuzzy species boundaries and complex antimicrobial antagonism. **Microorganisms**, 8(7), 1029.

Sipiczki, M., Horvath, E., Pfliegler, W. P. (2018). Birth-and-death evolution and reticulation of ITS segments of *Metschnikowia andauensis* and *Metschnikowia fructicola* rDNA repeats. **Frontiers in Microbiology**, 9, 1193.

Sipiczki, M., Pfliegler, W. P., Holb, I. J. (2013). *Metschnikowia* species share a pool of diverse rRNA genes differing in regions that determine hairpin-loop structures and evolve by reticulation. **PloS One**, 8(6), e67384.

Smith, G. P. (1976). Evolution of repeated DNA sequences by unequal crossover: DNA whose sequence is not maintained by selection will develop periodicities as a result of random crossover. **Science**, 191(4227), 528-535.

Soares, M. R. P. S., Caneschi, C. A., Chaves, M. D. G. A. M., Mota, M., Stroppa, P. H. F., Barbosa, W., Raposo, N. R. B. (2018a). In vitro antifungal activity and cytotoxicity screening of dry crude extracts from Brasilian Amazonia plants. **African Journal of Traditional, Complementary and Alternative Medicines**, 15(4), 13-21.

Soares, M. R., et al. Raposo, N. R. (2018b). Biosynthesis of silver nanoparticles using *Caesalpinia ferrea* (Tul.) Martius extract: physicochemical characterization, antifungal activity and cytotoxicity. **PeerJ**, 6, e4361.

Somers, J. M., Bevan, E. A. (1969). The inheritance of the killer character in yeast. **Genetics Research**, 13(1), 71-83.

Soto-Robles, L. V., Torres-Banda, V., Rivera-Orduña, F. N., Curiel-Quesada, E., Hidalgo-Lara, M. E., Zúñiga, G. (2019). An overview of genes from *Cyberlindnera americana*, a symbiont yeast isolated from the gut of the bark beetle *Dendroctonus rhizophagus* (Curculionidae: Scolytinae), involved in the detoxification process using genome and transcriptome data. **Frontiers in Microbiology**, 10, 2180.

Spitaler, U., et al. (2020). Yeast species affects feeding and fitness of *Drosophila suzukii* adults. **Journal of Pest Science**, 93, 1295-1309.

Stanke, M., Morgenstern, B. (2005). AUGUSTUS: a web server for gene prediction in eukaryotes that allows user-defined constraints. **Nucleic acids research**, 33(suppl_2), W465-W467.

Starmer, W. T., Fogleman, J. C. (1986). Coadaptation of *Drosophila* and yeasts in their natural habitat. **Journal of Chemical Ecology**, 12, 1037-1055.

Starmer, W. T., Ganter, P. F., Aberdeen, V., Lachance, M. A., Phaff, H. J. (1987). The ecological role of killer yeasts in natural communities of yeasts. **Canadian journal of microbiology**, 33(9), 783-796.

Starmer, W. T., Lachance, M. A. (2011). Yeast ecology. **The yeasts**, 65-83.

Stefanini, I. (2018). Yeast-insect associations: It takes guts. **Yeast**, 35(4), 315–330.

Stefanini, I., Dapporto, L., Berná, L., Polsinelli, M., Turillazzi, S., Cavalieri, D. (2016). Social wasps are a *Saccharomyces* mating nest. **Proceedings of the National Academy of Sciences USA**, 113, 2247–2251.

Stefanini, I., et al. (2012). Role of social wasps in *Saccharomyces cerevisiae* ecology and evolution. **Proceedings of the National Academy of Sciences**, 109(33), 13398-13403.

Sternberg, L. D. S., Pinzon, M. C., Moreira, M. Z., Moutinho, P., Rojas, E. I., Herre, E. A. (2007). Plants use macronutrients accumulated in leaf-cutting ant nests. **Proceedings of the Royal Society B: Biological Sciences**, 274(1608), 315-321.

Stoeck, T., Przybos, E., Dunthorn, M. (2014). The D1/D2 region of the large subunit ribosomal DNA as barcode for ciliates. **Molecular Ecology Resources**, 14(3), 458-468.

Stopiglia, C. D. O., Heidrich, D., Sorrentino, J. M., Vieira, F. J., Landell, M. F., Valente, P., Scroferneker, M. L. (2014). Susceptibility of species within the *Sporothrix schenckii* complex to a panel of killer yeasts. **Journal of Basic Microbiology**, 54(6), 578-584.

Stöver, B. C., Müller, K. F. (2010). TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. **BMC bioinformatics**, 11(1), 1–9.

Stumm, C., Hermans, J. M. H., Middelbeek, E. J., Croes, A. F., De Vries, G. J. M. L. (1977). Killer-sensitive relationships in yeasts from natural habitats. **Antonie van Leeuwenhoek**, 43, 125-128.

Suesdek, L., Lima, F. C. T. (2011). Association of the borer *Spermophthorus apuleiae* (Coleoptera; Curculionidae; Scolytinae) with the" pau-ferro" tree *Caesalpinia ferrea* (Leguminosae). **Biota Neotropica**, 11, 21-23.

Suh, S. O., Blackwell, M. (2004). Three new beetle-associated yeast species in the *Pichia guilliermondii* clade. **FEMS Yeast Research**, 5(1), 87-95.

Suh, S. O., Blackwell, M. (2005). Four new yeasts in the *Candida mesenterica* clade associated with basidiocarp-feeding beetles. **Mycologia**, 97(1), 167-177.

Suh, S. O., McHugh, J. V., Pollock, D. D., Backwell, M. (2005). The beetle gut: a hyperdiverse source of novel yeasts. **Mycological Research**, 109(3), 261–265.

Suh, S. O., Nguyen, N. H., Blackwell, M. (2008). Yeasts isolated from plant-associated beetles and other insects: seven novel *Candida* species near *Candida albicans*. **FEMS yeast research**, 8(1), 88–102.

Toki, W. (2021). A single case study of mycetangia-associated fungi and their abilities to assimilate wood-associated carbon sources in the ship timber beetle *Elateroides flabellicornis* (Coleoptera: Lymexylidae) in Japan. **Symbiosis**, 83(2), 173-181.

Toki, W. (2023). Fungal community of mycetangia in the ship-timber beetle *Elateroides dermestoides* (Coleoptera: Lymexylidae) in Japan. **Symbiosis**, 1-7.

Toki, W., Tanahashi, M., Togashi, K., Fukatsu, T. (2012). Fungal farming in a non-social beetle. **PLoS ONE** 7(7), e41893.

Torto, B., et al. (2007). Composition of volatiles from fermenting pollen dough and attractiveness to the small hive beetle *Aethina tumida*, a parasite of the honeybee *Apis mellifera*. **Apidologie**, 38(4), 380-389.

Trindade, R. C., Resende, M. A., Silva, C. M., Rosa, C. A. (2002). Yeasts associated with fresh and frozen pulps of Brasilian tropical fruits. **Systematic and Applied Microbiology**, 25(2), 294-300.

Ueda, H., Tachibana, Y., Moriyasu, M., Kawanishi, K., Alves, S. M. (2001). Aldose reductase inhibitors from the fruits of *Caesalpinia ferrea* Mart. **Phytomedicine**, 8(5), 377-381.

Urbina, H., Schuster, J., Blackwell, M. (2013). The gut of Guatemalan passalid beetles: a habitat colonized by cellobiose-and xylose-fermenting yeasts. **Fungal ecology**, 6(5), 339–355.

Vadasz, A. S., Vadasz, P., Gupthar, A. S., Abashar, M. E. (2003). Theoretical and experimental evidence of extinction and coexistence of killer and sensitive strains of yeast grown as a mixed culture in water. **International journal of food microbiology**, 84(2), 157-174.

Valzano, M., et al. (2016). A yeast strain associated to *Anopheles* mosquitoes produces a toxin able to kill malaria parasites. **Malaria journal**, 15, 1-9.

Vaughan-Martini, A. (1995). *Saccharomyces barnetti* and *Saccharomyces spencerorum*: two new species of *Saccharomyces* sensu lato (van der Walt). **Antonie van Leeuwenhoek**, 68, 111-118.

Vega, F. E., Biedermann, P. H. (2020). On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses. **Fungal Ecology**, 44, 100909.

Vital, M. J. S., Abranches, J., Hagler, A. N., Mendonça-Hagler, L. C. (2002). Mycocinogenic yeasts isolated from Amazon soils of the Maracá ecological station, Roraima-Brasil. **Brasilian Journal of Microbiology**, 33, 230-235.

Vu, D., et al. (2016). DNA barcoding analysis of more than 9000 yeast isolates contributes to quantitative thresholds for yeast species and genera delimitation. **Studies in Mycology**, 85(1), 91-105.

Walker, G. M., Mcleod, A. H., Hodgson, V. J. (1995). Interactions between killer yeasts and pathogenic fungi. **FEMS microbiology letters**, 127(3), 213-222.

Wang, Y., Zhang, Z., Ramanan, N. (1997). The actinomycete *Thermobispora bispora* contains two distinct types of transcriptionally active 16S rRNA genes. **Journal of Bacteriology**, 179(10), 3270-3276.

Weber, N. A. (1972). The fungus-culturing behavior of ants. **American Zoologist**, 12(3), 577–587.

White, T. J., Bruns, T., Lee, S. J. W. T., Taylor, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. **PCR protocols: a guide to methods and applications**, 18(1), 315-322.

Wickham, H. **Ggplot2: Elegant Graphics for Data Analysis**; Springer: New York, NY, USA, 2016; ISBN 978-3-319-24277-4. https://ggplot2.tidyverse.org.

Witzgall, P., et al. (2012). "This is not an apple"–yeast mutualism in codling moth. **Journal of chemical ecology**, 38, 949-957.

Wloch-Salamon, D. M., Gerla, D., Hoekstra, R. F., de Visser, J. A. G. (2008). Effect of dispersal and nutrient availability on the competitive ability of toxin-producing yeast. **Proceedings of the Royal Society B: Biological Sciences**, 275(1634), 535-541.

Wójcik, M., Kordowska-Wiater, M. (2015). The occurrence of killer activity in yeasts isolated from natural habitats. **Acta Biochimica Polonica**, 62(4).

Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. **Great Basin Nat. Mem**. 6: 1-1356.

Woods, D. R., Bevan, E. A. (1968). Studies on the nature of the killer factor produced by *Saccharomyces cerevisiae*. **Microbiology**, 51(1), 115–126.

Wu, Z. W., Wang, Q. M., Liu, X. Z., Bai, F. Y. (2016). Intragenomic polymorphism and intergenomic recombination in the ribosomal RNA genes of strains belonging to a yeast species *Pichia membranifaciens*. **Mycology**, 7(3), 102-111.

Yamamoto, D., Toki, W. (2023). Presence of non-symbiotic yeasts in a symbiont-transferring organ of a stag beetle that lacks yeast symbionts found in other stag beetles. **Scientific Reports**, 13(1), 3726.

Yamamoto, T., Hiratani, T., Hirata, H., Imai, M., Yamaguchi, H. (1986). Killer toxin from *Hansenula mrakii* selectively inhibits cell wall synthesis in a sensitive yeast. **FEBS letters**, 197(1-2), 50-54.

Yurkov, A. M. (2018). Yeasts of the soil–obscure but precious. **Yeast**, 35(5), 369–378.

Zorg, J., Kilian, S., Radler, F. (1988). Killer toxin producing strains of the yeasts *Hanseniaspora uvarum* and *Pichia kluyveri*. **Archives of microbiology**, 149, 261-267.