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Article

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Overview of the global research on dung-inhabiting fungi: trends, gaps, and biases

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Abstract

Dung-inhabiting fungi are specialized to grow on dung. The coprophilous habit required these fungi to have physiological adaptations to survive on dung, so they developed a variety of metabolites to exploit the resource and tolerate intra and interspecific competition. These fungi are important cyclers of matter/energy in terrestrial ecosystems, but they are poorly studied. We analyzed the global scientific production involving these fungi, using a systematic review and scientometric methods. We found 661 publications, with temporal distribution showing a marked increase in publications from the 1970s onwards with the widespread of the moist chamber technique facilitating the studying these fungi. Twelve journals account 37% of publications, with Fungal Biology with most publications (33). A total of 15 countries from a total of 54 concentrate more than half (65%) of the publications, with the USA (79), United Kingdom (66), Brazil (36), and India (33) having the greatest production (≥ 30), but there are lots of unexplored geographic areas regarding this biodiversity, to which attention should be given. Most studies are divided between paleobiological or taxonomic/ecological approach, with the latter group being trend among studies produced in developing countries. Fifty-eight species were involved in studies on secondary metabolites or another biological processes, with *Podospora anserina* (syn. *Triangularia anserina* and *Thermochaetoides thermophila* (syn. *Chaetomium thermophilum*) being the most studied. We hope our data reinforce the need for new research/funding aimed this fungal group with the purpose of learning its potential and guaranteeing conservation and knowledge of their biodiversity through the valuation of the goods and services they can generate.

Keywords – biotechnology – coprophilous fungi – dung-inhabiting microorganisms – scientometrics – secondary metabolites

Introduction

Dung-inhabiting fungi comprise a vast set of coprophilic fungi (fungi with morphological, physiological and behavioral adaptations that allow their spores to be ingested by animals, defecated and develop on dung), or fimicolous fungi, which do not have these adaptations but are able to develop on this type of substrate, mainly as opportunists (Bell 1983, Doveri 2004, Calaça et

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al. 2017). There are representatives of the phyla *Basidiomycota*, *Mucoromycota* and *Ascomycota* among coprophilous fungi (*stricto sensu*), belonging to the Fungi Kingdom. Among fimicolous fungi (*lato sensu*), in addition to some not dung-adapted fungi, we also include some species of myxomycetes (*Amoebozoa*) and myxobacteria (*Proteobacteria*), commonly studied in mycology.

Fimicolous organisms have the ability to use dung as a substrate for growth and dispersion and can even live on other substrates, such as decomposing plant residues and soil, among others (Araújo et al. 2014). In fact, some myxomycetes species are only known from dung, such as *Kelleromyxa fimicola* (Dearn. & Bisby) Eliasson, and *Trichia fimicola* (Marchal) Ing (Doveri 2004, Calaça et al. 2020a).

Regardless of the coprophilous or fimicolous life style, dung-inhabiting fungi are important matter and energy cyclers, which is their most relevant ecosystem role. The energy egested in dung, meaning part of the energy not absorbed by the animals during digestion, is available to be cycled by these organisms, along with the bacteria, to be used at other trophic levels (i.e., in photosynthesis) (Ricklefs & Relyea 2018). Dung-inhabiting fungi are excellent sources of a wide range of secondary metabolites of relevant industrial interest, including those with antibiotic potential, enzymes that degrade plant residues, compounds of interest in medicine, among other resources with biotechnological potential (Bills et al. 2013, Sarrocco et al. 2014, Sarrocco 2016).

However, there are still large gaps in the knowledge of this neglected fungal group, either due to a lack of knowledge about the group or even due to the lack of interest of mycologists in studying this group of organisms, due to their coprophilous lifestyle. In this sense, a knowledge review about the biology and ecology of these fungi will point out trends and gaps that can guide future studies. Thus, herein we propose a systematic review and scientometric evaluation of research with these fungi at a global level, seeking to assess trends, gaps, biotechnological uses, and future directions in the scientific production on dung-inhabiting fungi (*stricto sensu*).

Materials & Methods

Data collection and processing

Data were collected from a search of global publications indexed in the Web of Science and Scopus databases during the period from 1901 (year of the oldest available publication) to 2020. Different combinations of terms and Boolean indexes were applied: coprophilous fung* OR dung fung* OR fimicolous fung* OR coprophil* fungi OR fimicol* fungi OR *dung fung*. The asterisk was used for the algorithm to include variations of terms during the search. The bibliometric information of the 2,811 documents retrieved in the searches were downloaded in bibtex (.bib) format and then we removed all duplicate records (596) using the bibliometrix package for the R environment (Aria & Cuccurullo 2017, R Core Team 2023). After removing the duplicate publications, a total of 2,215 records were retrieved, which were screened again to include only studies focused on fungi which inhabit dung (coprophilous and fimicolous). Thus, the final database consisted of 661 documents. This final database is publicly available as a supplementary material at Figshare® repository (https://doi.org/10.6084/m9.figshare.22300636.v2).

Statistical analyzes

The following bibliometric parameters were analyzed using the bibliometrix package for the R environment: keywords, journals where the documents were published, year of publication, authors, author's institution and country of affiliation, when available. We then performed a Pearson's correlation (r) ($P < 0.05$) between the total number of articles published for each year to determine the trend in the increase in the number of publications for each approach. We similarly verified the increase or decrease of citations of these publications over time. To avoid the effect of outliers on this correlation, we removed documents with more than 100 citations in these analyses, to balance the total of citations among all documents, whose average citations were equal to 11 per document. We subsequently performed a principal component analysis (PCA), using a correlation matrix with the 20 most used keywords (27.4% from a total of 73) per period using the PAST statistical environment v. 4.03, in order to verify the temporal variation of keywords which allows us to visualize trends and gaps in the research for a given period of time (Hammer et al. 2001). Keywords with similar meanings (e.g., *dung fungi* and *coprophilous fungi*) were combined to avoid bias. The other scientometric analyses were performed using the biblioAnalysis function of the bibliometrix package for the R environment (Aria & Cuccurullo 2017, R Core Team 2023).

Of the 661 studies found, 85 of them focused on prospecting bioactive compounds and/or applying these fungi in biotechnological processes. By using this 85-studies database, we constructed a second database to analyze all data on all cited dung-inhabiting species used on metabolites screening or other biotechnological applications. With the objective of compiling these records in a single source and facilitating access to information on the use of these fungi, aiming to direct future studies, we tabulated this information, extracting all the secondary metabolites or biotechnological processes mentioned. The species nomenclature was updated using the Mycobank database (https://www.mycobank.org/) or, when necessary, the most recent literature available. Finally, we built a distribution map of publications by country with the available country data using the ARCGIS software (v. 10.1) to better visualize the total number of studies for each nation.

Results

Scientific production on dung-inhabiting fungi

A total of 661 publications were obtained based on the established criteria (Supplementary Material). The oldest date from 1901 and 1902, entitled *Researches on coprophilous fungi*, parts I and II, respectively, published in the Annals of Botany (ISSN 1095-8290), by the eminent mycologists George Edward Massee (1850–1917) and Ernest Stanley Salmon (1871–1959) (Massee & Salmon 1901, 1902). There was a high growth of publications from the 1970s continuing until the present, with a new peak of production observed from 2010 (r = 0.63, P-value <0.001), with an annual growth rate (AGR) percentage of 3.70 (Fig. 1).

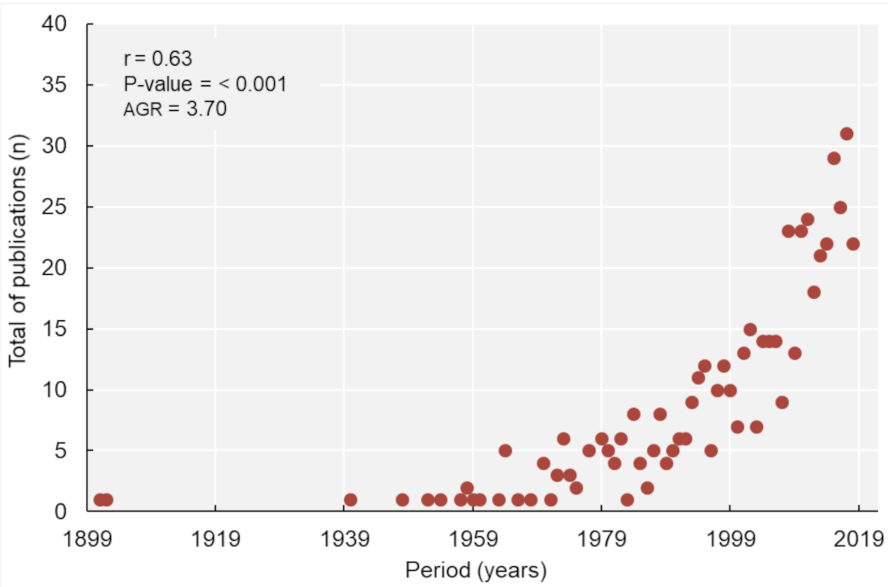

Fig. 1 – Temporal distribution of the number of articles on dung-inhabiting fungi. A greater number of publications is observed from the 1970s onwards. A new peak in productivity is observed from 2010 onwards. The annual growth rate (AGR) for the period evaluated is equivalent to 3.70.

This quantity of articles is distributed in 275 journals, with 12 journals concentrating 37% of the publications and having at least 10 articles published in each one. The Fungal Biology Journal (ISSN 1878-6146) has the largest number of publications (33), with different themes (Fig. 2a). The most cited work (312 citations; 17.3 citations/year) was the study by van Geel et al. (2003), published in the Journal of Archaeological Science (ISSN 0305-4403), which was followed by the study by Gill et al. (2009) (260 citations; 21.6 citations/year), published in the Science journal (ISSN 1095-9203); then the study by van Geel & Aptroot (2006) (251 citations; 16.7 citations/year), published in the Nova Hedwigia Journal (ISSN 0029-5035) and by Espagne et al. (2008) (191 citations; 14.6 citations/year), published in the Genome Biology Journal (ISSN 1474-760X). With the exception of the study by Espagne et al. (2008), which presents the genomic sequence of the fungus *Podospora anserina* (Rabenh.) Niessl, recently relocated to the new family *Podosporaceae* (Wang et al. 2019), the other three most cited studies address paleontological aspects of dung-inhabiting fungi (Table 1). Few works had more than 100 citations and most of these studies had more citations from the year 2000, a period in which there is also an increase in the number of publications. With few exceptions, the total number of citations was inversely proportional to the publication time, meaning the articles tended to have fewer citations as the time since publication increased (Fig. 2b).

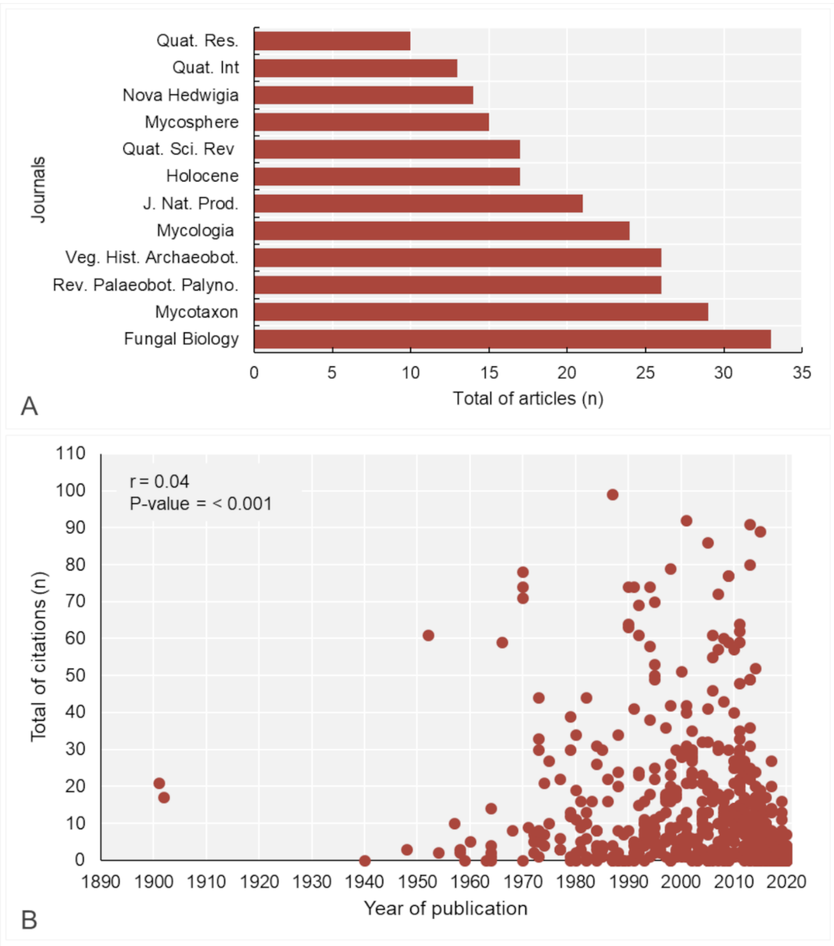

Fig. 2 – a Total publications on dung-inhabiting fungi between 1901 and 2020 for the 12 scientific journals that concentrated 10 or more publications. b Total citations per year.

Furthermore, 15 out of a total of 54 countries concentrate more than half (65%) of the productions. Africa has the fewest studies and consequently the greatest gaps in knowledge about these fungi (Fig. 3). The distribution of the number of articles produced per author, following the Lotka's Law (1926), showed that 1,438 of the 1,897 authors produced only one article, representing 75% of the total number of authors, while only one author, Professor Dr. James B. Gloer (University of Iowa) produced 33 publications, equivalent to 0.05% of publications, which shows the low number of studies dedicated exclusively to this group of organisms (Fig. 4).

Table 1 Most cited articles on dung-inhabiting fungi, listed by their total of citations in the studied period (1901 to 2020). DOI: digital object identifier; TC: total of citations; TC. year: mean of the total of citations by year.

Article	Approach	Journal	DOI	TC	TC. year
van Geel et al. (2003)	Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi	Journal of Archaeological Science	10.1016/S0305-4403(02)00265-0	312	17.33
Gill et al. (2009)	Pleistocene Megafaunal collapse, novel plant communities, and enhanced fire regimes in North America	Science	10.1126/Science.1179504	260	21.67
van Geel & Aptroot (2006)	Fossil ascomycetes in Quaternary deposits	Nova Hedwigia	10.1127/0029-5035/2006/0082-0313	251	16.73
Espagne et al. (2008)	The genome sequence of the model ascomycete fungus *Podospora anserina*	Genome Biology	10.1186/gb-2008-9-5-r77	191	14.69
Burney et al. (2003)	*Sporormiella* and the late Holocene extinctions in Madagascar	Proceedings of the National Academy of Sciences	10.1073/pnas.1534700100	143	7.94
Cugny et al. (2010)	Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity	Vegetation History and Archaeobotany	10.1007/S00334-010-0242-6	132	12
Davis & Shafer (2006)	*Sporormiella* fungal spores, a palynological means of detecting herbivore density	Palaeogeography, Palaeoclimatology, Palaeoecology	10.1016/J.Palaeo.2005.11.028	125	8.33
Whyte et al. (1996)	Cercophorins A-C: novel antifungal and cytotoxic metabolites from the coprophilous fungus *Cercophora areolata*	Journal of Natural Products	10.1021/np9603232	104	4.16
Davis (1987)	Spores of the dung fungus *Sporormiella*: abundance in historic sediments and before Pleistocene Megafaunal Extinction	Quaternary Research	10.1016/0033-5894(87)90067-6	99	2.91
Richardson (2001)	Diversity and occurrence of coprophilous fungi	Mycological Research	10.1017/S0953756201003884	99	4.38

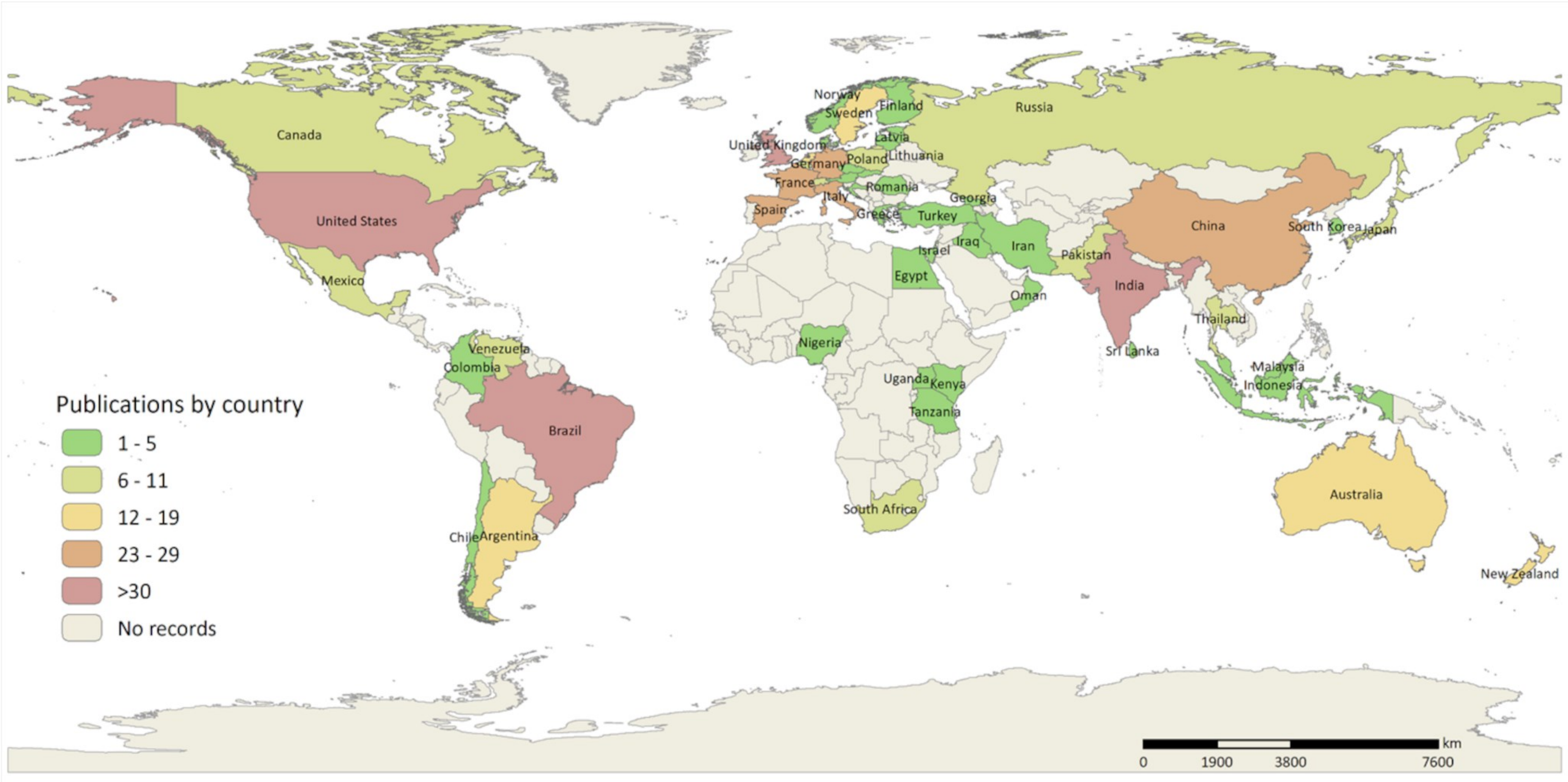

Fig. 3 – Global distribution of studies on dung-inhabiting fungi published between 1900 and 2020, based on the methods used herein.

Table 2 presents data about the top 10 most productive countries on dung-inhabiting fungi, where SCP is the abbreviation of a single country publications, MCP is a multiple country publication (a bibliometric analysis that identify and count scientific productions that were produced by authors from different countries), and MCP ratio is the MCP as a proportion of total number of publications, in percentage. The United States presented 79 productions, of which only 17 represent productions made in cooperation with other countries, which in turn shows a low collaboration network between countries, with a low MCP ratio (21.5%). The United Kingdom presented 66 productions, but only 10 are in cooperation with other countries, representing one of the lowest MCP ratios, ahead only of India and Italy (12.1 and 14.3% respectively). Brazil is the third country in terms of production with 36 articles, of which 14 had cooperation with other countries (MCP ratio = 38.9%). Germany and Netherlands were the countries with higher MCP ratio (58.3 and 57.9 respectively), that means most than half of its dung-inhabiting fungi production had international cooperation (Table 2). In terms of international cooperation among the most productive countries, Canada did not develop any studies with international collaboration.

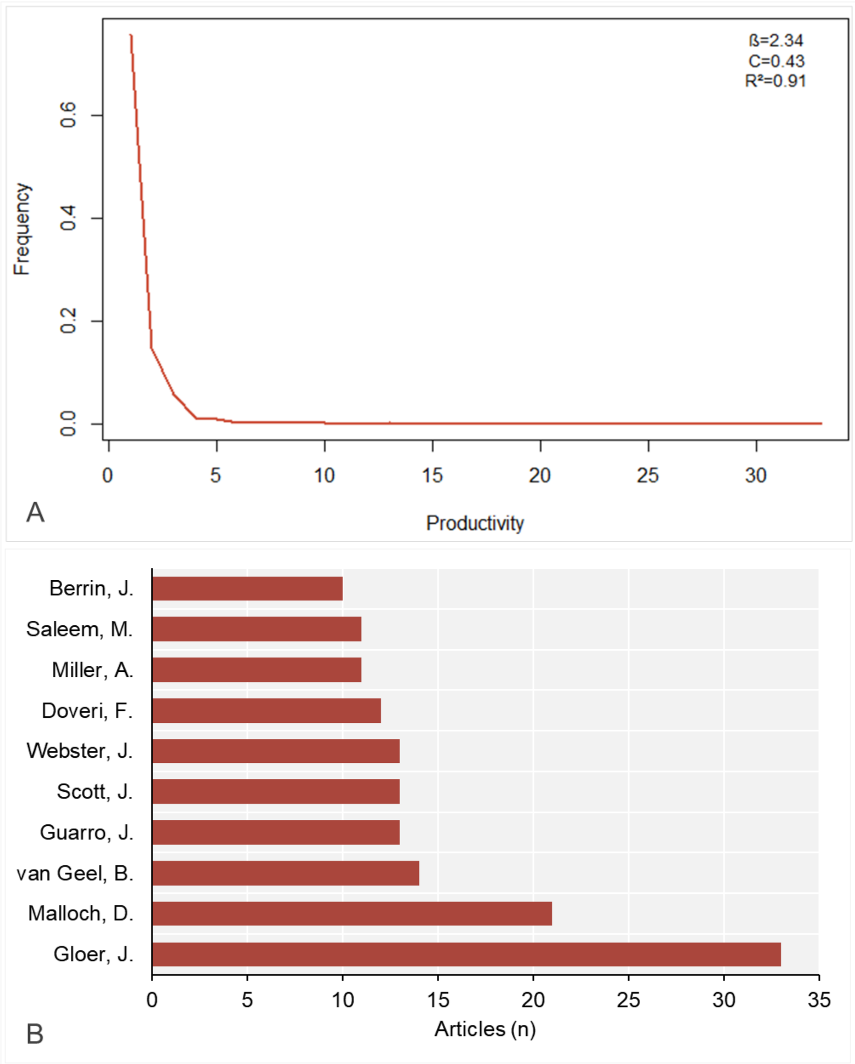

Fig. 4 – a Lotka coefficient for scientific productivity of authors on dung-inhabiting fungi. As expected by Lotka's law coefficient estimation, most authors have only one publication on dung-inhabiting fungi, which represents a frequency of 75% of authors for only one publication, while few researchers are authors in more than 10 publications. b Authors with more than 10 publications on dung-inhabiting fungi.

The principal component analysis (PCA) between the frequencies of use of keywords, showed that most of the studies retrieved can be divided into two large groups: studies with a *paleobiological approach* which involves the research of dung-inhabiting fungi in coprolites, and other paleontological proxies to determine different aspects of past fauna and landscapes; and studies with *taxonomic and ecological approaches*, which involve descriptions of species, their phylogenetic relationships and ecology. The other studies can be classified as generalist, addressing a mix of themes about the group, such as fungi in biological control, nematophagous fungi, fungal drugs, climate change, secondary metabolites, and cellulose degradation (Fig. 5). The use of these main keywords seems to remain stable among these groups over space and time, as they are concentrated in different years within the evaluated period.

Table 2 Countries with highest number of publications, according with the nationality of the corresponding authors, of articles on dung-inhabiting fungi worldwide and data on single/multiple countries publications, based on the methods used herein.

Country	Publications (n)	SCP	MCP	MCP ratio (%)
USA	79	62	17	21.5
United Kingdom	66	56	10	15.2
Brazil	36	22	14	38.9
India	33	29	4	12.1
France	29	20	9	31
Italy	28	24	4	14.3
Spain	27	20	7	25.9
Germany	24	10	14	58.3
China	23	19	4	17.4
Netherlands	19	8	11	57.9

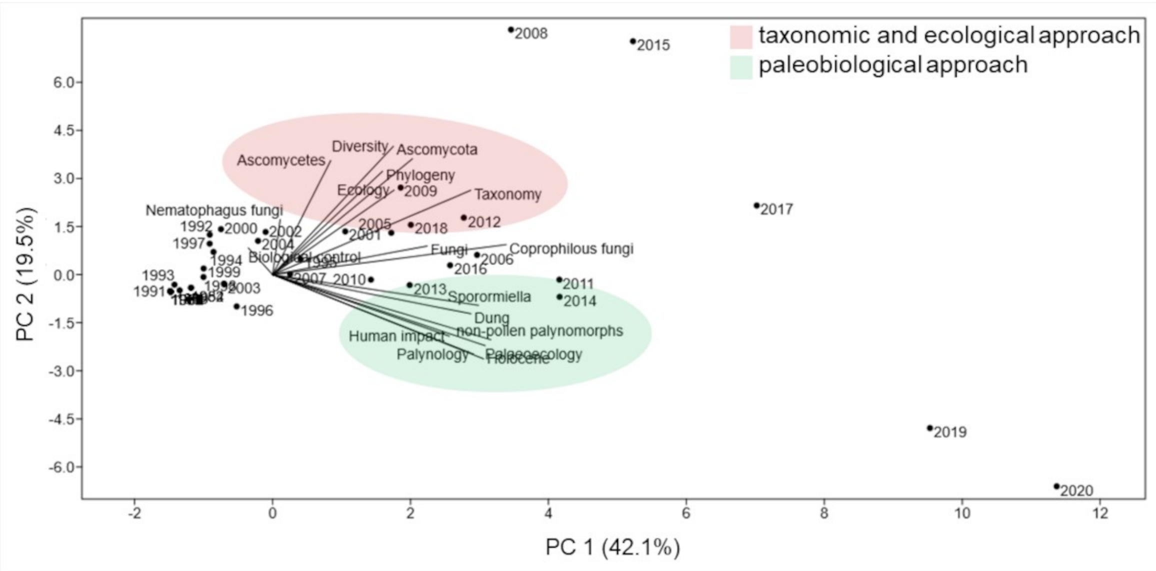

Fig. 5 – Temporal variation of keywords between studies on dung-inhabiting fungi based on principal component analysis (PCA) performed between the frequencies of use of the 20 most used keywords. The scatter plot shows how and how much these keywords contribute to the temporal variation in terms of variance retained in each principal component (PC), and showing how they are related to the years. The set shaded in pink (upper) indicates studies tending to the taxonomic and ecological approach, while the green set (lower) indicates studies tending to the paleobiological approach.

Dung-inhabiting fungi in secondary metabolites screening and other biotechnological processes

We found 85 articles addressing different aspects of secondary metabolites screening and other biotechnological processes involving species of dung-inhabiting fungi (Table 3, Supplementary Material). Eighty taxa were listed in these articles. Of this total, 58 were determined at species level while 22 represent unidentified and/or identified taxa only up to genus level. Of the 80 taxa evaluated, 82.5% belong to the phylum *Ascomycota*, 8.7% to *Basidiomycota*, 6.2% to *Mucoromycota*, and 2.5% were not identified in any higher taxon (Table 3). Most studies show the use of these species in the search for secondary metabolites, especially those with antimicrobial (i.e., antifungal, antibacterial) activities. Studies focused on the selection of enzyme complexes with potential for biodegradation, bioethanol production or enzymes with medicinal interest are also relevant. Thirty species were associated with antimicrobials production and/or antimicrobial activities, and 25 species were associated with enzymes production and/or enzymatic activities (Table 3). *Podospora anserina* (*Podosporaceae*) and *Thermochaetoides thermophila* (*Chaetomiaceae*) were the most frequent species in the publications (10 and 7 articles found, respectively), basically focusing on their enzymatic potential with enzymes involved in the cellulose/hemicellulose degradation process and glucose conversion.

Table 3 Secondary metabolites and/or biotechnological processes of dung-inhabiting fungi covered in the selected literature, according to our methodology. The nomenclature was updated according to the Mycobank database (https://www.mycobank.org), scientific names authorities were removed to table brevity, authorities can be consulted at Mycobank.

Taxon	Secondary metabolites and/or biotechnological processes mentioned	Reference
Apiotrichum scarabaeorum	bioethanol production	Makhuvele et al. (2017)
Apiospora montagnei	apiosporamide (4-hydroxy-2-pyridone alkaloid)	Alfatafta et al. (1994)
Ascobolaceae sp.	cellulolytic activity	Levin et al. (1996)
Ascobolus gamundiae	xylanase and cellulase	Sivori et al. (1996)
Ascobolus saccoboloides	cellulase complex	Magnelli & Forchiassin (1999)
Ascodesmis sphaerospora	arugosin F (antifungal and antibacterial)	Hein et al. (1998)
Ascobolus stercorarius	glycogen	Groisman et al. (1981)
Aspergillus flavus	undefined antibiotics	Kumar et al. (2010)
Aspergillus fumigatus	undefined antibiotics	Kumar et al. (2010)
Aspergillus niger	undefined antibiotics	Kumar et al. (2010)
Aspergillus versicolor	undefined antibiotics	Kumar et al. (2010)
Aspergillus sp.	polyethylene terephthalate polystyrene foam degradation	Umamaheswari et al. (2014)
Aureobasidium sp.	bioethanol production	Makhuvele et al. (2017)
Bombardioidea anartia	bombardolides (γ-lactones)	Hein et al. (2001)
Byssochlamys sp.	degradation of lignocellulose, fibrolytic and lipid accumulating activities	Liu et al. (2014)
Candida spp.	bioethanol production	Makhuvele et al. (2017)
Cephalotrichum stemonitis	extracellular hydrolases	Peterson et al. (2010)
	plant cell wall degrading enzymes	Peterson et al. (2011)
Cercophora areolata	cercophorins A–C (isocoumarin derivatives)	Whyte et al. (1996)
Cercophora sordarioides	1-dehydroxyarthrinone	Whyte et al. (1997)
	Cerdarin (anti-*Candida* activity)	
	arthrinone	
	3a,9a-deoxy-3a-hydroxy-1-dehydroxyarthrinone	
Circinella sp.	degradation of lignocellulose, fibrolytic and lipid accumulating activities	Liu et al. (2014)
Cladosporium sp.	degradation of lignocellulose, fibrolytic and lipid accumulating activities	Liu et al. (2014)
Cleistothelebolus nipigonensis	n-hexane extract and dichloromethane extract	Sarrocco et al. (2014)
	fusaproliferin and terpestacin	Cimmino et al. (2016)

Table 3 Continued.

Taxon	Secondary metabolites and/or biotechnological processes mentioned	Reference
Coelomycetes (unidentified)	preussomerins and deoxypreussomerins	Singh et al. (1994)
Coniochaeta saccardoi	coniochaetones A–B	Wang et al. (1995b)
Coprinellus radians	peroxidase and laccase activities	Anh et al. (2007)
Coprinopsis cinerea	lactonases	Stöckli et al. (2017)
	laccases	Rühl et al. (2013)
Coprinopsis verticillata	peroxidase and laccase activities	Anh et al. (2007)
Cryptococcus spp.	bioethanol production	Makhuvele et al. (2017)
Curvularia sp.	undefined antibiotics	Kumar et al. (2010)
Cutaneotrichosporon jirovecii	bioethanol production	Makhuvele et al. (2017)
Cylindrocladiella peruviana	hydrolases	Peterson et al. (2010)
Deconica coprophila	tryptophan biotransformation	Alarcón et al. (2014)
Delitschia confertaspora	benzophenone derivatives	Jayanetti et al. (2015)
	delicoferones A–B and fimetarone	Jayanetti et al. (2017)
Fusarium oxysporum	hydrolases	Peterson et al. (2010)
Fusarium sp.	polyethylene terephthalate polystyrene foam degradation	Umamaheswari et al. (2014)
Gelasinospora spp.	antagonistic effect against plant pathogenic fungi	Piasai & Sudsanguan (2018)
Guanomyces polythrix	naphthopyranone derivatives 1–5	Macías et al. (2000, 2001)
	rubrofusarin B	
	emodin	
	citrinin	
	4-hydroxybenzoic acid methyl ester	
Hypocopra rostrata	hypocoprins A–C	Jayanetti et al. (2015)
Lasiodiplodia theobromae	undefined antibiotics	Kumar et al. (2010)
Mariannaea camptospora	hydrolases	Peterson et al. (2010)
Mucor spp.	polygalacturonase, amylase, protease and lipase activities	Alves et al. (2002)
Neogymnomyces virgineus	n-hexane extract and dichloromethane extract	Sarrocco et al. (2014)
	fusaproliferin and terpestacin	Cimmino et al. (2016)
Neurospora cratophora	hydrolases	Peterson et al. (2010)
Nigrosabulum globosum	pseudodestruxins A–B	Che et al. (2001)
Onychophora coprophila	aphidicolin	Fisher et al. (1984)
Penicillium sp. 1	eremophilane-type, sporogen AO-1 and dihydrosporogen AO-1	Del Valle et al. (2015)
	isopetasol	
Penicillium sp. 2	polyethylene terephthalate polystyrene foam degradation	Umamaheswari et al. (2014)
Petriella sordida	petriellin A	Lee et al. (1995)

Table 3 Continued.

Taxon	Secondary metabolites and/or biotechnological processes mentioned	Reference
Phycomyces sp.	phenolic acid	Brucker & Drehmann (1958)
Pichia kudriavzevii	bioethanol production	Makhuvele et al. (2017)
Pichia methanolica	bioethanol production	Makhuvele et al. (2017)
Pilobolus sp.	oxylipins	Kock et al. (2001)
Pilobolus spp.	coprogen (ferric hydroxamate)	Hesseltine et al. (1952)
Pleosporaceae (unidentified)	pleosporin A (cyclodepsipeptide)	Isaka et al. (2014)
Podosordaria tulasnei	tulasnein and podospirone	Ridderbusch et al. (2004)
Podospora anserina	carbohydrate esterase (CE16), acetyl esterase	Puchart et al. (2015)
	anserinones A–B	Wang et al. (1997)
	cello-oligosaccharide oxidation	Bey et al. (2013)
	lytic polysaccharide monooxygenase	Fanuel et al. (2017)
	hemicellulases	Couturier et al. (2010)
	mannanases	Couturier et al. (2013)
	secretome (lignocellulose activity)	Poidevin et al. (2014)
	plant biomass hydrolysis	Katsimpouras et al. (2014)
	multicopper oxidase genes	Pöggeler (2011)
	endoglucanase	Poidevin et al. (2013)
	plant biomass hydrolysis	Mäkelä et al. (2017)
Podospora appendiculata	appenolides A–C	Wang et al. (1993)
Podospora australis	emestrins H–K epipolythiodioxopiperazines	Li et al. (2016)
Podospora communis	communiols A–D	Che et al. (2004)
	communiols E–H	Che et al. (2005)
	communiols A–C	Enomoto & Kuwahara (2008)
Polytolypa hystricis	polytolypin	Gamble et al. (1995)
Poronia gigantea	poronitins A–B	Isaka et al. (2012)
	(R)-5-methylmellein	
	isocoumarin	
Poronia punctata	punctatin A	Anderson et al. (1984a)
	punctatins B–C	Anderson et al. (1984b)
Preussia fleischhakii	2,3'-dihydroxy-4-methoxy-5',6-dimethyldiphenyl ether	Weber and Gloer (1988)
Preussia isomera	preussomerin A	Weber et al. (1990)
	preussomerines A–F	Weber & Gloer (1991)
Psilocybe cubensis	toxic for nauplii and adults of *Artemia franciscana* (Crustacea)	Vega-Villasante et al. (2013)
Rhypophila decipiens	podosporin A	Weber et al. (1988)

Table 3 Continued.

Taxon	Secondary metabolites and/or biotechnological processes mentioned	Reference
	decipinin A	Che et al. (2002)
	decipienolides A–B	
Rhypophila pleiospora	sordarin A–B	Weber et al. (2005)
	hydroxysordarin	
	sordaricin	
Rodentomyces reticulatus	n-hexane extract and dichloromethane extract	Sarrocco et al. (2014)
Sordaria fimicola	laccase	Ishfaq et al. (2017a)
	superoxide dismutase	Ishfaq et al. (2017b)
	glucose and sucrose metabolization	Rees et al. (1984)
Sordaria superba	hydrolases	Peterson et al. (2010)
Sporormiella similis	similins A–B	Weber et al. (1992)
Sporormiella teretispora	terezines A–D	Wang et al. (1995a)
	hyalopyrone	
Sporormiella vexans	sporovexins A–C	Soman et al. (1999)
	3′-O-desmethyl-1-epipreussomerin C	
Stilbella fimetaria	antiamoebins	Lehr et al. (2006)
	myrocin B	
Thermochaetoides thermophila	α-glucosidase	Giannesi et al. (2006)
	trehalase	Jepsen & Jensen (2004)
	β-glucosidase	Lusis et al. (1973)
	trehalase	Almeida et al. (1999)
	cellobiohydrolases I–II	Ganju et al. (1989)
	β-glucosidase	Venturi et al. (2002)
	cellulases	Ganju et al. (1990)
Trichoderma atroviride	hydrolases	Peterson et al. (2010)
Trichoderma reesei	hydrolases	Peterson et al. (2010)
Trichoderma sp.	bioethanol production	Stevenson & Weimer (2002)
unidentified	sonomolides A–B	Morris et al. (1995)
	coprophilin	Ondeyka et al. (1998)
	crude fiber degradation	Morinaga & Arimura 1984
	lignin and cellulose components modification	Wicklow et al. (1980)
	lignin decomposition	Gupta & Agrawal (1988)
unidentified (PM0651419)	metallic silver (Ag) nanoparticles	Rangarajan et al. (2018)

Discussion

Dung-inhabiting fungi make up an ecological group that has been still little studied considering their biological and ecological aspects compared to other fungal groups (Singh et al. 2019). The first studies observed according to the methodology adopted in this work date from 1901-2, which address aspects of the biology of this group (Massee & Salmon 1901, 1902). The use of the moist chamber, a technique consisting of creating a microcosm where the incubated substrate (i.e., the dung) is kept under moist conditions which favor the development of fungi, was a milestone in the study of these fungi, as it facilitated their development in the laboratory and allowed new approaches in research with them (Lundqvist 1972, Bell 1983). Although Massee & Salmon (1901) had already mentioned the use of similar artifacts to the moist chambers currently used to monitor the succession of fungi in dung, which contained small amounts of naphthalene to avoid the development of interspecific competitors in the substrate, the use of the moist chamber technique for inducing the development of fungi and other fungi-like microorganisms (i.e., myxomycetes) in the laboratory was only observed from the 1940s to the 1960s (Calaça et al. 2020a).

The 661 retrieved works were published in 275 journals (Fig. 2a); most of these studies are focused on taxonomic aspects, from the first works to the present day. Although the most recent studies on dung-inhabiting fungi are based on molecular biology, taxonomy still predominates in these studies, many of which describe new species for the group, expand its biogeography or present taxonomic revisions based on phylogeny (e.g., Wang et al. 2019, Ament-Velásquez et al. 2020, Lima et al. 2020, Richardson 2020).

Hawksworth & Lücking (2017) pointed out characteristics that should be observed in fungal groups to predict and direct studies aimed at the discovery of new species. In addition to the technical difficulties in dealing with cryptic species, like many members of *Sordariales*, there are large gaps in knowledge about these organisms in biodiversity hotspots (Calaça et al. 2020b). It is also important to consider that there is a great deficit of human resources dedicated to the study of this group, and this limits our knowledge. This situation reinforces the need for training human resources and new studies aimed at research with dung-inhabiting fungi, which may contribute to the discovery of new fungal species.

The citations of works on dung-inhabiting fungi also significantly increased from the 1960s onwards in proportion to the number of publications (Fig. 2b), which is due to the increase in publications, although a few individual works had more than 150 citations. Although most studies focus on taxonomic aspects, the most cited works are studies which address the application of dung-inhabiting fungi in paleontological studies, which present paleoenvironmental reconstructions based on paleoecological proxies, such as spores of dung fungi or pollen grains. These studies describe how past human populations altered local landscapes through introducing herbivores, or describe the composition of past mycobiota, as well as trace the stages of megafauna decline in the late Pleistocene by verifying the variation in the number of spores in sediments over time (van Geel et al. 2003, van Geel & Aptroot 2006, Gill et al. 2009).

However, recent studies suggest that the use of this proxy to determine the dynamics and abundance of megafauna and other aspects related to vegetation should be done with caution due to limitations in the dispersion of dung-inhabiting fungi, whose spore spread ranges from a few centimeters to a few meters away (Davies 2019, Richardson 2019). Despite this, the high number of citations of these works (Table 1) may be associated with the fact that these studies are cited in introductions, even in works focused on taxonomy, to address the importance and applicability of dung-inhabiting fungi, since many are pioneering studies involving paleontological aspects of these fungi.

The African continent has areas with one of the most biodiverse savannas in the world (Solbrig 1996), both in terms of vegetation and fauna. However, it is the continent with the fewest studies of all, presenting several gaps in knowledge about the diversity of dung-inhabiting fungi in these savannas, and especially their relationship with the unique fauna of the region (Fig. 3). Despite the low contributions, important taxonomic and biogeographic studies have been carried out in Kenya in recent years, focusing on the *Ascobolus*, *Chaetomium*, *Podospora*, *Saccobolus*, *Schizothecium*, and *Sporormiella* genera, for example (Mungai et al. 2012a, b, c, d, e, f). These studies give us an indication of the high diversity of dung-inhabiting fungi in these ecosystems and of the countless possibilities of research that still need to be done in these unexplored areas regarding this diversity.

The low number of countries developing studies with this group of fungi in partnerships/collaborations may indicate a reduced number of researchers devoted to the group acting in these locations. This scenario also shows us that there are no new specialists to this group of fungi being formed recently in postgraduate courses dedicated to mycology. Additionally, many pioneer researchers from this group have both retired (e.g., Francesco Doveri, Michael J. Richardson) or passed away in the last years (e.g., Roy F. Cain, Richard P. Korf, Gastón Guzmán Huerta).

The United States of America is the country with the highest number of publications, almost all without international collaborations (Table 2). A similar situation was observed in a study on collaboration between researchers on fimicolous myxomycetes, in which little international collaboration is observed (Calaça et al. 2020a). The same is observed between the United Kingdom, Brazil, and India second, third and fourth in the number of publications respectively, but also with a low number of collaborations. The analysis of the principal components of the keywords used in these publications (Fig. 5) shows that there are two major groups of studies involving dung-inhabiting fungi: studies focused on paleobiology and studies with taxonomic and ecological approaches. These groups show the existing research focuses for each region according to the nationality of the authors who lead these publications. For example, the works developed by Brazilian authors are focused on taxonomy (mainly classical), while the Americans and the British develop general and/or paleobiological studies. As discussed by Calaça et al. (2020a), the availability of financial resources and administration of each location influences the types of studies developed, since authors with more resources can explore methods and approaches which are not easily accessible to authors from developing countries.

Our results show that the biotechnological aspects of dung-inhabiting fungi are much less studied compared to the amount of work with taxonomic, ecological and paleontological approach, being represented by few studies (13% of the total of 661 articles recovered). The United States of America dominates the authority of publications evolving biotechnological uses of dung-inhabiting fungi. Almost all these studies were published in the Journal of Natural Products (21 papers, Fig. 2a), among which, one of the top 10 most cited works (Table 1) (Whyte et al. 1996). This journal specializes in publications involving research on the biochemistry of products of natural origin and has an impact factor IF = 4,803 (Impact Factor 2021). Our results suggest that biotechnological application of dung-inhabiting fungi as an underexplored area, despite the already known potential of these fungi in several sectors of biotechnological interest (Sarrocco et al. 2014, Sarrocco 2016). The use of fungi in biotechnology is well reported (Hawksworth 1985); however, it is still not widespread with regard to underexploited groups, such as dung-inhabiting fungi.

Additionally, our results highlight the wide diversity of species of economic interest in the development of diverse inputs for industry, medicine and environmental sciences. The sesquiterpenoids are the most diverse group of terpenoids. Some of those metabolites, produced by dung-inhabiting fungi species, for example, such as *Hypocopra rostrata* Griffiths, *Rhypophila decipiens* (G. Winter ex Fuckel) Y. Marín, A.N. Mill. & Guarro, *Poronia punctata* (L.) Fr., are important sources of antimicrobial compounds. Some of these compounds have also the potential for use in the production of drugs for the treatment of cardiovascular diseases, protection against neurodegeneration, and antimalarial action (Chadwick et al. 2013). As can be seen, the future research potential for the application of these fungi in biotechnology is extremely viable and relevant. The biggest trend is the prospection of secondary metabolites, especially those with applications in the control of plant pathogens or with antimicrobial activity, including antifungals, antibacterials and antibiotics in general. The prospect of enzymes with potential in degrading plant residues and bioethanol production is also relevant (Table 3). *Podospora anserina* is a well-known biological model of the 58 species of dung-inhabiting fungi found in the publications, whose genome has already been sequenced and is currently one of the most used model organisms in genetic studies (Espagne et al. 2008, Ament-Velásquez et al. 2020, Vogan et al. 2021). The species was the most frequent in studies involving biotechnological aspects (Table 3).

Final considerations

The results presented in this study showed that: (i) there was an increase in the number of publications on dung-inhabiting fungi over time, especially from the 1960s, with the widespread use of the moist chamber as a necessary tool for studying these organisms in the laboratory. (ii) Few countries hold most of the publications, however international collaboration is low. The United States, the United Kingdom, Brazil, and India stand out among the countries that publish the most about dung-inhabiting fungi. (iii) Two research lines hold almost all publications: studies with a paleontological approach and a taxonomic and ecological approach. Studies with a biotechnological approach (constituting a theme in which dung-inhabiting fungi have high potential) are few and represent a gap in the knowledge about these fungi. (iv) Authors from more developed countries generally publish studies that vary between the two broad lines of research, while authors from developing countries tend to publish works with a taxonomic and ecological focus.

Even after more than a century of research, our data showed that the study of these fungi is still considerably low and there are still unexplored geographic areas, mainly on the African continent, regarding the diversity of this group of organisms for which more attention should be given. Dung-inhabiting fungi are valuable sources for mycological research, both in terms of taxonomic and biogeographic studies, as well as their biotechnological potential. We hope that the results presented herein reinforce the need for future research and funding aimed at this fungal group, with the purpose of knowing the potential of these organisms and guaranteeing their conservation and biodiversity knowledge through appreciating the goods and services they can generate.

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