Human-mediated introductions of macrofungi worldwide: Distribution patterns and impacts

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THESIS PRESENTED TO OBTAIN THE DOCTOR DEGREE IN

ENVIRONMENTAL ENGINEERING

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Abstract

Fungi remain one of the lesser-known kingdoms, both in terms of their ecology and their significance in invasive species research. This underrepresentation reflects limited knowledge about the distribution of these taxa as a whole, and most likely stems from many of these organisms being inconspicuous and difficult to identify. In this work, we specifically analyzed the biogeographical patterns and impacts of alien macroscopic fungi, a non-pathogenic fungal group composed mainly of ectomycorrhizal and saprotroph species with a huge lack of available information about their introductions. Firstly, we created a global repository of distribution records of macrofungi outside their native ranges. This enabled us to provide a detailed representation of the distribution of alien macrofungi worldwide. Furthermore, we carried out the first comprehensive evaluation of the spatio-temporal patterns of alien macrofungi distributions and how these patterns are driven and shaped by some geographical, socio-economic and climatic factors. Thus, it was possible to observe a considerable increase in the number of alien macrofungi species over time, but especially during the last century. In addition, economic development and mean annual temperature were found to drive regional differences in alien species richness, while geographic distance and thermal similarity were significant drivers of compositional similarities between regions. Finally, we also provided the first comprehensive global database on negative and positive impacts of alien macrofungi. It was observed that recorded impacts of these species encompass a wide variety of effects on humans, native and alien plant taxa, other fungi and animal species and soil biochemistry. Altogether, this work showed the constraints of studying some of the most unknown alien groups, presented methods to understand their current situation as well as gave some ideas and suggestions for further studies.

Keywords: alien species, impact analysis, introduction drivers, mushrooms, observational data

Resumo

O reino Fungi é considerado um dos menos conhecidos tanto em relação à sua ecologia como em relação à sua importância para o estudo das espécies invasoras. Essa sub-representação reflete um conhecimento limitado sobre a distribuição destas espécies, e provavelmente é uma consequência da complexidade deste grupo e das dificuldades associadas à sua identificação taxonómica. Neste trabalho foram analisados os padrões biogeográficos e os impactos associados aos macrofungos, um grupo de fungos não patogénico composto principalmente por espécies ectomicorrizas e saprotróficas, que apresentam uma grande falta de informação relativamente às suas introduções. Primeiramente, começou-se por criar um repositório global de registos de distribuição de macrofungos fora das suas áreas nativas. Deste modo, este trabalho conseguiu fornecer uma representação detalhada dos registros de distribuição global de macrofungos introduzidos. Além disso, também foi realizada uma avaliação geral dos padrões espaciotemporais das distribuições destes macrofungos e como estes são conduzidos e moldados por fatores geográficos, socioeconómicos e climáticos. Esta avaliação permitiu concluir que houve um aumento considerável de espécies introduzidas de macrofungos ao longo do tempo, especialmente no século XX. Verificou-se também que o desenvolvimento económico e a temperatura média anual impulsionaram as diferenças regionais na riqueza de espécies introduzidas, enquanto a distância geográfica e a similaridade térmica influenciaram significativamente as parecenças composicionais de espécies entre regiões. Finalmente, foi criada a primeira base de dados global sobre impactos negativos e positivos de macrofungos introduzidos. Aqui verificou-se que os impactos destas espécies abrangem uma ampla variedade de efeitos em seres humanos, plantas nativas e exóticas, outros fungos, espécies animais e na bioquímica do solo. Em suma, este trabalho demonstrou as limitações de estudar um grupo taxonómico pouco conhecido e apresentou novos métodos e soluções para perceber a sua situação atual. Por último, foram ainda apresentadas algumas ideias e sugestões para estudos futuros.

Palavras-chave: análise de impactos, cogumelos, dados de ocorrência, espécies exóticas, fatores de introdução

Resumo alargado

Apesar de os estudos em invasões biológicas serem principalmente focados em animais e plantas, as atividades humanas têm sido responsáveis por transportar outros grupos taxonómicos para além das regiões de distribuição nativas. Um desses grupos é o dos fungos que, por ser bastante complexo e desconhecido, ainda é pouco citado em listas de espécies invasoras. Somente algumas espécies que causam doenças infeciosas em plantas e animais têm sido mencionadas em alguns trabalhos. No entanto, muitas outras espécies de fungos foram introduzidas massivamente em todo o mundo, nomeadamente espécies de macrofungos. Este grupo, composto principalmente por espécies ectomicorrízicas e saprotrófitas que exibem estruturas macroscópicas portadoras de esporos, é um dos mais excluídos deste tipo de estudos. Isto porque é maioritariamente composto por espécies não patogénicas com impactos pouco visíveis nas áreas onde foram introduzidas. Desta forma, esta tese pretende colmatar este deficit de conhecimento e reunir toda a informação possível sobre a atual distribuição e impactos destes organismos em áreas onde foram introduzidos.

A tese é composta por um total de 3 artigos científicos. No primeiro artigo, referente ao segundo capítulo da tese, o objetivo foi o de criar um repositório global de registos de ocorrência de macrofungos introduzidos de forma a aumentar a representatividade destas espécies em estudos relacionados com padrões de invasão globais. Com esse fim, foi criada a base de dados "*Global Alien Macrofungi Database*" que agregou ocorrências de macrofungos introduzidos em todos os continentes, à exceção da Antártida. Estes registos foram retirados de várias tipologias de fontes nomeadamente artigos, relatórios, bases de dados de espécies invasoras e portais de ciência cidadã. No total, a base de dados reuniu 1966 registos (ou seja, combinações de espécies x regiões) em que estão representados 2 filos, 7 classes, 22 ordens, 82 famílias, 207 géneros, 648 espécies e 31 variedades, formas ou subespécies. Cada registo coletado também incluiu informações do local da ocorrência e, quando disponível, a data da primeira observação, o nome da espécie hospedeira ou outras informações relevantes. Desta forma, este trabalho forneceu uma representação detalhada da distribuição de macrofungos introduzidos pelo mundo.

O segundo artigo, referente ao terceiro capítulo da tese, efetua a primeira avaliação global dos padrões espaciotemporais dos macrofungos introduzidos e como esses padrões são determinados por fatores geográficos, socioeconómicos e climáticos. Neste trabalho foram utilizados os dados da *Global Alien Macrofungi Database* para os quais

se analisou (1) os padrões de acumulação temporal, (2) os fatores responsáveis pela variação regional da riqueza de espécies e (3) as similaridades na composição de espécies entre regiões. Destas análises observou-se um aumento considerável no número de espécies introduzidas especialmente no século passado, com muitas destas já presentes em muitos países pelo mundo. Além disso, verificou-se que o poder económico de cada região e a temperatura média anual estão relacionadas significativamente com as diferenças regionais na riqueza de espécies exóticas, enquanto a similaridade térmica foi um determinante significativo da similaridade composicional entre diferentes regiões. Estes resultados demonstram uma ação conjunta da atividade socioeconómica e do clima na determinação dos conjuntos regionais de espécies introduzidas, o primeiro a atuar sobre o número de espécies introduzidas e o segundo a 'filtrar' aquelas que possuem requisitos ambientais incompatíveis com os que se encontram disponíveis em cada região. Assim, as introduções de macrofungos parecem ser não apenas impulsionadas por atividades humanas, mas também por restrições térmicas para os fungos ou os seus hospedeiros.

No último artigo, referente ao quarto capítulo, foi criada a primeira base de dados global de registos de impactos negativos e positivos de macrofungos introduzidos. Esta base de dados reuniu 1440 registos pertencentes a 374 *taxa*, dos quais 869 eram referentes a impactos negativos e 571 a impactos positivos. Com recurso a estes dados foram avaliadas i) a tipologia e a frequência dos impactos registados; ii) a diversidade taxonómica das espécies associadas a esses impactos, e iii) a sua distribuição geográfica. Com as análises realizadas verificou-se que os impactos de macrofungos introduzidos abrangem uma ampla gama de efeitos, nomeadamente em populações humanas, em plantas nativas e exóticas, em outros fungos e espécies animais e na bioquímica do solo. Os impactos reportados com maior frequência relacionam-se com as relações mutualísticas com as plantas, sendo estas interpretadas como positivas quando as espécies de plantas são de interesse comercial e negativas quando são espécies invasoras. Adicionalmente, também verificámos uma elevada diversidade de espécies de macrofungos para as quais pelo menos um tipo de impacto é relatado, sugerindo que a gestão e prevenção desses impactos requer a adoção de medidas que possam ter um efeito multi-espécie, assim como desenvolvimento de estratégias de cooperação transnacional. Finalmente, é destacado que muitos tipos de impactos são provavelmente subestimados (por exemplo, alterações causadas à biodiversidade local e nas relações tróficas) e mais dados são certamente necessários para descobrir a sua verdadeira magnitude.

Como um todo, este trabalho deu um passo significativo para o entendimento da biogeografia e diversidade de macrofungos introduzidos. Por fim, permitiu ainda fazer uma primeira análise integrada dos impactos conhecidos para estas espécies e que até ao momento permaneciam largamente desconhecidos devido a não serem tão percetíveis como os de outras espécies de fungos.

Palavras-chave: análise de impactos, cogumelos, dados de ocorrência, espécies exóticas, fatores de introdução

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Chapter 1

General introduction

1.1 Biological invasions

1.1.1 The importance of biological invasions

Species dispersal is a key process determining the biogeography of our planet. However, in recent decades, humans increased the rate and scale of this dispersal, being responsible for many introductions of non-native species in all types of ecosystems, from the tropics to the poles and from terrestrial to aquatic environments (Mack et al. 2000). Although, not all the translocated species are able to establish and become invasive (Jeschke et al. 2014). Only a proportion of them find suitable environmental conditions and are resilient enough to outcompete native species for resources, populating the regions where they have been introduced (Crystal-Ornelas et al. 2020). These species are called Invasive Alien Species (IAS) and can become a serious threat by causing serious environmental, economic, and human health issues (Pyšek et al. 2020). As a result, given the unprecedented magnitude of recent species introductions (Seebens et al. 2017) plus social and economic concerns, research programs on IAS have increased enormously and attracted great scientific interest (Richardson & Pyšek 2008; Gallardo et al. 2019; Linders et al. 2020). This topic has actually been gaining momentum in both theoretical and empirical ecology and is an important field of research with broad implications in biogeography, ecology, genetics, and evolution (e.g., Fridley et al. 2007; Hufbauer & Torchin 2008; Capinha et al. 2015).

Therefore, biological invasions are nowadays recognized as one of the most important threats to global diversity, challenging the conservation of biodiversity and natural resources (Hall 2019). They have been shown to have many effects on ecosystems, potentially disrupting species interactions and global ecological processes (Pearson et al. 2018). As a result, the introduction of non-native species can cause both ecological and economic impacts on ecosystem services worldwide through their impacts on biodiversity and ecosystem processes (Simberloff et al. 2013). In fact, over the last decades, unprecedented globalization and intensification of human activities have significantly accelerated the frequency and geographical reach of this phenomenon (Bullock et al. 2018; Seebens et al. 2018; Schmeller et al. 2020). For that reason, our ability to successfully minimise the impacts of those invasions depends strongly on our capacity to anticipate their global spread and establishment in new regions (Kamenova et al. 2017; Capinha et al., 2023).

Invasive alien species are in fact responsible for substantial losses of goods, services and production capacity (such as reduced crop yield, damaged infrastructure and altered use values of ecosystem services), and economic resources are spent each year for their management (Reaser et al. 2007). There are few global attempts of cost assessments, which all suffer recognized flaws and the majority of assessments are restricted to particular taxa (Haubroc et al. 2021). As biological invasions are an increasingly planetary issue, a worldwide reliable economic impact assessment is needed to quantify more precisely patterns and trends of associated costs (Kumschick et al. 2012). For that reason, efficiently mitigating this major driver of global change requires the improvement of public awareness and policy regarding its substantial impacts on our socio-ecosystems (Burgiel & Muir 2010). One option to contribute to this overall objective is to inform people on the economic costs linked to these impacts; however, until now, a reliable synthesis of invasion costs has never been produced at a global scale (Diagne et al. 2020).

In order to prevent any adverse consequences of these invasions, an efficient forecasting of their impacts is required in order to draw appropriate management actions (Jarnevich et al. 2018). However, successful forecasts directly depend on our capacity to quantify such impacts in terms of biodiversity dynamics, evolutionary history, or ecosystem functioning (Hulme 2017) at relevant spatial and temporal scales. Such an endeavor currently constitutes one of the biggest challenges in invasion ecology, still hindering our ability to prompt any general, evidence-based conclusions or management recommendations. Not only is the acquisition of large-scale empirical data methodologically demanding, but there is also a general lack of conceptual agreement upon how to define or quantify the impact of invasive species (Stohlgren & Schnase 2006; Hulme 2015).

1.1.2 The importance of accessing data in invasive alien species research

Science-based strategies to tackle biological invasions depend on recent, well-documented, standardized and openly accessible information on alien species (Hulme et al. 2009; Kerns et al. 2021). However, globalization has forced us to think from a dynamic and long-distance perspective for a whole suite of organisms, particularly with regard to invasive alien species (IAS) (Groom et al. 2017). Hence, the rate of change has been a challenge for managers, policy makers and researchers who have to deal with information that is rapidly out-of-date (Lucy et al. 2016). Besides, currently and historically, alien species data are scattered in numerous disconnected data silos that lack interoperability, not allowing an efficient retrieval, combination, and use of these kinds of information for research and policymaking (Simpson et al. 2009). Thus, there is a necessity to improve the availability of accessible and up-to-date data regarding alien species because it is an essential key to address this problem and a help to potentially find and prioritize new introduced species which are not yet well established (Shackleton et al. 2019).

For those reasons, IAS science keeps struggling to meet the current growing demand for accurate information sources despite the obvious advantages of reliable, fast and free data availability (Kerns et al. 2021). The reasons for this are many and range from lack of awareness of the importance of sharing that data to technical and operational constraints (Groom et al. 2015). Hence, the best way forward is for researchers to publish their data openly, by making use of repositories in which the data are licensed in a permissive manner, while making sure they are credited by the adequate provision of citation (Assante et al. 2016). Besides, reducing the barriers to data sharing will significantly improve our ability to react as quickly as possible to the challenge of biological invasions (Groom et al. 2015, Jarić et al. 2020).

1.2 The introductions of macrofungi species

1.2.1 The fungal dimension of biological invasions

Research on biological invasions has focused mainly on vascular plants and animal invaders (Pyšek et al. 2008; Seebens et al. 2017). As a result, only a few publications and comprehensive datasets dealing with the spread of fungi in different regions were published (e.g., Desprez-Loustau et al. 2007, 2010; Vellinga et al. 2009; Wood 2017). The under-representation of this group is largely the result of a lack of scientific knowledge on fungal biodiversity and ecology. With the exception of pathogenic fungi, which cause emerging infectious diseases specially in agronomically important plants, the impact of fungal invasions is often difficult to quantify owing to limited baseline data on fungal communities (Desprez-Loustau 2009).

These pathogens can be highly destructive to species that are closely related to their host species, which are relatively unaffected in the native range of the fungus, presumably due to host–pathogen co-adaptations (Loo 2008). Their impacts can differ in the magnitude or speed of the ecological change that they trigger on susceptible plant communities. For that reason, they provide a reminder of the powerful evolutionary forces that pathogens have exerted on plants (Prospero & Cleary 2017). They also illustrate the extremely varied impacts that even closely related organisms can have on community structure and dynamics, and the challenges ecologists can face when predicting their introductions (Vandenkoornhuyse et al. 2015). Some notorious examples of invasive pathogens include chestnut blight (*Cryphonectria parasitica (Murr.) Bar*, Rigling & Prospero 2008; Dutech et al. 2012; Gruenwald 2012), Dutch elm disease (*Ophiostoma ulmi* (Buisman) Melin & Nannf, Brasier 1991; Bartnik et al. 2015), and *Puccinia striiformis* Westend., the cause of yellow rust on wheat (Ali et al. 2014).

One of the most common pathways for the introduction of these non-native fungal species is the movement of infected planting stock or infested wood (Paap et al. 2022). In fact, although there is a general trend amongst pests and pathogens introduced around the world that dispersed range increases with wider host range, introduced fungi have the narrowest host range but the widest introduced range, suggesting that many fungi species are well adapted to human-assisted dispersal (Bebber et al. 2014; Chaloner et al. 2021). Hence, this has been, and remains, the most important pathway of their introduction (Desprez-Loustau et al. 2007, 2010; Liu et al. 2021). For those reasons, alien fungal distributions deserve some additional considerations, not just because of the relevance of this group of organisms, but also because improvements in fungal ecology can provide insights that are important to general issues of biological invasions (Gladieux et al. 2016).

1.2.2 The introductions of less known macrofungi species

Other introduced fungal species have been even more ignored (Desprez-Loustau 2009). Most of the data regarding these introduced species are in fact still scattered in the unconventional literature, or as anecdotal records in formal checklists (Desprez-Loustau et al. 2007). Therefore, groups like macrofungi that are mostly comprised by saprotrophic and ectomycorrhizal species with macroscopic spore bearing structures are still poorly studied and are usually excluded from invasive species checklists (Vellinga et al. 2009). For example, as far as saprotrophic taxa are concerned, only a few in-depth studies have been carried out with species like *Clathrus archeri* (Berk.) Dring (Pietras et al. 2016, 2021), *Leucocoprinus cepistipes* (Sowerby) Pat. (Motiejunaite et al. 2016; Szczepkowski et al. 2014) and *Favolaschia calocera* R. Heim (Vizzini et al. 2009). While, regarding ectomycorrhizal fungi mainly the introduction and spread of *Amanita phalloides* (Vaill. ex Fr.) Link (Pringle et al. 2009; Wolfe et al. 2010), *Amanita muscaria* (L.) Lam. (Dickie et al. 2008; Sawyer et al. 2001; Wood et al. 2015) and some Australian fungi associated with *Eucalyptus* species (Díez 2005) has been carefully studied and monitored.

Therefore, these macrofungi species have mainly been accidentally introduced when allochthonous trees are planted for agriculture and reforestation (Elmostapha et al. 2022) or in infested wood and soil. Although, the deliberate movement of ectomycorrhizal fungal species and strains is also a growing phenomenon as a consequence of the promise of using beneficial soil mutualist organisms to improve agriculture (Khade & Adholeya 2009; Cornejo et al. 2017; Igiehon & Babalola 2017), habitat restoration (Asmelash et al. 2016), bioremediation (Harms & Wick 2011), reforestation (El Mrabet 2014, Sanon et al. 2010), and edible basidiomata production (Barroetaveña et al. 2008; Dickie et al. 2016). Hence, it is necessary to keep increasing the research and data availability of introduced macrofungi in order to understand their current alien distributions, as well as to uncover the mechanisms controlling their presence in novel habitats and potential positive and negative impacts in non-native regions.

1.2.3 The most common introduced macrofungi species around the world

Knowledge on the movement, establishment, and spread of fungi is limited, perhaps because of their cryptic nature (Dickie et al. 2017). As we mentioned in the previous section, information regarding macrofungi are especially uncommon, as the effects of pathogens on animals and plants are more obvious than effects caused by them (Vizinni et al. 2009). Only recently have there been some comprehensive studies of the occurrence of introduced macrofungi outside native ranges in order to understand their current status of these species in regions outside their native range (Vellinga et al. 2009; Deprez-Loustau et al. 2009, 2010). Some of the most recorded ones are *Suillus luteus* (L.) Roussel, *Pyrrhoderma noxium* (Corner) L.W.Zhou & Y.C.Dai), *Amanita phalloides* (Vaill. ex Fr.) Link and *Amanita muscaria* (L.) Lam. (Vellinga et al. 2009).

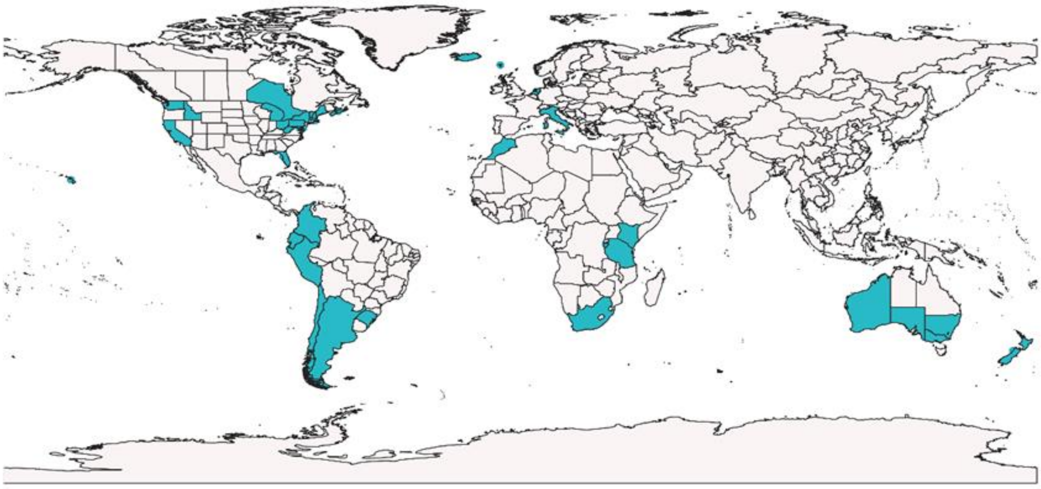
First, *Suillus luteus* (slippery jack) (Figure 1.1a) is a typical pioneer ectomycorrhizal (EM) basidiomycete that forms associations with roots of young pine trees (Bending et al. 2002). It is a species native to the Eurasian region that presents a high degree of host specificity, and its native distribution coincides with the natural distribution of Pinaceae species (Pildain et al. 2021). Therefore, it is a common ectomycorrhizal mushroom in coniferous forests associated with two-needle pine trees (*Pinus sylvestris*, *Pinus radiata*, *Pinus ellioti*) on sandy and acid soil, throughout the area where *Pinus* spp. occur naturally or have been planted (Hayward et al. 2015). This species has been widely introduced into North America, South America, Africa, and Oceania (Figure 1.2a) during afforestation with pines (Policelli et al. 2019). Indeed, *S. luteus* is one of the most abundant exotic EM mushrooms found under pines across the Southern Hemisphere (Dickie et al. 2010). Besides, it is one of the most important wild edible mushrooms harvested and exported around the world. For those reasons, it is the most introduced species in the highest number of non-native countries, as it is the most well recorded species per country outside its native range.

Pyrrhoderma noxium (Figure 1.1b) is an alien aggressive pathogenic fungus indigenous to some rainforests throughout the tropics (Stewart et al. 2020). Currently, it has been widely introduced among several tropical countries, where it causes a brown root rot disease responsible for the decline of numerous orchard and forest tree species (Hsiao et al. 2019). It was introduced in different countries of Southeast Asia, Africa, Oceania, Central America and the Caribbean region (Figure 1.2b) (GISD, 2022). In all of these regions, it has a wide host range which encompasses more than 200 plant species representing 59 families (Ann et al. 2002). It can devastate agricultural plantations of tea, rubber, cocoa, avocados, and oil palm; tropical fruit trees such as longan, breadfruit, litchi, carambola, and loquat; timber trees including hoop pine (*Araucaria* sp.), eucalypts (*Eucalyptus* sp.), mahogany (*Swietenia* sp.); as well as many ornamental trees and shrub (Ashiglar et al. 2015). Impacts of the fungus on native forests are less known, though native species have been reported vulnerable (Brooks 2002).

Amanita phalloides (Figure 1.1c), commonly known as the death cap, is a well recorded alien ectomycorrhizal species mostly for being a notorious deadly poisonous species of ectomycorrizhal fungus, that is involved in the majority of human fatal cases of mushroom poisoning worldwide (Garcia et al. 2015). This usually happens because they resemble several edible species commonly consumed by humans, increasing the risk of accidental poisonings (Ye & Liu 2018). The species is native to the European continent, where it is well widespread (Wolfe & Pringle 2012). Outside of its native range (Figure 1.2c), it has been established in Oceania in countries like New Zealand and Australia under planted alien trees stands such as *Quercus* sp. (Roberts et al. 2013). Besides, in South America it has been reported from Uruguay, Argentina and Chile associated with exotic trees, like oaks (e.g., *Quercus ilex*), chestnut (e.g., *Castanea sativa*) and pinus (e.g., *Pinus* sp.) (Lechner & Albertó 2008; Valenzuela et al. 2018. Meanwhile, in North America, it has been introduced into urban landscapes and undisturbed native forests in some states of the United States and Canada (Pringle et al. 2009). Finally, in Asia is reported from a few countries like China or India whilst in Africa is reported as introduced in South Africa, Malawi, Zambia, Zimbabwe and Tanzania where it was found in pine plantations and in association with exotic trees such as pines (*Pinus* sp.), oak (*Quercus* sp.) and poplar (*Populus* sp.)' (Yang et al. 2001; Hallen et al. 2002; Pringle & Vellinga 2006).

Finally, *Amanita muscaria* (Figure 1.1d), or fly agaric, is another iconic poisonous ectomycorrhizal species of fungi: it is the classic mushroom of fairy tales and children's cartoons (Satora et al. 2005). Native to the northern hemisphere, it has been introduced mostly throughout the southern hemisphere including different countries of South America, Africa and Oceania (Figure 1.2d). It is usually found associated with exotic northern hemisphere pine trees (*Pinus nigra* or *Pinus radiata*), being a classic case of 'co-invasion' (Vargas et al. 2019). However, it can also form 'novel associations' with native trees such as *Fuscospora cliffortiodies* (mountain beech), or 'co-xenic novel associations' with alien trees from outside its natural distribution range, including *Eucalyptus* from Australia (Robinson 2010). Hence, this species can contribute to pinus introductions worldwide, although it is considered to be a 'late-stage' fungus by only infecting trees once they are several years old (Wood et al. 2015). As such, it may play a role in the impact of pine invasion on ecosystem function, but is unlikely to drive the actual invasion front (Policelli et al. 2019).

Figure 1.1. The most record species of introduced macrofungi. (a) *Suillus luteus* (L.) Roussel (Björn 2017); (b) *Phellinus noxius* (Corner) G. Cunn. (Brooks 2009); (c) *Amanita phalloides* (Vaill. ex Fr.) Link (Spraag 2013); (d) *Amanita muscaria* (L.) Lam (Storbylomices 2013).



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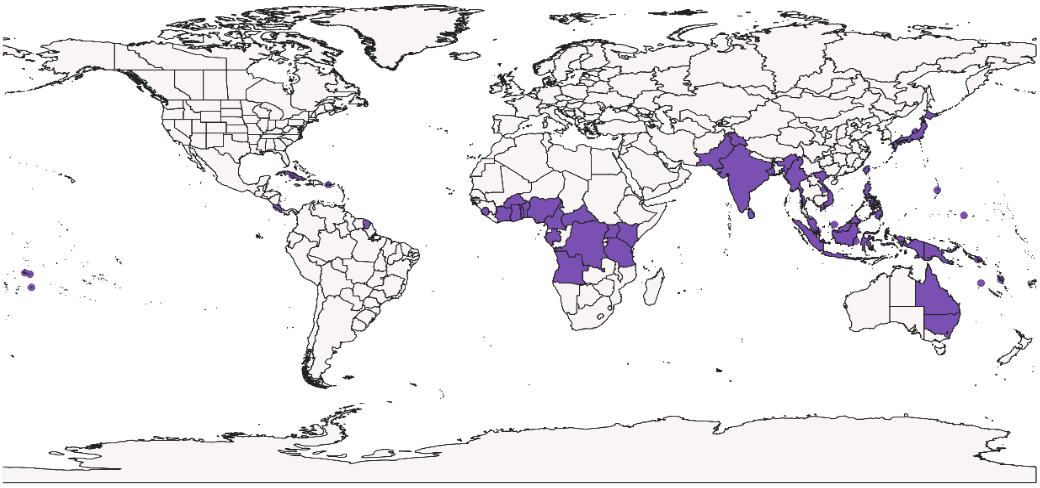

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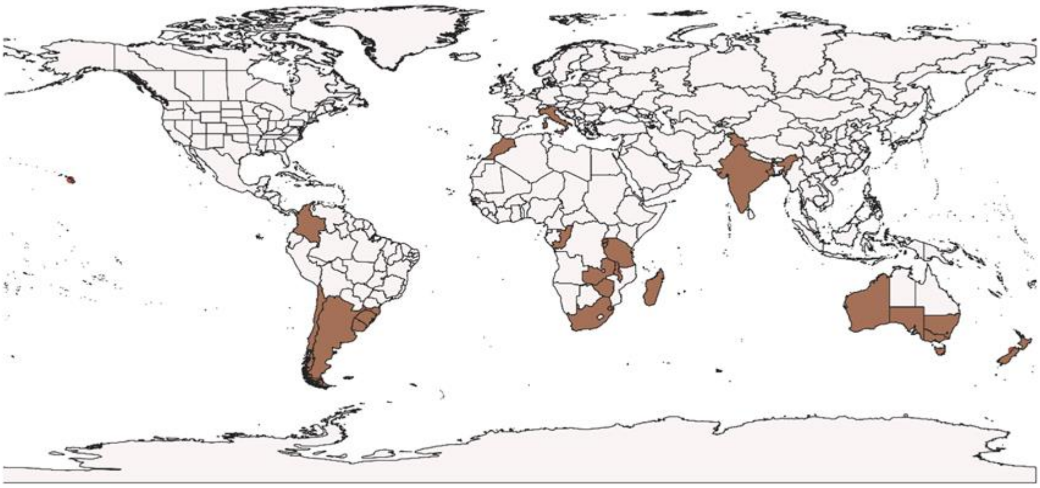

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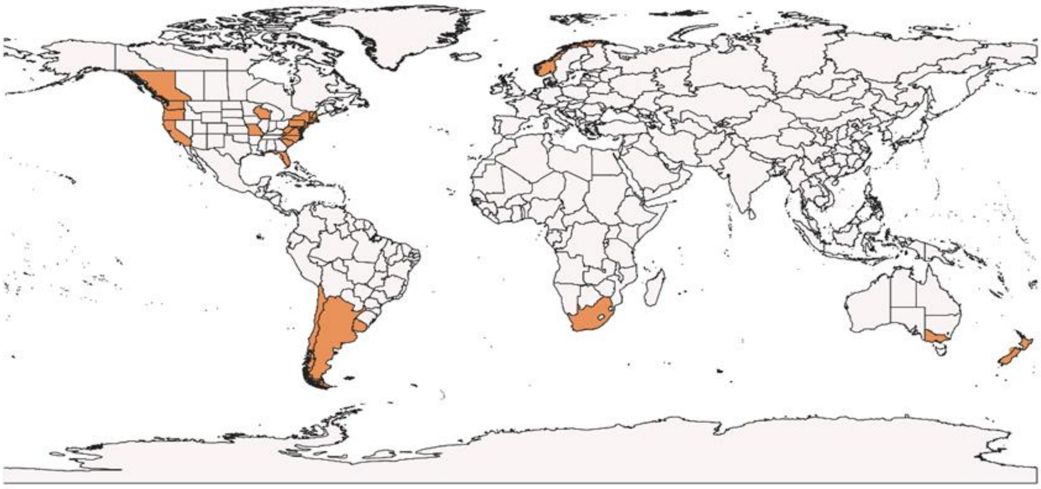

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Figure 1.2. The global distribution of the most introduced macrofungi species in different countries and first administrative divisions of the six largest countries in the world (Australia, Brazil, Canada, China, Russia and United States). (a) *Suillus luteus* (L.) Roussel; (b) *Phellinus noxius* (Corner) G. Cunn.; (c) *Amanita phalloides* (Vaill. ex Fr.) Link; (d) *Amanita muscaria (L.) Lam*. The data represented in maps is taken from the database mentioned in chapter 2 of the thesis.

1.2.4 Impacts of introduced macrofungi in non-native regions

There is still little practical information on the impacts of macrofungi in non-native regions as well advice regarding strategies to manage them (Dickie et al. 2016). That lack of practical advice stands in contrast with the abundant literature on control strategies for invasive groups of plants and animals (Shine 2007). Although, in the last decades the availability of studies regarding this matter is increasing. Currently, we know that introduced fungi can negatively affect non-native ecosystems by causing severe diseases to some economically important plants for agriculture and forestry, being toxic to humans through their consumption, may compete with native, edible or otherwise valuable fungi, facilitate the co-invasion of exotic trees, or by causing major changes in soil biota (Dickie et al. 2016). Meanwhile, some species can positively contribute to these ecosystems by enabling plantation forestry and, in some cases, being a valuable food source or economic resource (Sitta & Davolli, 2012; Liao et al. 2016). For those reasons, it is necessary to increase our knowledge and appropriately manage the massive import of these species to avoid their negative impacts (Hulme 2007).

Several of these impacts are caused by introduced ectomycorrhizal fungi (Dickie et al. 2016). These species are usually restricted to alien plant hosts and may not influence much native plants directly, but they can have strong indirect effects by facilitating plant invasions (Richardson et al. 2000). Besides, the phenomenon suggests tree species not currently widely invasive may become more invasive if compatible fungi were to co-invade (Vellinga & Kuyper 2012). A few introduced species from the suilloid genus, as well as *Amanita phalloides* and *Amanita muscaria* are some examples of introduced fungi that facilitated the establishment of exotic plants like pines (Pérez-Pazos et al. 2021, Sapsford et al. 2022) and eucalyptus (Sulzbacher et al. 2018; Wilgan 2020). Even though, in cases related to economically important exotic tree plantations, they can also become an economic advantage for forestry industries by contributing to their establishment outside native range (Moeller et al. 2015). For example, after failed attempts to establish pine plantations in the Southern Hemisphere in the 1800s and early 1900s, it was quickly discovered that pines, which are obligatorily associated with symbiotic EM fungi, cannot survive without soil inoculum from previously established nurseries or pine forests (Hoeksema et al. 2020). Besides, species like *Suillus luteus* (L.) Roussel, *Boletus edulis* Bull. and *Suillus granulatus* can serve as a valuable food source in some introduced countries of South America and Africa (Barroetaveña et al. 2008; Buyck 2008; Dickie et al. 2016).

Pathogenic fungi are another group of species that commonly has negative impacts in introduced regions by causing severe diseases especially in economically important plantations (Dickie et al. 2017). They are often highly destructive to species that are closely related to pathogens' host species, which are unaffected in the native range of the fungus, presumably due to host-pathogen co-adaptation (Loo 2008). For example, the aggressive *Pyrrhoderma noxium* responsible for causing the root-rot disease and can damage forest and hardwood plantations, fruit orchards, and landscapes (Ann et al. 2002). Besides, these plantations cannot be replanted for many years due to the longevity of *P. noxium* in the soil and its broad host range (Mohammed et al. 2014). Mahogany, rubber, hoop pine, and cocoa have been some of the plnts most seriously affected by its presence during the last decades (Ashiglar et al. 2015). Another fungus with recorded impacts on introduced ecosystems is *Entoleuca mammata* (Wahlenb.) J.D. Rogers & Y.M. Ju. It causes hypoxylon canker, a damaging disease that affects hardwoods, most commonly in poplars and willows (Kasanen et al. 2004). When affected by this disease, the trees usually develop stem cankers and die within 5 years or are structurally weakened and break in the wind (Ostry 2013). Finally, some species of the genus *Heterobasidion* such as *Heterobasidion irregulare* Garbel. & Otrosina and *Heterobasidion annosum* (Fr.) Bref. can be responsible for causing root and butt rot of conifer trees (Gonthier et al. 2013). These fungi thrive in many sites, especially in commercial forests and like all wood decayers, influences species composition, ecosystem diversity, stand structure and direction and rate of forest succession (Zaļuma et al. 2019).

1.2.5 Management strategies to control introduced macrofungi species

The decision to control or remove an invasive species is often based in policy, not science, as financial constraints, public perceptions, and feasibility should also be considered (Larson et al. 2011). For example, alien fungi valued for food or timber production provide ecosystem services that may drive conflict over invasive species removal (Sladonja et al. 2015). Moreover, even understanding which species are invasive can be problematic, as determining any species' native or alien status can require extensive literature review or detailed DNA analyses (Boon et al. 2020). Nonetheless, there are clear examples where a desire to remove alien ectomycorrhizal fungi has been expressed by land managers. Two good examples are the interest in removal of *Tuber indicum* Cooke & Massee and *Tuber brumale* Vittad. from the lands of commercial growers of higher value truffles in Italy (Liu et al. 2014) and the expressed concerns over *Amanita muscaria* invasion into native forests by regional councils in

Australia (Sawyer et al. 2001; Robinson 2010). Thus, it is essential to formulate possible management strategies, based on aspects of basic fungal biology and comparison with other, better studied, invasive taxa (e.g., vascular plants and mammals) (Pyšek et al. 2008).

Therefore, the best method to deal with fungal invasions is simply to prevent them from establishing in the first place (Koide et al. 2011). Many countries now have barriers to the importation of new species, including fungi (Pyšek et al. 2020). Although, there are persons who continue to undertake and promote the cross-continental translocation of fungi into natural ecosystems (Dickie et al. 2008a). Plus, advocacy to move species may be a particular issue for macrofungi species, which can be seen as ‘‘beneficial’’ and therefore not-of-concern (Sukumar et al. 2013). Despite, clear evidence of negative impacts confirms that the global spread of these fungi can come with significant risks (Dickie et al. 2017). For that reason, even if prevention can be considered a good control strategy, its efficacy is limited by economic pressures for allowing the movement of plants and fungi (Pyšek et al. 2010). Even in countries with a high level of biosecurity awareness, nursery stock is typically screened for disease symptoms and culturable fungi, but not for the generally difficult to culture ectomycorrhizal fungi (Liebhold et al. 2017). Further, plants are frequently moved by people to gardens or yards, with little to no consideration of which fungi may also be moved (Donaldson et al. 2014).

As a result, where alien fungi are already widespread, or where economic or other benefits of fungi make eradication impossible, there may still be options for reducing associated undesirable impacts (Mueller et al. 2007; Wojewoda & Karasiński 2010). For example, many future macrofungi invaders are likely already present, as mycorrhizas on roots of amenity plantings and forest plantations or potentially as spores in the soil and infested wood (Szczepkowski et al. 2014). In fact, alien trees often occur around farmsteads, research stations, and campgrounds within high conservation-value landscapes, and many are likely to support populations of alien fungi (Urcelay et al. 2019). Nonetheless, ecosystem management to avoid soil disturbance, and protect or restore native ecosystems may contribute to maintaining native fungal populations and reducing co-invasion, despite being unlikely to eliminate invasive ectomycorrhizal fungi altogether (Tedersoo 2017). For those reason, proposing potential strategies is an essential key to facilitating coordinated research and control efforts across international boundaries (Lodge et al. 2016).

Notwithstanding, at present the control of invasive ectomycorrhizal fungi seems stuck at an impasse (Lai et al. 2008). Land managers are interested in trying to remove invasive fungi, but are unable to find evidence-based guidance on how to do so (Kesäniemi et al. 2019). Therefore, the only way to improve is to create approaches that take into account both management guidance and research knowledge (Lodge et al. 2016). Land managers who are contemplating control efforts should seek out scientific advice on possible strategies and on robust experimental design of trials (Chandrasekar 2011). In particular, partnerships should be designed where land managers benefit from scientific expertise while contributing to furthering scientific knowledge. Contrariwise, scientists need to recognize that land managers have their own constraints, including limited budgets, and a need for timely, clearly presented results (Dickie et al. 2016). Further, many species of macrofungi are charismatic and for that reason they are ideal systems for engaging the public in conservation and biosecurity (Dunn & Hatcher. 2015). Besides, the large, prominent and large sporocarps of many introduced macrofungi species make them easier to study than invasive pathogens, and hence create a model system for understanding fungal introductions (Taylor & Alexander 2005).

1.3. Thesis objectives

In this thesis, our main goal was to uncover the current situation of alien macrofungi distribution and impacts around the world. For that reason, we focused the studies in uncovering the patterns and drivers of their alien distribution and species diversity, as well as the main environmental and socio-economic impacts that they can potentially cause (Figure 1.3). This has a special importance because they are part of a *taxonomic group* with a huge lack of information regarding their alien status in non-native areas because they are complex organisms with a still poorly known biology and ecology. As a result, we intended to contribute for the development of this kind of research regarding the introduction capabilities of such an unknown group.

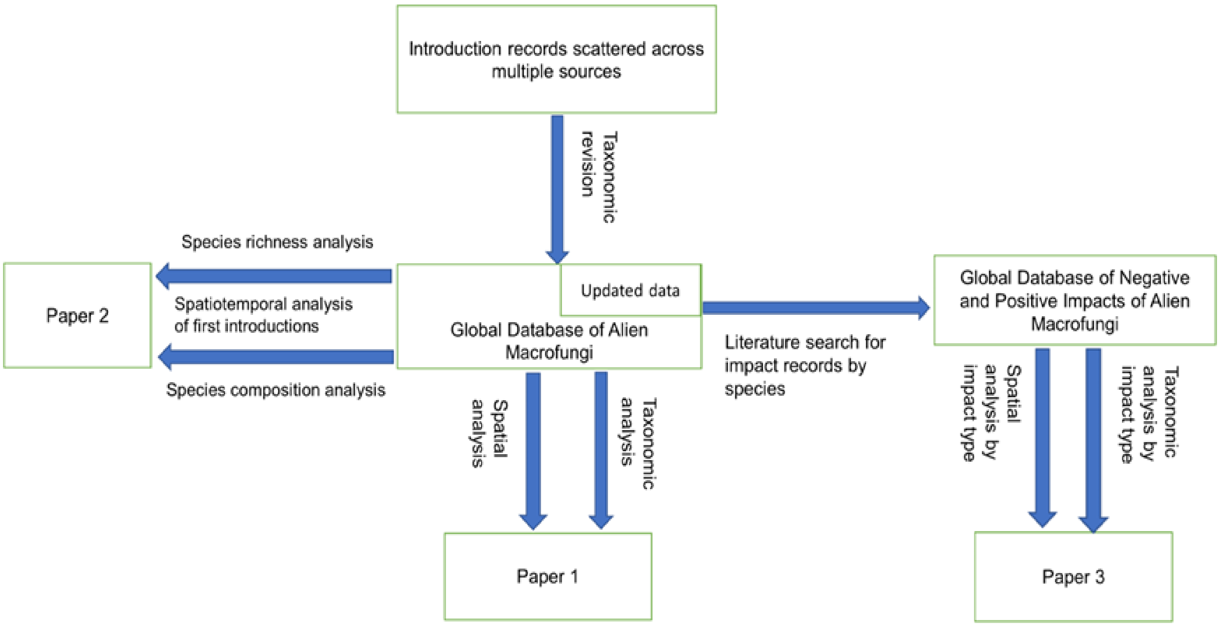

Figure 1.3. Outline of the work to be carried out in this thesis.

Thus, the article entitled “**A database of the global distribution of alien macrofungi**” (Chapter 2) had a purpose to present the new and most complete global database of alien macrofungi (GDAM) that gathered as much information as possible regarding macrofungi alien distributions as well as other important remarks from all different types of sources such as publications, reports, global alien species databases and citizen-science data repositories. Through this database, we were able to understand and visualize the current spread of macrofungi introductions worldwide.

The article “**Patterns and drivers of the global diversity of non-native macrofungi**” (Chapter 3) used the previous dataset gathered in the first paper with the purpose of analysing patterns and drivers of (1) regional variation in species richness, (2) compositional similarity between regional species assemblages and (3) the spatiotemporal trends of first records. With that, we could understand which are the regions with high and low diversity of non-native macrofungi, what socio-economic and environmental factors drive the increase of species diversity and how the trend of introductions evolved along the time.

Finally, the article “**Negative and positive impacts of alien macrofungi: a global scale database”** (Chapter 4) had the purpose to identify the negative and positive impacts of these species in non-native regions, as their effects have often received little or no attention, and are still poorly understood. To do that, we built a dataset of impact records based on a comprehensive literature search. With that we were able to identify the main alien species that cause impacts worldwide as well as understand the different socio-economical and environmental impacts that they can cause.

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Chapter 2

A database of the global distribution of alien macrofungi

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A database of the global distribution of alien macrofungi

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2.1 Abstract

Background

Human activities are allowing the ever-increasing dispersal of taxa to beyond their native ranges. Understanding the patterns and implications of these distributional changes requires comprehensive information on the geography of introduced species. Current knowledge about the alien distribution of macrofungi is limited taxonomically and temporally, which severely hinders the study of human-mediated distribution changes for this taxonomic group.

New information

Here, we present a database on the global alien distribution of macrofungi species. Data on the distribution of alien macrofungi were searched in a large number of data sources, including scientific publications, grey literature and online databases. The database compiled includes 1966 records (i.e. species x region combinations) representing 2 phyla, 7 classes, 22 orders, 82 families, 207 genera, 648 species and 31 varieties, forms

or subspecies. Dates of introduction records range from 1753 to 2018. Each record includes the location where the alien taxon was identified and, when available, the date of first observation, the host taxa or other important information. This database is a major step forward to the understanding of human-mediated changes in the distribution of macrofungal taxa.

2.2 Introduction

In this publication, we present the recently completed Global Alien Macrofungi Database, a database of distribution records of alien macrofungi aggregated from all relevant sources we could identify, namely publications, reports, databases on invasive alien species and citizen science observations. In total, the dataset contains occurrences for nearly 650 alien species, registered in more than 140 countries and sub-national administrative divisions. This represents an increase of nearly 2.5 times the number of alien records and 3.2 times the number of alien species found in the most comprehensive distribution database for alien ectomycorrhizal fungi available prior to our work (Vellinga et al. 2009). The presented database is expected to provide a valuable contribution towards the increasing understanding of the spatial and temporal dynamics of biological invasions worldwide.

2.3 General description

Purpose: The main goal was to create a comprehensive global repository of distribution records of macrofungi outside their native ranges, as the under-representation of these species in studies of broad-scale invasion patterns reflects a lack of readily available synthesised information about their distribution in the world (Troudet et al. 2017). Macrofungi, i.e. fungi that exhibit macroscopic spore bearing structures, are an artificial group mostly comprised of ectomycorrhizal and saprotroph fungal species. Those are widely missing in alien invasive species databases, such as the CABI Invasive Species Compendium (https://www.cabi.org/ISC; CABI 2019) and Global Invasive Species Database (http://www.iucngisd.org/gisd; IUCN 2019), because their impacts on native biota are hard to assess and remain largely unknown (Desprez-Loustau 2009, Desprez-Loustau et al. 2010, Vizzini et al. 2009). Nevertheless, macrofungi have been massively introduced into new geographic regions particularly as hitchhikers of exotic plants, in infested wood or soil (Desprez-Loustau 2009).

The specific objectives of our work were:

1. To update and expand previous compilations of the global alien distribution of macrofungi, particularly the work of Vellinga et al. (2009), who compiled data on the distribution of alien ectomycorrhizal fungi worldwide. Here we integrate their data and extend it both taxonomically (i.e., by considering all macrofungi) and temporally (i.e., by including records published more recently).

2. To highlight the relevance of data circulating outside the scientific community, and its importance for the comprehensive representation of alien fungal distributions. A substantial number of alien records were collected from citizen-science-based websites. Often these data sources were the only mentioning alien distributions of taxa for given regions, particularly for species best known by the general public, such as the Fly agaric (*Amanita muscaria* (L.) Lam.) or the Oyster mushroom (*Pleurotus ostreatus* (Jacq.) P. Kumm.). Two notable examples of such online databases of biodiversity observations used in the research process were iNaturalist (https://www.inaturalist.org/; iNaturalist 2019) and mushroom observer (https://mushroomobserver.org/; Wilson and Hollinger 2019).
3. To provide a detailed representation of the distribution records of alien macrofungi worldwide, which will be pivotal for advancing current knowledge about the spatio-temporal and taxonomic patterns of fungal invasions and establishing a baseline for comparison with new data collected in the future.

2.4 Project description

Title: A global database of alien macrofungi.

Personnel: Monteiro, M.; Reino, L.; Schertler, A.; Essl, F.; Figueira, R.; Ferreira, M.T.; Capinha, C.

Study area description: Countries from all continents except Antarctica and the first-order administrative divisions of the six largest countries in the world (Australia, Brazil, Canada, China, Russia and United States).

Design description: The creation of the “Global Alien Macrofungi Database” followed a two-step approach. First, we performed an exhaustive search for data sources supplying occurrence records of macrofungi. Then, we critically assessed and harmonised the collected data and entered it into a standardised database. Our search and collation of alien macrofungi records were carried out during the years 2017-2019. For the first step, we analysed the database made available by Vellinga et al. (2009), who collected a total of 770 distribution records of ectomycorrhizal fungi from more than 190 publications. However, given the exclusive focus of the database on ectomycorrhizal fungi and the consequential absence of data on saprotrophic species, it can hardly be assumed that the patterns represented in Vellinga et al. (2009) provide a comprehensive portrayal of the global biogeography of alien macrofungi. Hence, we performed a complementary search for alien saprotroph fungi and searched for new records of alien ectomycorrhizal fungi. For the second step, all collected records were entered into two different datasets. First, we compiled a taxonomic checklist that accounts for all macrofungi taxa we found to be introduced outside their native range. Secondly, we described the alien occurrences of those taxa by including additional data when available, such as dates of introduction, host information and invasion status (e.g. casual, established) in the invaded regions. Here, each entry corresponded to a single record described as an alien taxon in a specific location. If a taxon in a given locality were reported multiple times by different sources, we merged the information into a single database entry and cited the earliest reference in time reporting the record.

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2.5 Sampling methods

Study extent: We built our database by compiling occurrences of introduced macrofungal species based on an exhaustive search in published and unpublished sources. Data were extracted from peer-reviewed articles, scientific and technical reports, books and book chapters, alien species databases and online citizen-science repositories. Finally, we also approached selected mycologists via email. These experts were contacted and asked if they were aware of records of alien macrofungi or of data resources other than the ones we identified through online searches.

Sampling description: The data collection process consisted of three different procedures, as is explained below.

Identifying and obtaining relevant records from publications

During the search process, we initially looked for records in broader introduced taxa databases, such as the ones for Delivering Alien Invasive Species Inventories for Europe (Hulme et al. 2019), the Global Register of Introduced and Invasive Species (Pagad et al. 2019) and the European Alien Species Information Network (Katsanevakis et al. 2019). In addition, we used general-purpose search engines (i.e. Google) and scientific search engines (Google Scholar, Science Direct and JSTOR) to gather more information from relevant literature. We entered key terms related to fungal invasions in different languages including English, German, French, Spanish and Portuguese. The terms used were ‘introduced´, ’invasive’, ‘established’, ‘alien’, ‘non-native’ and ‘exotic’, which were combined with fungal taxonomic terms, ranging from a generic and higher denomination (e.g. ‘fungi’, ‘macromycetes’, ‘basidiomycota’) to a more specific designation, such as the scientific name (e.g. *Amanita muscaria (L.) Lam., Amanita phalloides* (Vaill. ex Fr.) Link) or a common name (e.g. fly agaric, death cap). For each combination, we repeated the searches by adding the name of one continent or country, until all continents and countries were being considered. As examples, final search terms would be like ‘European alien fungi’, ‘introduced basidiomycota in United States’ or ‘introduced *Amanita muscaria* + South America’.

Cross-checking of alien status: For each record, we assessed the reliability of the alien status given by the original data sources. Records collected from sources explicitly dealing with alien taxa (e.g. Vellinga et al. 2009), retained the nativity status given by the data. These statuses corresponded either to ‘alien’ or to ‘cryptogenic’ (*sensu* Essl et al. 2018). Records collected from nonspecialized sources (e.g. species checklists not considering nativity, grey literature and citizen-science data) were cross-checked against biogeographical information available in scientific literature or with mycologists. Cases where the records referred to regions outside known native ranges, were coded as ‘alien’. Cases in clear biogeographical conflict with known native ranges were not considered for inclusion in our database. Finally, cases where the native or alien status was not possible to identify unambiguously were also not considered.

Occurrence data entry: To be included in our database, records had to meet specific criteria regarding taxonomy and locality description. First, a record must describe a macrofungal species having sporocarps of at least 2 mm in size, irrespective of phylogenetic placement (Senn-Irlet et al. 2007). As this was not always clear, we had to double-check our data with relevant fungal literature to be sure that the families or even the orders of the referred species were cited as part of the macroscopic fungi checklists. We also had to be certain that the records were identified at least to the species level, as a way of knowing that all contemplated species were, in fact, alien organisms in the non-native places. Furthermore, the records had to be accompanied by geospatial coordinates or, at minimum, an unambiguous textual designation of location level reference (e.g. region, country and locality). Finally, the record had to represent a fungal species introduced by human activity to a region outside its native range. These tasks were accomplished by the main author (MM) during the years 2017-2019 with the supervision of experts in fungal ecology and biogeography. These experts were also consulted and asked if they were aware of records of alien macrofungi or of data resources other than the ones we identified through online searches.

Quality control: For the development of the dataset, the records from the original sources were revised by the first author because some of the names of the species were not updated or sometimes misspelled. As a result, some changes at any of the taxonomic ranks (e.g. order, family, genus or species) had to be adopted in conformity with the used nomenclature. Even though, in cases of synonyms, both scientific names were included. The taxonomic revision of scientific names and data checking were performed by using Index Fungorum (Index Fungorum 2019) and Mycobank (Robert et al. 2019). To publish our dataset in the GBIF network, we adjusted our records with the Darwin Core specifications (Wieczorek et al. 2012).

2.6 Geographic coverage

Description: Geographic coverage corresponded to all continental areas, except Antarctica. We collected data from 81 different countries and 61 first-order administrative divisions of the six largest countries. The continent with the highest number of records was Europe (38.78% of records) and the one with the lowest number was Asia (4.7% of records) (Figure 2.1). A map showing the number of introduced species per country and administrative divisions, respectively is presented for the world and Europe (Figure 2.2). For 26 of the records collected, only the continental-level distribution was possible to assign, as more precise geographical information was unavailable.

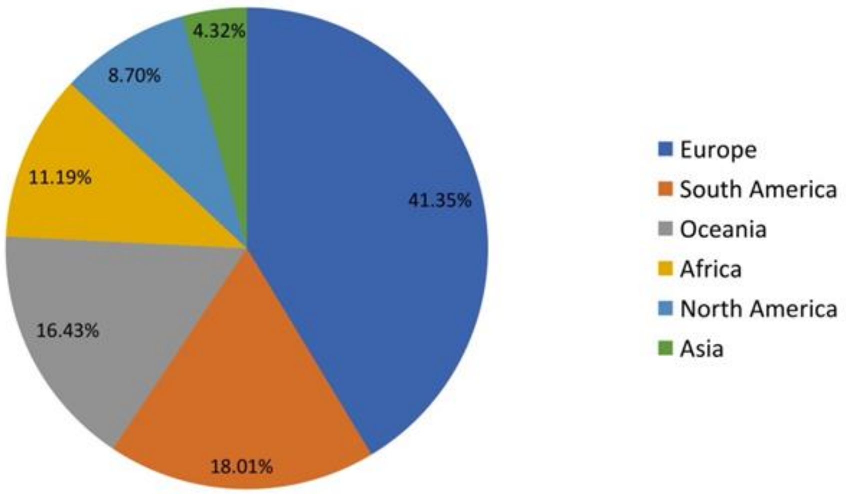

Figure 2.1. Percentage of introduction records per continent.

2.7 Taxonomic coverage

Description: The dataset includes distribution records of alien macrofungi taxa from 2 phyla, 7 classes, 22 orders, 82 families, 207 genera, 648 species and 31 varieties, forms or subspecies (Monteiro et al. 2020). Agaricales is the best represented order (44.2% of the records), followed by Boletales (29.2% of records) and Russulales (6.7% of records). The Suillaceae, Agaricaceae and Sclerodermataceae are the families with most alien records (224, 199 and 135 records, respectively) (Figure 2.3). Twelve records belong to taxa that were placed incertae sedis within their orders as the assignment to a family is yet unclear. Finally, the species with the highest number of alien records are *Suillus luteus* (L.) Roussel (44 records), *Phellinus noxius* (Corner) G. Cunn. (43 records), *Amanita muscaria* (L.) Lam. (38 records), *Amanita phalloides* (Vaill. ex Fr.) Link (37 records), *Suillus granulatus* (L.) Roussel (34 records) and *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya (34 records).

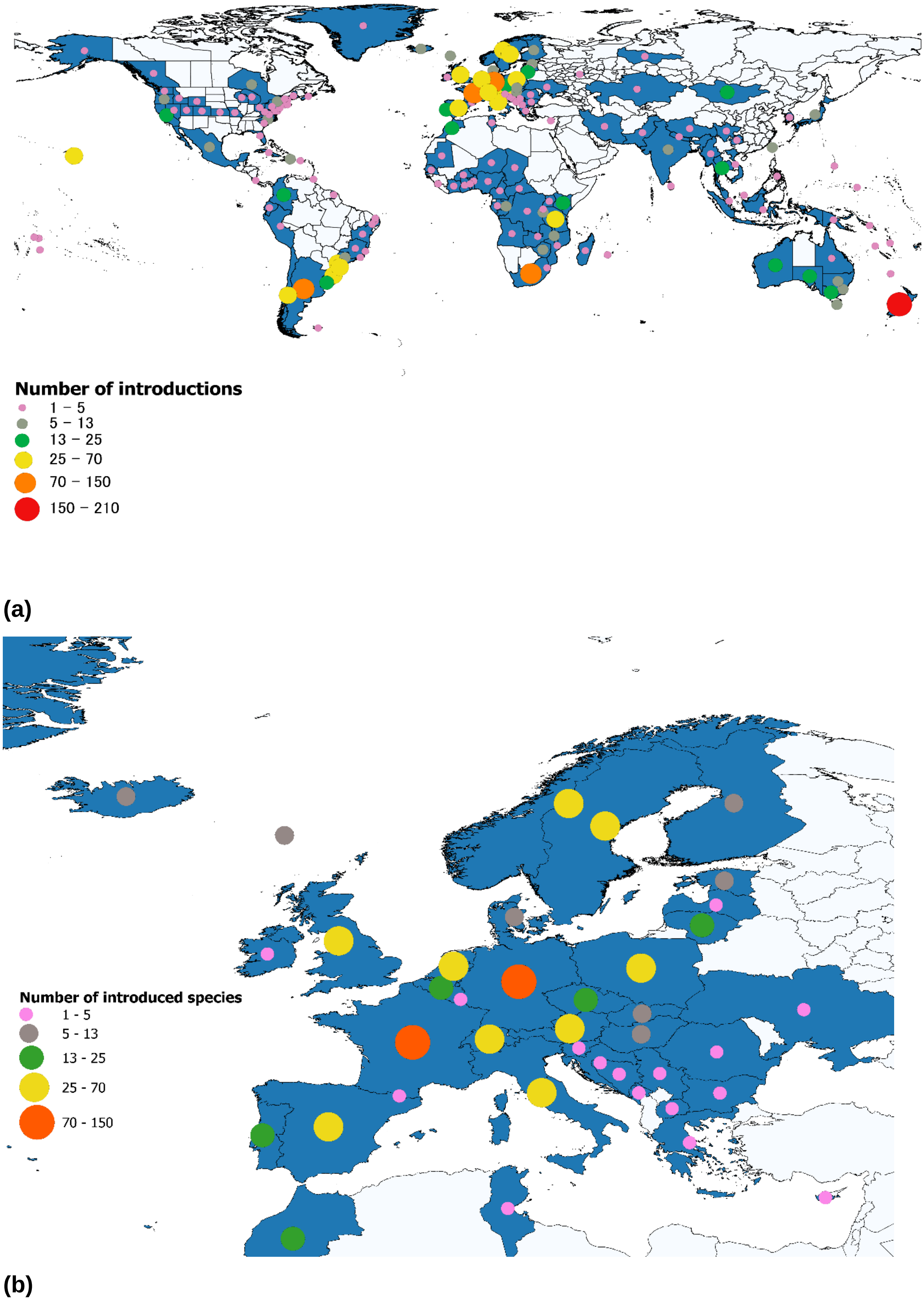

Figure 2.2. (a) The global distribution of the introduced macrofungi species. (b) The European distribution of macrofungi species. Blue color represents countries/administrative divisions with at least one introduced species. Circles represent the number of species that have been reported as introduced by both size and color.

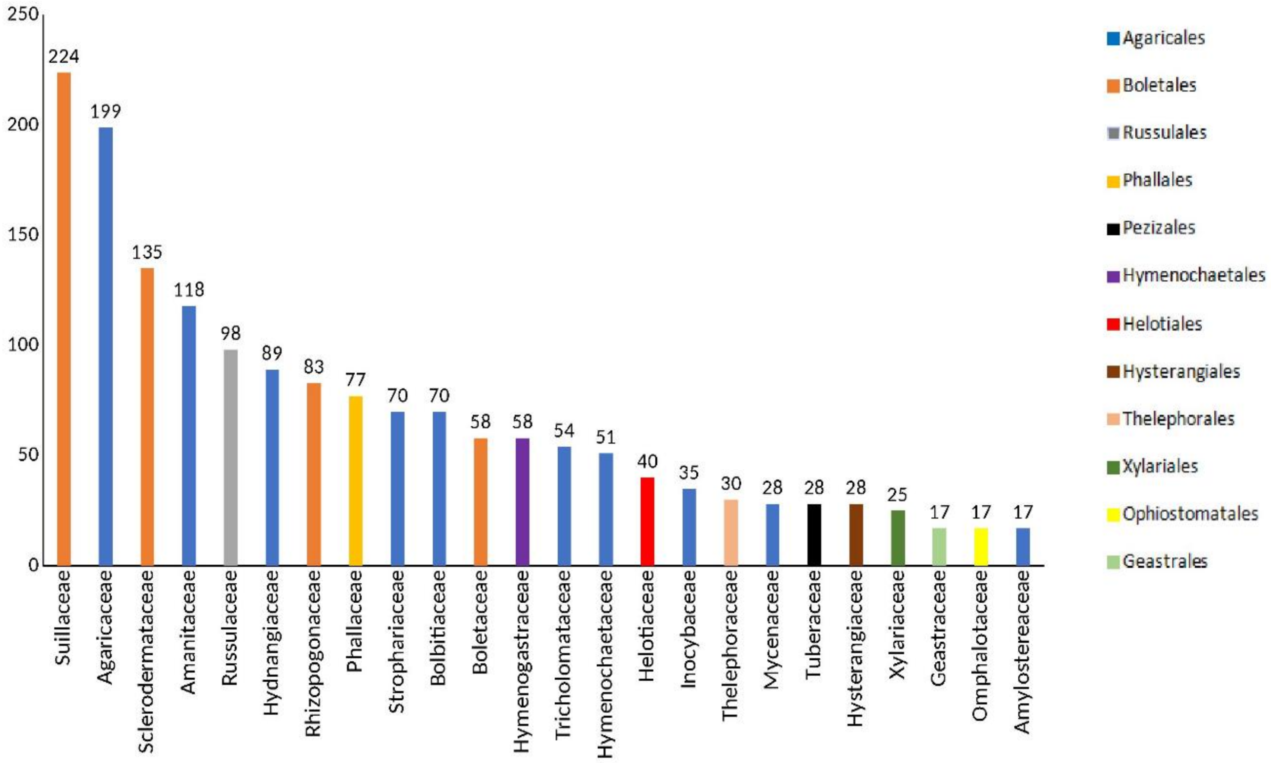

Figure 2.3. Number of introduction records per family. Only families with more than 17 records are shown. All families were coloured according to their associated order.

Two official fungal nomenclatural repositories, Index Fungorum (Index Fungorum 2019) and Mycobank (Robert et al. 2019), were used to resolve taxa and properly attribute the most recent valid names. Index Fungorum was considered our main reference and Mycobank was a secondary resource for some ambiguous cases. Both repositories are currently responsible for documenting the list of scientific names that have been validly defined for fungal taxa (Table 2.1).

Table 2.1. Taxa included in the database

Rank	**Scientific Name**
phylum	Basidiomycota
kingdom	Fungi
phylum	Ascomycota
class	Agarocomycetes
order	Agaricales
order	Amylocorticiales
order	Auriculariales
order	Boletales
order	Cantharellales
order	Geastrales
order	Gloeophyllales
order	Gomphales
order	Hymenochaetales
order	Hysterangiales
order	Phallales
order	Polyporales
order	Russulales
order	Thelephorales
class	Dacrymycetes
order	Dacrymycetales
class	Tremellomycetes
order	Tremellales
class	Dothideomycetes
order	Pleosporales
order	Helotiales
class	Leotiomycetes
class	Pezizomycetes
order	Pezizales
class	Sordariomycetes
order	Xylariales

2.8 Temporal coverage

Data range: 1785-1-01 - 2018-12-31.

Notes: Data sources provided the dates when the species was detected for the first time in a given region for 755 of the 1966 records included in the dataset. The earliest first record dates back to 1753 and the most recent event occurred in 2018. The lowest number of first records is reported between 1900-1925 and the highest number occurred between 1975-2000. Nevertheless, the cumulative number of those introductions grew in a steady way during the referenced period (Figure 2.4).

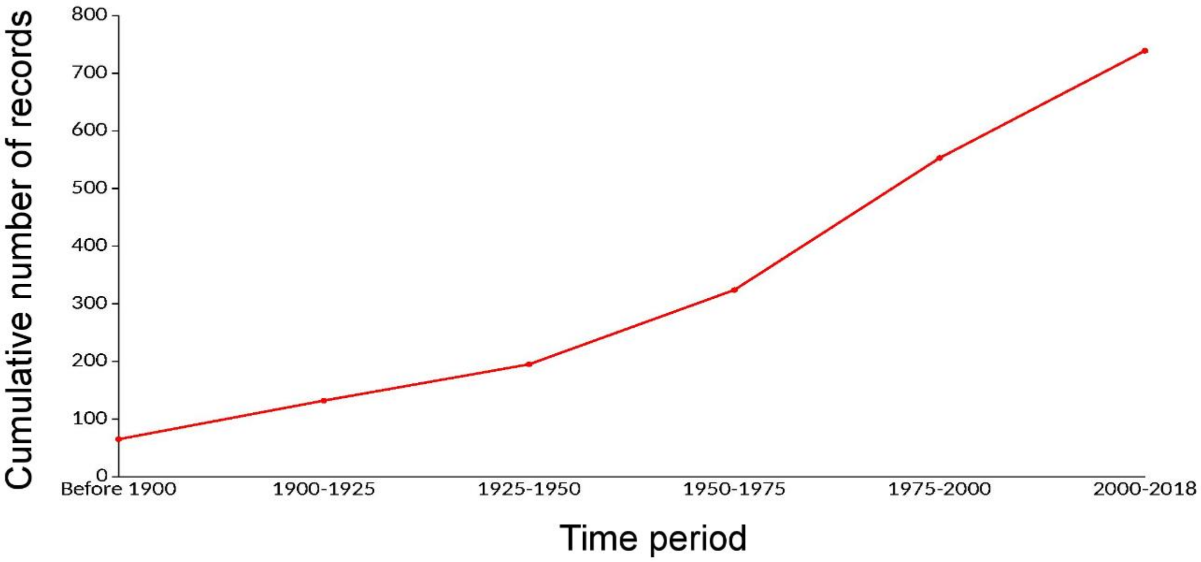

Figure 2.4. Temporal accumulation of the number of first records in 25-year periods. The temporal progression is based on 38% of the total of distribution records included in the dataset.

2.9 Usage rights

Use license: Other

IP rights notes: CC-BY 4.0

2.10 Data resources

Data package title: Global database of alien macrofungi

Resource link: https://www.gbif.org/dataset/da3542b4-9a73-4054-b9a3-2d762e172199

Alternative identifiers: https://doi.org/10.15468/2qky1q

Number of data sets: 2

Data set name: Darwin Core Archive Occurrence dataset

Character set: UTF-8

Download URL:
https://www.gbif.org/dataset/da3542b4-9a73-4054-b9a3-2d762e172199

Data format: Darwin Core Archive format

Data format version: 2.0

Data fields in Occurrence dataset:

Column label	Column description
id	Record identifier
basisOfRecord	The specific nature of the data record
occurrenceID	Occurrence identifier
occurrenceRemarks	Occurrence remarks
establishmentMeans	Establishment means
associatedReferences	Associated references
associatedTaxa	Associated taxa
eventDate	Event date
countryCode	Country code
locality	Locality
taxonID	Taxon identifier

Data set name: Darwin Core Archive Taxon dataset

Character set: UTF-8

Download URL: https://www.gbif.org/dataset/da3542b4-9a73-4054- b9a3-2d762e172199

Data format: Darwin Core Archive format

Data format version: 2.0

Data fields in Taxon dataset:

Column label	**Column description**
id	Record identifier
taxonID	Taxon identifier
scientificName	The full scientific name, with authorship
acceptedNameUsage	The full name, with authorship and date information, if known, of the currently valid taxon
namePublishedIn	A reference for the publication in which the scientificName was originally established under the rules of the associated nomenclaturalCode
namePublishedInYear	The four-digit year in which scientificName was published
kingdom	Kingdom name
phylum	Phylum name
class	Class name
order	Order name
family	Family name
genus	Genus name
specificEpithet	Specific epithet
infraspecificEpithet	Infraspecific epithet
taxonRank	Taxonomic rank
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode
language	Language of the resource
datasetName	Dataset name

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Chapter 3

Patterns and drivers of the global diversity of non-native macrofungi

The article was mentioned by the journal as the “Editor's choice” of the respective monthly publication where it was included (Vol. 28, Issue 11 in October 2022).

The article corresponding to this chapter was published in *Diversity and Distributions*

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https://doi.org/10.1111/ddi.13607

Patterns and drivers of the global diversity of non-native macrofungi

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3.1 Abstract

Aim To uncover the biogeography of non-native macrofungal diversity worldwide, by analysing patterns and drivers of (1) regional variation in species richness, (2) compositional similarity between regional species assemblages and (3) the spatiotemporal trends of first records.

Location Global.

Methods We used a database providing 1608 distribution records of 554 non-native macrofungal species in 167 national and sub-national regions worldwide. Regression models accounting for regional levels of recording capacity, were used to relate spatial variation of non-native macrofungal richness and of regional compositional similarities to variables representing geographic, socio-economic, and biophysical characteristics of regions. Temporal trends of first records were assessed at the global and continental scales and for distinct ecofunctional groups.

Results Regions reporting higher diversity of non-native species occur mainly in Europe, the Americas and Oceania. Regression models showed that regions with greater gross domestic product per capita, areal extent and in the Southern Hemisphere have higher non-native species richness, while regions with similar mean temperatures and latitudinal position share higher compositional similarities. Numbers of first records of non-native macrofungi have grown quasi-exponentially between 1753 and 2018, reflecting improved recoding capacities but also likely an increasing number of introductions.

Main Conclusions We find that many regions of the world already harbour a high diversity of non-native macrofungi, with economic, climatic and introduction pathway-related factors explaining a relevant portion of the geographic patterns formed by these taxa. Given that socio-economic activity has increased strongly in recent decades, the global anthropogenic redistribution of macrofungi is likely to intensify further in the near future.

Keywords: biological invasions, drivers, ectomycorrhiza, observational data, saprotrophs, species richness.

3.2 Introduction

The intensification and globalization of human activities is increasingly leading to the introduction of species outside their native ranges (Pyšek et al., 2020; Seebens et al., 2017; Seebens et al., 2021). Although many of these species fail to establish in non-native regions (Jeschke et al., 2018), a fraction eventually succeeds (Dawson et al., 2017) changing the composition, structure and functioning of ecosystems (Capinha et al., 2020; Linders et al., 2019). Established non-native species often have no apparent negative impacts on native biodiversity and human welfare (Tobin, 2018), but some are responsible for major biodiversity losses (Bellard et al., 2016; Bellard et al., 2021), economic costs (Diagne et al., 2021) and human health threats (Hulme, 2014). Worryingly, recent research suggests that the numbers of established non-native species will continue to grow globally in the coming decades (Seebens et al., 2021), with likely major negative impacts for biodiversity (Essl et al., 2019).

As a result of the changes and impacts caused, interest has grown in investigating patterns of biological invasions at large geographical scales and in how these patterns are driven by human activity and environmental factors (e.g., Dawson et al., 2017; Guo et al., 2021). Despite this interest, the patterns and drivers of invasion remain poorly known for many taxonomic groups, including fungi. Fungi form a hyper-diverse kingdom that plays a crucial role in ecosystems. Saprobes are essential to the recycling of nutrients being dominant decomposers of the complex components of plant debris (Tedersoo et al., 2014). Other fungi engage in symbiotic relationships, e.g., mutualistic ones, such as different types of mycorrhiza (e.g. ectomycorrhiza), or antagonistic ones, e.g., plant pathogens (Willis, 2018). In addition to their relevance in natural ecosystems, fungi are also economically and socially important resources for direct human usage (e.g., for antibiotics and as food source; Frąc et al., 2018; Kendrick, 2011). Notwithstanding these features and the identification of a considerable number of known non-native species (Desprez-Loustau, 2009; Desprez-Loustau et al., 2010; Monteiro et al., 2020; Santini et al., 2013; Vellinga et al., 2009; Vizzini et al., 2009), fungi are still largely missing in macroecological and biogeographical analyses of invasion patterns, particularly at the global scale.

With the aim of reducing this research gap, we recently compiled the Global Alien Macrofungi Database (‘GAMD’; Monteiro et al., 2020), the largest and most complete source of information on the global distribution of non-native macrofungi, i.e., the subset of fungi that form visible fruiting bodies (Senn-Irlet et al., 2007), consisting mostly of saprobes and ectomycorrhiza. This database identifies the non-native occurrences of taxa (at the genus or species level) in countries and major subnational divisions worldwide. It results from the compilation, harmonization, and verification of published information identifying macrofungi as introduced or possibly introduced (i.e., ‘cryptogenic’; Essl et al., 2018) by human agency into an area outside of its native range. These records were comprehensively searched and collected from a wide variety of sources, including scientific publications, technical reports, online databases and citizen science projects (see Monteiro et al., 2020). In addition to distribution records per se, the database also includes the dates of first observation of taxa in each non-native region, when these are supplied by the original sources.

As for fungi in general the invasion patterns and drivers of non-native macrofungi remain poorly known, despite comprising some of the most easily recognised and widely known fungal species (e.g., the fly agaric; *Amanita muscaria*). This could be because most macrofungi are saprotrophic or ectomycorrhizal and the ecological changes and impacts they cause are less obvious than those of pathogenic fungi (Desprez-Loustau et al., 2007). Indeed, the biogeography and macroecology of several non-native, often microscopic, fungal pathogens are well studied, driven by their socio-economic or environmental damages, for example on agricultural crops (e.g., Bebber et al., 2014; Bufford et al., 2016; Fones et al., 2017; Scott et al., 2019) − but see for example Paap et al. (2022), for a discussion of knowledge limitations even for these taxa. On the other hand, knowledge on patterns of macrofungal invasions is geographically restricted (e.g., Szczepkowski et al., 2014; Wood, 2017) and biased towards mycorrhizal taxa (e.g., Dickie et al., 2017; Nuñez et al., 2014; Vellinga et al., 2009). Of particular relevance is the work of Vellinga et al., (2009), who mapped the distribution patterns of non-native ectomycorrhizal fungi and found, for example, that these taxa are strongly associated with the movement and planting of a few economically important tree genera, such as *Pinus spp.* and *Eucalyptus spp.*. However, given the mutualistic nature of ectomycorrhizal fungi, the findings of Vellinga et al., (2009) may not be representative of non-native macrofungi in general and saprotrophic species in particular, the largest group of fungi in soil (Bridge & Spooner, 2001).

Based on the knowledge available for some regions of the world, macrofungi subgroups and non-native taxa in general, some testable hypotheses can be made about the biogeography, drivers and temporal trends of non-native macrofungi worldwide (Santini et al., 2013; Wood, 2017). Variation in richness of non-native species is likely positively related to the geography of economic wealth and human population size, expressing the cumulative role of economic and trading activities in generating introduction opportunities (Desprez-Loustau et al., 2010; Dawson et al., 2017). In addition, forest area, particularly of planted trees, is also likely associated with the richness of non-native macrofungi, considering the importance that this habitat has for many species and the known role of commercial forestry as a pathway of species introductions (Vellinga et al., 2009). In this regard, it can even be expected that species numbers will be higher in regions of the Southern Hemisphere where tree species native to the Northern Hemisphere (e.g., pines) were intensively planted (Richardson and Higgins, 1998; Vellinga et al., 2009; FAO, 2015). The richness of non-native macrofungi is likely higher on islands. This is because the diversity of native taxa in many of these regions is low (Delavaux et al., 2019), increasing the pool of potential non-native species. Finally, climate likely also plays an important role, determining where introduced species will meet their climatic requirement (Větrovský et al., 2019) and, to some extent, the distribution of symbionts and availability of dead organic matter (Tedersoo et al., 2014). Concerning regional compositional similarities, it is likely that regions that are geographically close and have similar socioeconomic (e.g. human population size, economic wealth) and biophysical conditions (e.g. climate, island communities) will share higher proportions of the same species, reflecting similarities in the identity of the species that are introduced (Richardson and Higgins, 1998; Velllinga et al., 2009) and the environmental 'filtering' of those that become established (Capinha et al., 2015). Finally, as is the case for most other taxonomic groups (e.g., Bertelsmeier et al., 2017; Seebens et al., 2017), we expect the number of new introduction records to have increased over time and in different regions of the globe.

Here, we provide the first comprehensive analysis of the patterns and determinants of the spatial and temporal distribution of non-native macrofungi worldwide. While doing so we consider the challenges associated with using these data, coming from multiple regions, and published over a wide period of time, which inherently includes recording deficits and spatiotemporal biases. Specifically, our objectives are, i) to identify regional hotspots and coldspots of non-native species richness and the environmental and socioeconomic drivers of these patterns; ii) to map patterns of taxonomic similarity between regional assemblages of non-native species and identify the drivers of their geographical variation and iii) to examine the temporal trends of the first records of non-native macrofungi worldwide, on distinct continents and for distinct ecofunctional groups.

3.3 Methods

3.3.1 Global distribution data for non-native macrofungi

We used distribution data of non-native macrofungi from GAMD (Monteiro et al., 2020). This database is a comprehensive source of information for known non-native macrofungi across regions of the world, with regions consisting of countries and the first-order administrative divisions of Australia, Brazil, Canada, China, Russia, USA (the six largest countries in the world). The database comprises a single occurrence record per taxon-region pair, which means that during data compilation multiple records of the same taxon in a region were converted into a single, region-level, record. For this work, we only considered taxa having accepted species names based on two nomenclatural repositories, the Index Fungorum (www.indexfungorum.org) and MycoBank (www.mycobank.org). Considering the uncertainty of their nativity status, we also excluded all records referring to cryptogenic species. The data used for analyses comprised a total of 1608 distribution records, representing 554 species, distributed across 2 phyla, 6 classes, 21 orders, 80 families and 204 genera. Of these species, 255 are ectomycorrhizal, 292 are saprotrophic and 7 are parasitic/pathogens. A total of 167 regions are comprised (mean number of records per region = 9.63 ±19.04 standard deviation), of which New Zealand (n = 169), Germany (n = 87) France (n = 69), South Africa (n = 64) and Argentina (n = 60) hold the highest numbers of records. In addition, we also used data on the year of the first record of the species in each region, which was available for 648 of the 1608 records.

3.3.2 Predictor variables and associated hypotheses

To investigate the drivers of regional variation in non-native macrofungal richness and compositional similarity worldwide, we compiled a set of variables representing plausible geographic, climatic, socio-economic and land use drivers, reflecting the hypotheses raised in the introduction section, (1) per capita GDP (gross domestic product) (2) human population size; (3) mean population density; (4) insularity (i.e., if the region is an island; yes/no); (5) total land area; (6) latitude; (7) mean annual temperature (8) mean annual precipitation, (9) total forest area and (10) total area of planted forests (see a list of these variables with measurement units and data sources in Table 3.1). These variables were collected or aggregated at a country or state level, matching the study units of the Database of Global Administrative Areas v. 3.6 (GADM, 2012).

Table 3.1. Description and sources of the socio-economic, geographic and climatic variables that were considered as predictors of non-native macrofungal diversity worldwide.

Variable	Description	Sources
Sampling effort	Percentage completeness of native species inventories per region.	Meyer et al., 2015, 2016.
Gross domestic product (GDP) per capita	Mean income (in US$) in 2019 (or closest year available).	Worldbank (data.worldbank.org; Worldbank, 2019).
Human population size	Total number of individuals per country or first administrative area in 2019 (or closest year available).	Worldbank (data.worldbank.org; Worldbank 2019), Worldometer (www.worldometers.info; Worldometer, 2020), Worldpopulationreview (worldpopulationreview.com; World Population Review, 2020).
Human population density	Number of individuals per km2 in 2019 (or closest year available).	Same as for ‘Human population size’ and Worldatlas (www.worldatlas.com; Worldatlas 2020).
Insularity	1 = island 0 = not island	No specific source.
Total land area	The aggregate of all land within international boundaries and coastlines (in km2).	Calculated in GIS using the shapefile of the Database of Global Administrative Areas GADM v 3.6 (https://gadm.org), after reprojection into a Mollweide equal-area projection.
Latitude	Centroid latitude (in decimal degrees). (Note, that we use plain, rather than absolute values, distinguishing the Northern and Southern Hemisphere)	Calculated in GIS using the shapefile of the Database of Global Administrative Areas GADM v 3.6 (https://gadm.org).

Mean annual precipitation	The average annual total precipitation from 1981 to 2010 (in millimetres).	Calculated in GIS using the CRU 4.01 gridded climate dataset (Harris et al., 2020).
Mean annual temperature	Average annual temperature from 1981 to 2010 (in degrees Celsius).	Calculated in GIS using the CRU 4.01 gridded climate dataset (Harris et al., 2020).
Total forest area	The aggregate of all areas occupied by primary, naturally regrown, planted and unclassified forests (in km2).	Calculated in GIS using the ‘forest classes level 1’ theme (Schulze et al., 2019).
Total area of planted forests	The aggregate of all areas occupied by planted forests (in km2).	Calculated in GIS using the ‘forest classes level 1’ theme (Schulze et al., 2019).

3.4. Data analyses

3.4.1 Spatial patterns and drivers of non-native macrofungi richness

To analyse the relationships between richness of non-native macrofungi and geographical, socio-economic and biophysical characteristics of regions, we used a generalized least squares (GLS) regression (Dormann et al., 2007). To conform with the availability of data for some of the variables (e.g., per capita GDP), the analysis was performed at the country scale. For that purpose, the non-native species richness of countries represented at the subnational scale in GAMD (i.e., Australia, Brazil, Canada, China, Russia and USA) were upscaled accordingly. The ten variables indicated in section 2.2. were considered for this analysis.

Because regional variation in sampling effort can bias the identification of richness drivers (i.e., observational bias), we considered an additional predictor variable representing sampling effort. Direct measurements of the degree of sampling effort for macrofungi are not available, so we used estimates of percentage completeness of native species inventories in the Global Biodiversity Information Facility (GBIF). These estimates are available for amphibians, mammals, plants, and reptiles (Meyer et al., 2015, Meyer et al., 2016), and we used their cross-taxonomic average as a proxy for the completeness of biodiversity information in each country (cf. Dawson et al., 2017). We note that while the absolute values of sampling effort for these taxa are likely higher than those of macrofungal taxa, their inter-regional differences (i.e., what is considered in the regression model) are likely to provide a good indication of interregional differences for macrofungi as well. This is because levels of sampling effort worldwide and their determinants are generally strongly correlated across taxa (Meyer et al., 2015, Meyer et al., 2016).

The variables non-native species richness (dependent), per capita GDP, human population size, population density, total land area, total area of forest and total area of planted forest (predictors), were $\log_{10}$-transformed to improve the robustness of the statistical significance of coefficients (Ives, 2015). Prior to the modelling, we tested for redundancies among the predictors using Pearson's pairwise correlation (r) and three strongly correlated ($|r| > 0.70$; Dormann et al., 2013) pairs of predictor variables were identified, human population size and land area extent, total forest area and land area extent, and total forest area and human population size. To avoid adding this redundancy to the models, the variables human population size and total forest area were no longer considered.

We performed two models aiming to identify the drivers of richness, one including the proxy for sampling effort and another without it. This allowed exploring the sensitivity of identified relationships to the use of this predictor.

In addition, we developed a third model aimed at providing a visual depiction of the distribution of hotspots and coldspots of richness, after accounting for the confounding effects of total land area and sampling effort. For this purpose, we ran a GLS model of richness values as a function of sampling effort, $\log_{10}$-transformed land area and the interaction of the two (Dawson et al., 2017). The residuals from this model were then ranked into deciles and mapped to identify hot- and coldspots of richness.

The GLS models were implemented using the 'nlme' package (Pinheiro et al., 2021) for R. version 4.0.3 (R Core Team 2020) and included a spatial term accounting for an exponential decrease in the correlation of residuals with increasing spatial distances (cf. Dormann et al., 2007).

3.4.2 Patterns and drivers of regional compositional similarity

To assess the biogeographic regionalisation of non-native macrofungi, we examined the similarity of species composition between each pair of regions by calculating the Simpson index of dissimilarity (Baselga, 2010). This index returns values from zero, corresponding to identical taxonomic composition (i.e., all species are shared between the two regions) to one (no species are shared). The Simpson index calculates the proportion of species shared with reference to the region having lower species richness i.e., it measures the turnover component of beta diversity; Baselga (2010). In the context of our study, this is a valuable property as it allows removing the potential effect of biases caused by differences in recording capacity of regions. Compositional dissimilarity calculations were performed using the 'betapart' package (Baselga & Orme, 2012) for R.

We then used the UPGMA clustering technique (Unweighted pair group method with arithmetic mean; (Weigelt et al., 2013) to visualise the grouping of regions according to observed levels of pairwise compositional similarity. In addition, we also analysed whether the grouping patterns were driven by geographic, biophysical and socio-economic factors. For this purpose, we used a multiple regression on distance matrices (MRM) available through the 'ecodist' package (Goslee & Urban, 2007) for R. This model uses a distance (or dissimilarity) matrix as response variable and any given number of distance matrices as predictor variables. In our model the response variable corresponded to the matrix of Simpson's dissimilarities and the predictor variables were

(1) geographic distance; (2) mean latitude; (3) insularity; (4) mean annual temperature; (5) mean annual precipitation; (6) per capita GDP; (7) human population size, (8) human population density; (9) total forest area and (10) total area of planted forest (see introduction section for rationale on the selection of variables). The geographic distance between the centroids of regions were calculated using the "r.dist.earth" function of R package 'fields' (Etten 2017). Pairwise differences for the remaining variables were obtained using Euclidean distance. Pairwise differences of considered variables were not strongly correlated (i.e., $|r| > 0.70$). As for the GLS model (previous section), these analyses were performed at the country scale, to conform with the availability of data on socioeconomic predictors.

Regional species assemblages with a low number of species are likely to be less representative of the cumulative effect of the processes determining the formation of these assemblages, as they are more sensitive to randomness in these processes and to potential data errors (caused, for example, by taxonomic errors in identification). Thus, to assess the robustness of results to these confounding factors, we performed three distinct UPGMA and MRM analyses, using all regions, using regions with 3 or more non-native species and using regions with 5 or more non-native species.

3.4.3 Temporal patterns of non-native macrofungal species accumulation

We plotted and compared the temporal trends of non-native species accumulation at the global scale, for each continent and for each of the species' ecofunctional types. These trends should exhibit relevant temporal bias driven by improvements of recording capacity of regions along time (La Salle et al., 2016; Andrew et al., 2017). However, because so far it is unclear how this bias could be addressed analytically (e.g., Bertelsmeier et al., 2017; Capinha et al., 2017; Seebens et al., 2017), we here perform a visual assessment of these trends and interpret them taking into account the potential role of this confounding factor. The assessment of these trends was considered for three ecofunctional types, ectomycorrhizal, saprotrophs, and pathogens/parasites. For that purpose, we identified the ecofunctional type of each species through a literature search, using scientific papers and Google Scholar (search terms used were, "species name", "ecofunctional type", "species ecology" and "habitat type"). The trends for pathogens/parasites were not assessed, due to the low prevalence of these species in the data (n = 19).

3.5 Results

3.5.1 Spatial patterns and drivers of non-native macrofungi richness

After accounting for sampling effort and spatial extent, regional hotspots of non-native macrofungi richness (defined as the top 10%) occur mainly in Europe (e.g., Poland, Switzerland, Netherlands, Italy, Lithuania and Austria), but also in South America (Brazil, Argentina and Chile) and Oceania (New Zealand and Norfolk Island) (Figure 3.1). On the other hand, coldspots (the lowest 10%) are mainly concentrated in Asia (Indonesia, Iran, Kazakhstan, Myanmar, Papua New Guinea, Philippines), but some also occur in Africa (Angola, Cameroon, Mozambique), Europe (Ireland) and Central America (Costa Rica).

Results from GLS models showed that inter-regional differences in richness of non-native macrofungi are significantly positively related with land area extent and per capita GDP and negatively to latitude (Table 3.2). Variables representing biophysical factors (mean annual temperature, mean annual precipitation and area of planted forest) and insularity were non-significant. These results are verified irrespectively of the use of sampling effort as predictor (Table 3.2AB), and despite the significant positive relationship of this variable with richness values when included in the model (Table 3.2A). Both GLS models, i.e., with and without sampling effort, explained a relevant amount of spatial variation in richness values (pseudo-$R^2 = 0.47$ and 0.40, respectively).

3.5.2 Patterns and drivers of regional compositional similarity

Concerning the taxonomic composition of non-native macrofungi assemblages, the UPGMA algorithm identified multiple macro-clusters (Figure 3.2). The highest geographical cohesion occurs among European countries, which consistently cluster with each other, particularly when considering only assemblages having 3 or more and 5 or more non-native species (Figure 3.2bc). A few clusters composed of multiple countries in distinct continents are also consistently identified. One of these is composed mainly of mid to high latitude countries in the Southern Hemisphere (e.g., New Zealand, South Africa, Zimbabwe, Argentina, Chile; Figure 3.2a-c), which also includes the USA and Australia when assemblages having 3 or more and 5 or more non-native species are used (Figure 3.2bc). Another cluster involves mainly low latitude countries in Africa (e.g., Burundi, Rwanda, Madagascar and Republic of Congo) and in South America (Colombia and Brazil).

The MRM regression identified mean annual temperature as the only significant predictor across all data sets analysed (Table 3.3). The coefficient for this predictor is positive, meaning that lower differences in mean annual temperature are associated with a higher similarity in species compositions. Differences in latitude were significant in two of the three models and also related positively with compositional dissimilarity. Two predictors were significant in only one of the models, geographical distance when using data on assemblages with three or more non-native species (in which latitudinal differences are not significant), and differences in per capita GDP for assemblages composed of five or more species. In both cases the predictors were positively associated with compositional dissimilarities. However, it is noteworthy that these models explained only a small portion of variation in compositional dissimilarities (R^2 from 0.19 to 0.21).

3.5.3 Temporal patterns of non-native macrofungal species accumulation

We found that the number of first records of non-native macrofungi increased strongly over time, particularly in the last century (Figure 3.3a). This pattern holds when the numbers of records are grouped by continents, with most records being made in Europe (399 records), followed by North America (81 records) and Oceania (68 records). Reporting started much earlier on the European continent than on the other continents (Figure 3.3b), particularly in Africa, Asia and South America, for which most of the first records were only reported in the last 45 years. First records of ectomycorrhizal and saprotrophic species increased similarly over time (Figure 3.3c). In the last period (2000 to 2018) there has been a decline in the number of first records for Europe and South America.

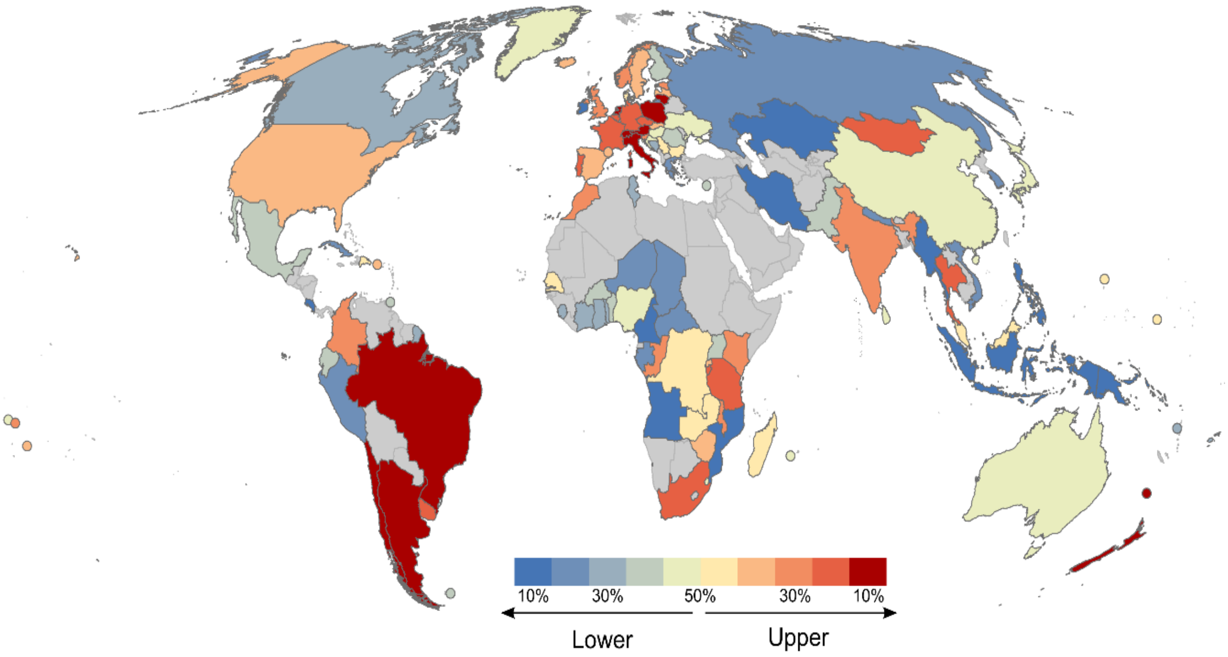

Figure 3.1. Hotspot and coldspot regions for richness of non-native macrofungi. The colour gradient shows the decile of residuals obtained from a regression model relating recorded richness values to area extent and sampling effort. Small regions are visualized by circles and regions without data are represented in grey.

3.6 Discussion

This study provides the first assessment of the biogeographical patterns and drivers of non-native macrofungal distribution in regions worldwide, covering more than 550 species from three ecofunctional types (ectomycorrhiza, saprotrophs and parasites/pathogens). After accounting for the effects of sampling effort and areal extent, we found that most hotspots of non-native species are found in Europe, South America and Oceania, while coldspots are mainly found in Asia and Africa. Macrofungal richness is positively associated with GDP per capita and negatively with latitude, suggesting a consistently higher richness of non-native macrofungi in wealthier regions and in the Southern Hemisphere. Inter-regional similarities in species identities are consistently related to temperature and geography, either in terms of geographical distance or latitudinal position, although the fraction of variance explained by these factors is small. Finally, the number of new first records of non-native fungi has been steadily increasing over time and across continental regions.

Table 3.2. Results of a generalized least squares regression (GLS) explaining the richness of non-native macrofungi species across countries (n=111). Results are given for a model with a predictor variable representing regional differences in sampling effort (A; Pseudo-R^2= 0.47) and for a model without this variable (B; Pseudo-R^2= 0.40). Significant predictors (α = 0.05) are marked with an asterisk.

	A			**B**		
Predictor	**Coeff.**	**Std Error**	**p**	**Coeff.**	**Std Error**	**p**
Intercept	-4.292	1.519	0.006	-4.648	1.590	0.004
Sampling effort	0.015	0.006	**0.014**	NA	NA	NA
Geographical factors						
Insularity	-0.193	0.346	0.579	-0.101	0.369	0.785
Area (log$_{10}$)	0.603	0.187	**0.002**	0.589	0.187	**0.002**
Latitude	-0.019	0.006	**0.003**	-0.020	0.008	**0.010**
Biophysical factors						
Mean Temperature	-0.031	0.024	0.197	-0.030	0.026	0.247
Mean Precipitation	-00004	0.0002	0.795	-00004	0.0002	0.816
Planted forest area	0.168	0.134	0.211	0.179	0.134	0.187
Socio-economic factors						
Per capita GDP (log$_{10}$)	0.558	0.268	**0.040**	0.717	0.270	**0.009**
Population density (log$_{10}$)	0.155	0.231	0.503	0.224	0.232	0.335

3.6.1 Spatial patterns and drivers of non-native macrofungi richness

The positive relationship identified between per capita GDP and richness of non-native species is unsurprising and is in line with results from previous studies showing that economic and commercial activities are a main driver of colonization pressure by non-native taxa (Dawson et al., 2017; Hulme, 2021), including some fungal groups (Bebber et al., 2014b; Deprez-Loustau et al., 2009; Santini et al., 2013; Scott et al., 2019). While specific economic activities (e.g., forestry) are important drivers of the introduction of macrofungi taxa, the aggregated effect of importation of multiple potential vector commodities, such as ornamental and forestry plants, their seeds, non-living plant material, wood, and other materials (Desprez-Loustau & Rizzo, 2011), is likely well captured by per capita GDP, explaining the relationship found. Some examples of the great diversity of potential vector commodities include eucalyptus trees leading to the occurrence of Australian ectomycorrhizal species in Spain (Díez, 2005), wool shipments, presumably leading to the introduction of the saprotrophic species *Clathrus archeri* from Australia to Europe (Desprez-Loustau et al., 2007), and bamboo, which is thought to be the cause of introduction of this species to North America (Arora & Burk, 1982).

The absence of a significant relationship for planted forest area is, on the other hand, relatively surprising but could be explained by the fact that area of tree plantations does not necessarily equate to a greater diversity of non-native tree taxa planted and thus to colonization pressures ensuing from this introduction pathway. For example, tree species native to the Northern Hemisphere, especially pines, were extensively planted in many countries in the Southern Hemisphere (Richardson & Higgins, 1998) − a factor that has been previously suggested to explain an observed higher number of non-native ectomycorrhizal fungi in these regions (Vellinga et al., 2009) and that plausibly explains the negative relationship we identified for latitude. On the other hand, in many important timber producing countries of the Northern Hemisphere (e.g., the USA, Canada, Russian Federation or Finland), tree crops are mainly composed of native taxa (MacDicken, 2015), reducing the influence of this factor as an introduction pathway. Hence, a more proximal representation of the origin of planted tree species and of the area they cover in each region would be valuable to better uncover the role of commercial forestry as driver of species introductions. While these data are available for some regions (e.g., FAO, 2015), its geographical coverage is yet far from suitable for a global-scale analysis.

The absence of significant relationships for climatic predictors is also unexpected. One possible explanation concerns the generally higher per capita GDP in temperate latitudes (Gallup et al., 1999), as is also reflected here by a relatively high correlation between mean annual temperature and this variable ($r = 0.65$ in our data). Hence, the relationship identified for per capita GDP may also reflect, to some extent, an effect of bioclimatic constraints or host availability. On a global scale, Tedersoo et al., (2014) found a peak in ectomycorrhizal richness in northern temperate biomes, coinciding with the distribution of most species of the Pinaceae, an important host plant family. Indeed, genera belonging to the suilloid group such as *Suillus* spp. and *Rhizopogon* spp. associate almost exclusively with this tree family (Vellinga et al., 2009) and comprise a relevant number of species included in GAMD (n = 24 and n = 16, respectively). Similarly, parasitic species, such as *Hymenoscyphus fraxineus* and *Entoleuca mammata* are also widespread in countries from temperate regions, reflecting the distribution of their host taxa. Thus, it may be the case that commercial activity leading to increased colonization pressures in temperate latitudes is compounded by the availability of suitable environmental and biological conditions for many of the species being transported and introduced.

The absence of a significant relationship for insularity is intriguing. A higher number of non-native taxa on islands is one of the most consistent features of non-native animal and plant biogeography (Dawson et al., 2017), a pattern believed to be driven by a higher colonization pressure in these regions, but also because the establishment of non-native species could be facilitated here (Moser et al., 2018). We suspect that the absence of this pattern for macrofungi could be related to an inversion in the role of the latter factor, owing to the complete absence or reduced availability of native symbiotic plant taxa in many of these regions (Delavaux et al., 2019; Vellinga et al., 2009). Hence, while this should not be a barrier for saprotrophic macrofungi, the capacity of ectomycorrhizal and host-specific parasitic species to establish independently (i.e., without an accompanying importation of non-native hosts) is likely minimal.

3.6.2 Spatial patterns of regional compositional similarity

A cluster analysis based on regional compositional similarities allowed the identification of three relatively cohesive country groups, one consisting mainly of European countries, another of mid- to high-latitude countries in the Southern Hemisphere, and a third of predominantly tropical countries in Africa and South America. These patterns together with results from MRM, suggest an interacting role between dominant introduction pathways and climatic filtering. The European cluster is likely a reflection of a smaller role (compared to the other clusters; see below) of introductions of ectomycorrhizal taxa from commercial tree plantations, as the most widespread species in this region are mainly non-ectomycorrhizal (e.g. *Hymenoscyphus fraxineus*; *Entoleuca mammata*; *Mutinus ravenelii*; *Clathrus archeri*). On the other hand, the other two clusters comprise mostly Southern Hemisphere countries (which likely justifies the significant relationship found for latitudinal differences), where the use of non-native tree species is much more prevalent in forestry (FAO, 2015) and has played an important role in the introduction of ectomycorrhizal fungi (Richardson & Higgins, 1998; Vellinga et al., 2009;). The division between these two clusters seems to be driven, in some extent, by climatic conditions (as supported by the significant relationship found for temperature), likely determining where species and their hosts will have their environmental requirements met. However, it should be noted that the MRM explained only about 20% of the variation in regional compositional dissimilarities, suggesting that the structuring of regional assemblages of non-native species results from a much greater variety of factors. This is not surprising given the often centuries-long action of human activities determining the geography and volumes of species introduction flows and that of multiple and interacting climatic and biotic factors determining the species' survival after introduction.

3.6.3 Temporal patterns of non-native macrofungal species accumulation

We also found that there has been a considerable increase in the number of first regional records of non-native macrofungal species over time, particularly during the 20th century − a trend that is also observed for other taxonomic groups sharing the same or related introduction pathways, such arthropods or forest pathogens (Roques, 2010; Santini et al., 2013). This increase is verified for the two ecofunctional groups assessed (saprobes and ectomycorrhiza) and in most continents. However, the extent to which this trend is driven by increased recording intensity, as resulting for instance from an improved fungal taxonomic knowledge and citizen science activities (e.g., Andrew et al., 2017), is unclear. It is likely that this factor plays an important role, considering for instance that the increase in recording rates was substantially higher in Europe, North America, and Oceania, where some countries have significant biodiversity monitoring capacity, facilitating the detection of non-native species (e.g., Bebber et al., 2014b). Despite the confounding effect of this factor, it also seems plausible that the identified trend expresses, to some extent, a true acceleration in the introduction of non-native macrofungal species worldwide, as driven by the increasing globalisation of trade and the many associated opportunities for macrofungi to be transported and introduced in new areas (Hulme, 2021). Indeed, international movement of live plants – the most common route by which associated organisms, such as fungi, reach non-native regions (Liebhold et al., 2012; Santini et al., 2013; Sikes et al., 2018) – has also increased consistently through time (Santini et al., 2018).

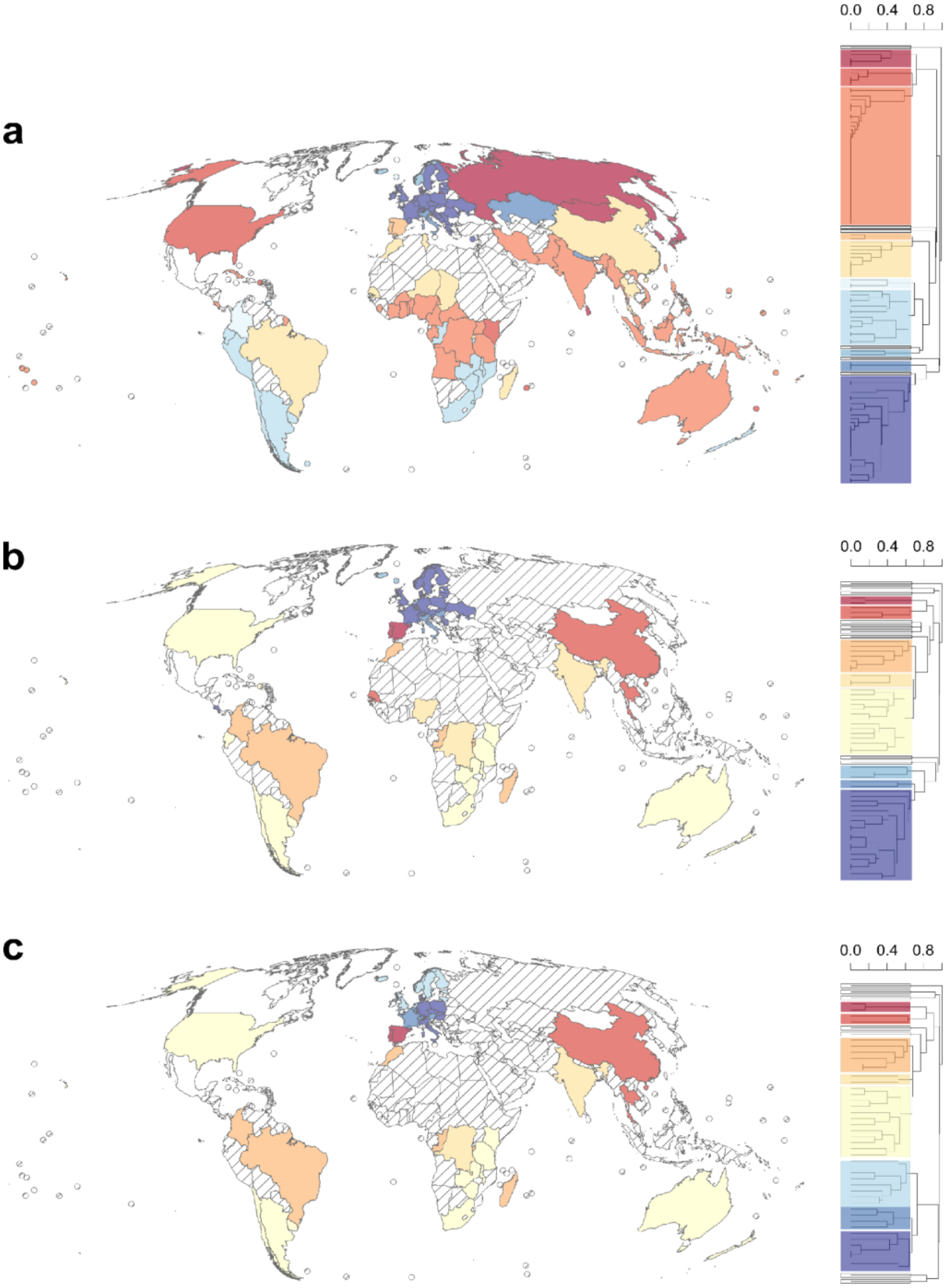

Figure 3.2. Dendrograms and geographical clusters of countries according to dissimilarities in the taxonomic composition of non-native assemblages of macrofungal species. Results are shown for (a) all countries having non-native macrofungal species, (b) countries having at least three non-native species and (c) countries having at least five non-native species. Single-country clusters are shown in white, while countries not used for clustering are shown with dashes.

Table 3.3. Results of the multiple regression on distance matrices explaining similarities in the identity of non-native macrofungi species between countries (n = 117). Significant predictors (α = 0.05) are shown in bold. Results are shown for three models, one using data for all countries (R^2 = 0.20), another for countries with three or more non-native species (R^2 = 0.19) and a third for five or more non-native species (R^2 = 0.21).

	All countries		**Countries with ≥3 non-native spp.**		**Countries with ≥5 non-native spp.**	
Predictor	**Coeff.**	**p**	**Coeff.**	**p**	**Coeff.**	**p**
Intercept	0.649	0.779	0.649	0.836	0.628	0.855
Geographical factors						
Geographical distance	2e-06	0.284	7.8-06	**0.002**	2.7e-6	0.349
Latitude	0.003	**0.001**	7.9	0.061	0.001	**0.009**
Island/not island	-0.018	0.286	-4.8e-04	0.987	-0.005	0.852
Environmental factors						
Mean temperature	0.014	**0.001**	0.009	**0.001**	0.008	**0.001**
Mean precipitation	7e-06	0.129	-7.4e-06	0.664	-1.7e-05	0.420
Forest area ($\log_{10}$)	-0.007	0.211	-0.008	0.126	-0.009	0.109
Socio-economic factors						
Per capita GDP	-3.6e-07	0.338	-2.3e-07	0.379	-6.6e-07	**0.027**
Population size ($\log_{10}$)	-0.003	0.558	0.008	0.148	0.009	0.149
Population density	-1.3e-05	0.487	5.2e-5	0.439	2.2e-5	0.767
Planted forest area ($\log_{10}$)	0.008	0.130	-0.005	0.319	-0.001	0.857

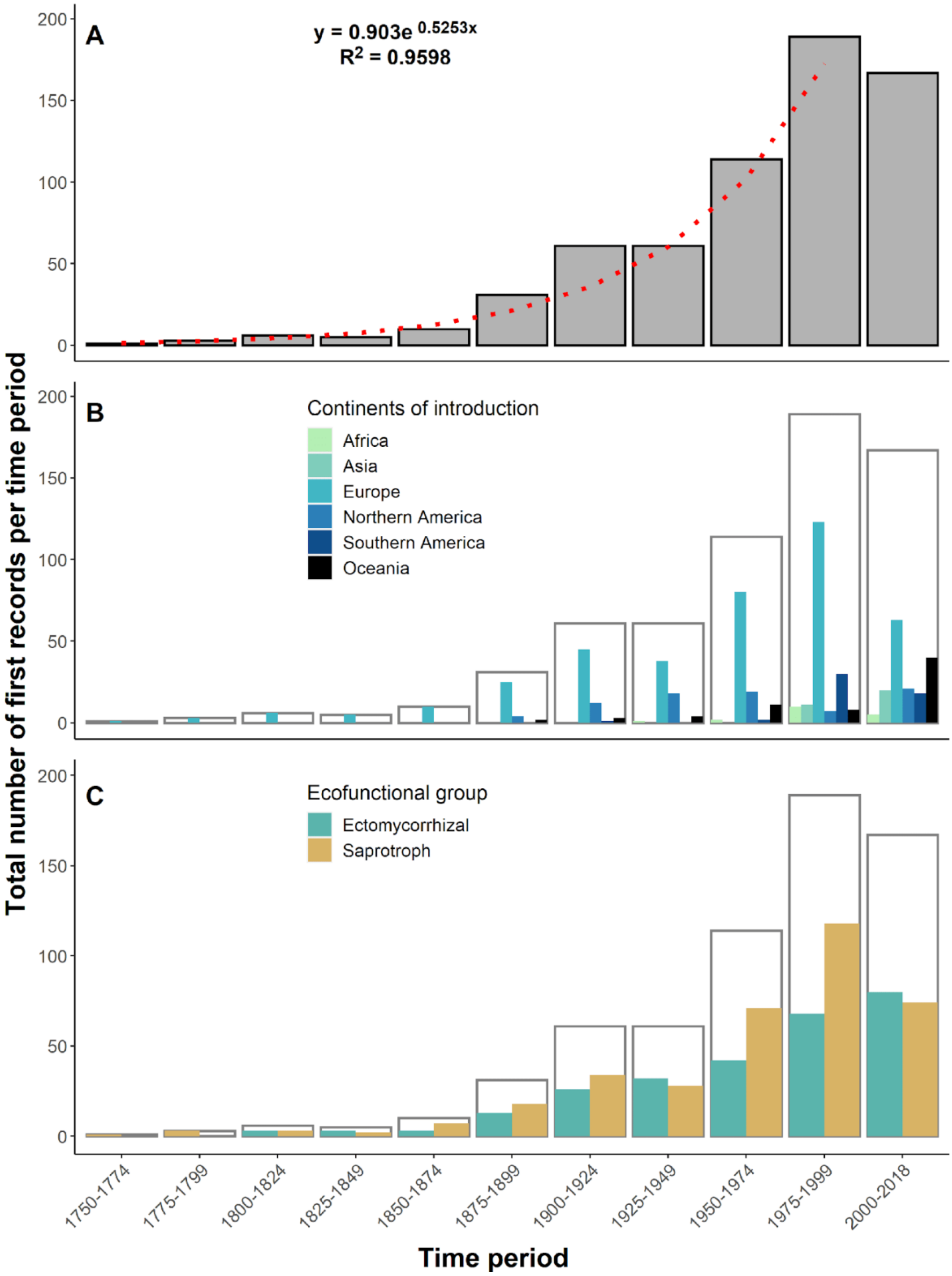

Figure 3.3. Temporal distribution of the number of first records per 25-year time period from 1750 to 2018. 1a) Total number of records (n=648; across 92 regions and 314 taxa). 1b) First records grouped by continental region of introduction (n = 648) 1c) First records of ectomycorrhizal (n=270) and saprotrophic (n=359) species.

Notwithstanding the general trend, we also identified a reduction in the numbers of first records in the most recent period (i.e., 2000 to 2018) for Europe and South America. This could indicate a slowdown in the rate of introduction of new species, as caused by a depletion of incoming species stocks (Seebens et al., 2017), or to an increased effectiveness of initiatives aimed at preventing new introductions (Sikes et al., 2018). However, it could also simply result from the smaller number of years covered (18 instead of the 25 considered in the other time periods) and from time lags between detection and reporting (Seebens et al., 2017).

3.7 Conclusions

Our study is an important step towards understanding the global biogeography of non-native macrofungi. The spatial variation in numbers of these species worldwide appears to be driven largely by levels of socioeconomic activity in interaction with the distribution of suitable environments for the species and their hosts. Regional similarities in taxonomic composition have shown limited predictability, although a role for distinct pathways of introduction in the Northern and Southern Hemispheres and environmental filtering is suggested. In addition, the number of non-native species also appears to have been increasing substantially over time in most regions of the globe. These results align with previous studies for other, often better-studied taxonomic groups, showing that human-mediated species introductions are greatly changing the distribution of biodiversity globally (Capinha et al., 2017, 2020; Dawson et al., 2017; Dyer et al., 2017; Pyšek et al., 2020; Tingley et al., 2015). Given that unintentional transport is the main mechanism of introduction of non-native macrofungi (Desprez-Loustau et al., 2011), current and potentially increasing levels of globalisation are likely to further accentuate the global redistribution of these taxa in the future.

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3. 9 Data availability statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.6572849**.**

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Chapter 4

Negative and positive impacts of alien macrofungi: a global scale database

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Negative and positive impacts of alien macrofungi: a global scale database

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4.1 Abstract

Advances in ecological research during the last decades have led to an improved understanding of the impacts of alien species. Despite that, the effects of alien macrofungi have often received little attention and are still poorly understood. With the aim of reducing this knowledge gap, we compiled a database of the recorded socio-economic and environmental impacts of alien macrofungi. This database was compiled from all relevant sources we could identify, through an exhaustive literature review, considering the identity of known alien taxa and explicit indications of impacts of any kind. In total, 1440 records of both negative and positive impacts were collected for 374 distinct species in different regions of all continents, except Antarctica. The most frequently recorded impacts are related to the mutualistic interactions that these fungi can form with their host plants. In total 47.8% of all records refer to the indirect negative effect of these interactions, by facilitating the colonization of invasive plants, while 38.5%

refer to their positive contribution to the growth of forestry species. Less frequently recorded negative impacts included, ectomycorrhizal interactions with native plants, plant pathogenicity and human poisoning after ingestion. Additional positive impacts include the use as a food source by native species and human populations and commercial exploitation. Alien macrofungi are an increasingly prevalent component of human-dominated ecosystems, having a diverse array of negative and positive impacts on native biota and human population. Our database provided a first step towards the quantification and mapping of these impacts.

Keywords: Biogeography, biological invasions, fungi, impact assessment, non-native species

4.2 Introduction

The introduction and naturalization of alien species are recognized as important threats to native biodiversity (Bellard et al. 2016, 2021; Simberloff et al. 2013) and major causes of impacts on socio-economic activities and human welfare (Diagne et al. 2021). Current understanding of the impacts of alien species is heavily skewed towards a few species (Marean 2015; Vilà et al. 2009), taxonomic groups (Evans et al. 2018; Bartz and Kowarik 2019) and geographical regions (Kumschick et al. 2013; Heringer et al. 2021). However, the potential underestimation of impacts by frequently ignored taxa is increasingly recognized (Vilà et al. 2010).

In recent years, fungi as alien species have received some attention, through a higher availability of distribution data and information about their impacts in introduced ecosystems (Vellinga et al. 2009; Dickie et al. 2016; Nuñez and Dickie 2014; Monteiro et al. 2020, 2022). However, knowledge on impacts of alien fungi has been mainly restricted to a few pathogenic, often microscopic, taxa which have been studied because of their potential to cause severe diseases in native biota (Desprez-Loustau et al. 2007), strong damages to both agricultural and forestry production (Panzavolta et al. 2021) and, in a few cases, human health risks (Page and Westcott 2014; Ye and Liu 2018). On the contrary, macrofungi, comprising ectomycorrhizal and saprotroph fungal taxa exhibiting macroscopic spore bearing structures, are in general still widely missing from cross-taxonomic alien species impact assessments (Evans et al. 2016, 2020; Kumschick et al. 2017), despite their potential to dramatically change ecosystem functions and cause problems for human health (Dickie et al. 2016). This likely originates from a prevalent view of these taxa as having limited impacts in naturalized ranges because they mostly comprise non-pathogenic species (Desprez-Loustau et al. 2010, Vizzini et al. 2009).

Despite being comparatively less represented in invasion studies than other groups, macrofungi comprise a large number of species that have been introduced widely across the globe over recent centuries (Desprez-Loustau et al. 2010; Monteiro et al., 2022), many of which moved inadvertently in the plant trade or in deadwood or soil (Vellinga et al. 2009). The increased occurrence of some macrofungi species as well as of their effects on invaded areas has led to an increased availability of reports on their negative impacts (Desprez-Loustau et al. 2007). These impacts include toxicity to humans (French et al. 2011; Santi et al. 2012), competition with native fungi (Murat et al. 2008), facilitating the co-invasion of invasive plants (Vlk et al. 2020), and changes to ecosystem functions (Chapela et al. 2001). Interestingly, macrofungi belong to one of the groups of alien taxa for which positive impacts are commonly reported, namely by improving or enabling forestry plantations (Dickie et al. 2010), constituting a commercially valued product (Buyck 2008) or being a local food source (Dickie et al. 2016). Despite the mounting evidence of impacts, their records remain scattered across scientific and non-scientific literature, impeding an integrated examination of multiple aspects of relevance, such as the taxa involved, the regions most affected, or the type and magnitude of impacts caused. Ultimately, this knowledge is crucial to better inform invasion prevention strategies as well as in the management of existing populations of alien macrofungi.

In this context, we compiled a database of the socio-economic and environmental impacts of macrofungi reported in all relevant sources we could identify, namely scientific publications, reports, citizen science websites and databases on alien species. We reviewed sources in multiple languages and considered not only information on negative impacts but also impacts perceived as positive. We applied the precautionary principle and categorized impacts as 'negative’ if they were known to have detrimental effects on native communities and human populations, or if they had no known beneficial effects (i.e., causing ecological change without any apparent gain to humans or native biota). In contrast, we categorized impacts as 'positive' if they were documented to have beneficial effects according to values associated with nature conservation or human interests (Vimercati et al. 2020). In addition, we distinguished between environmental and socio-economic impacts. Environmental impacts are those causing changes to the natural environment, whether positive or negative, resulting from effects on the air, land, water and the biota of the ecosystem. Socio-economic impacts refer to negative or positive effects on property values, agricultural productivity, public utility operations or human well-being (Simberloff et al. 2013). In total, 1440 impact records were collected for 374 different alien macrofungi species, and comprising all continents except Antarctica. Using these data, we assessed *i*) the taxonomic diversity of macrofungi for which impacts were recorded and ii) the typology and magnitude of recorded impacts and their geographical distribution worldwide.

4.3 Methods

We used as a starting point the recently published Global Database of Alien Macrofungi (Monteiro et al. 2020), which has allowed us to obtain a pre-identification of macrofungi taxa known to be occurring outside of their native ranges. Hence, focusing on each of these taxa, we conducted an extensive search for studies, reports and other sources that addressed impacts of any sort. Sources searched comprised broad databases on introduced taxa such as Delivering Alien Invasive Species Inventories for Europe (Hulme et al. 2019), the Global Register of Introduced and Invasive Species (Pagad et al. 2019) and the European Alien Species Information Network (Katsanevakis et al. 2019). In addition, we used general-purpose engines (i.e., Google) and scientific search-engines (Google Scholar, ScienceDirect and JSTOR) to identify relevant information from peer-reviewed literature. The reference lists from these articles were also searched to identify further papers or book chapters which may contain useful information. We used specific keywords related to fungal impacts in multiple languages including English, French, Portuguese and Spanish. Terms used in the search were ‘introduced´, ’invasive’, ‘established’, ‘alien’, ‘non-native’ and ‘exotic’, combined with fungal taxonomic terms, ranging from a generic and higher denomination (e.g., ‘fungi’, ‘macromycetes’, ‘basidiomycota’) to a more specific designation, such as the scientific name (*Amanita muscaria* (L.) Lam., *Amanita phalloides* (Vaill. ex Fr.) Link, *Boletus edulis* Bull., *Suillus luteus* (L.) Roussel and *Pyrrhoderma noxium* (Corner) L.W.Zhou & Y.C.Dai). For each combination, we added “impact” and “effect”. We also performed additional searches using specific terms related to more commonly reported impacts such as “competition”, “toxicity”, “plant diseases” and “ectomycorrizhal interactions”. We performed an individual search for each combination of country and taxa in the Global Database of Alien Macrofungi (Monteiro et al. 2020). Finally, some records were obtained by checking macrofungi observations in citizen science websites like iNaturalist (https://www.inaturalist.org; iNaturalist 2022) and Mushroom Observer (https://mushroomobserver.org; Wilson and Hollinger 2019). Records collected from nonspecialised sources were cross-checked against information available in scientific literature (e.g., species alien status) in order to assess their reliability. Only records of impacts in regions where the species are not native were included, i.e. impacts in native regions were not considered.

To classify species impacts, we first divided them into either positive or negative. Negative impacts – referring to detrimental effects on native communities and human populations, or ecological changes without any apparent gain to humans or native communities –, were divided into the following subcategories: human health problems, competition with native fungi, ectomycorrhizal interactions with native plants, plant disease agents, ectomycorrhizal interaction with alien invasive species and other ecosystem changes. Positive impacts, referring to recorded beneficial effects on nature conservation or human interests, were categorized into benefits for forestry plantations, as food source for local human populations, food source for other species, and commercial use (Table 1). Note that the previous classification is non-mutually exclusive, meaning for example that some records were simultaneously assigned to negative ectomycorrhizal interaction with alien invasive species and to positive impacts on forestry plantations. For each record, the ecofunctional type of the species (ectomycorrhizal, saprotroph or pathogenic) and a short description of the impact was also added (see online Appendices I and II regarding both negative and positive impacts of alien macrofungi for the data used in the analyses). The geographical examination of collected impacts followed the geographical scheme of GAMD (Monteiro et al. 2020), consisting of countries and the first-order administrative divisions for the six largest countries in the world (Australia, Brazil, Canada, China, Russia, USA).

At last, in order to evaluate if the number of negative and positive impacts was directly related with the wealth of each included region, we performed for both impact categories (negative vs positive impacts) a Spearman's rank correlation (r_s) between the number of impacts per region and their respective per capita GDP (gross domestic product). The GDP variable represents the mean income (in US$) in 2019 (or closest year available) and can be considered a proxy of wealth of the different introduced locations. Our hypothesis is that wealthier regions will have a higher number of recorded impacts (both negative and positive) owing to more introduction opportunities (Monteiro et al. 2022). To conform with the availability of data for the per capita GDP variable, the analysis was performed at the country scale. For that reason, the numbers of alien species impacts represented at the subnational scale in the database had to be upscaled accordingly. We collect the mean income in US$ data of the year 2019 (or closest year available) from the Worldbank website (https://data.worldbank.org/) (Worldbank, 2019).

4.4 Results

We collected a total of 1440 records of impacts from 246 data sources. Of these, 869 were identified in the sources as negative impacts and 571 as positive. Regarding negative impacts, most were related to mutualistic interactions that alien fungi form with alien plants (47.8% of the records; Table 1), followed by negative interactions with native plants (7.7% of the records), causing plant disease (3.6% of the records), human poisoning after ingestion (1.0% of the records), competition with other fungi species (0.1% of the records) and changes in soil biochemistry and biodiversity (0.1% of the record). On the contrary, positive impacts recorded in the descending order of frequency were: beneficial interactions with non-native plants of importance for forestry (38.5% of the records; Table 1), direct commercial exploitation by the canning and other food industry (0.8% of the records) and use as direct food source for human populations (0.2% of the records). Only 0.1% of the records reported consumption by native species.

In terms of the taxonomy, a total of 374 species belonging to 2 phyla, 5 classes, 15 orders, 50 families and 85 genera respectively were reported as having impacts. The families with the highest proportion of negative impacts were Suillaceae (110 records), Amanitaceae (96 records) and Russulaceae (65 records) (Fig 1a) meanwhile the families with most positive impacts were Sclerodermataceae (91 records), Suillaceae (80 records) and Amanitaceae (56 records) (Fig.1b). At the species level, the ones having most records of negative impacts were *Pyrrhoderma noxium* (Corner) L.W.Zhou & Y.C.Dai (43 records), *Amanita phalloides* (Vaill. ex Fr.) Link (28 records) and *Descolea alba* (Klotzsch) Kuhar, Nouhra & M.E.Sm. (25 records) whilst *Amanita muscaria* (L.) Lam. (28 records), *Suillus granulatus* (L.) Roussel (24 records) and *Suillus luteus* (L.) Roussel (24 records) were the species most frequently recorded as having positive impacts. Furthermore, some of the species with the greatest diversity of impact types from both negative and positive categories were *Suillus luteus* (L.) Roussel (6 impact types), *Amanita pantherina* (DC.) Krombh. (4 impact types), *Amanita phalloides* (Vaill. ex Fr.) Link (4 impact types), *Amanita muscaria* (L.) Lam. (4 impact types) and *Boletus edulis* Bull. (4 impact types) (Table 2).

The global distribution of recorded impacts is uneven between regions (Fig 2a and 2b), with the majority of negative ones being found in South America (225 records), Europe (190 records) and Africa (175 records) (Fig 3a). For positive impacts, the majority of records takes place in South America (191 records), Africa (154 records) and Oceania (85 records) (Fig 3b). Regions where the impacts of alien macrofungi were least recorded are North America and Asia. Negative impacts corresponded to 75 records and 45 records in North America and Asia, respectively and 39 records and 28 records of positive impacts for each.

Additionally, the results of the Spearman's rank correlation between the number of impacts per country and the per capita GDP were r_s =0.14 for the negative impacts and r_s =0.04 for the positive impacts.

Table 4.1. Percentage of each category of impacts on the total of records (n=1440). Environmental impacts are signaled by one asterisk (*) while socio-economical impacts are represented by two (**).

Impact categories	**Description**	**Percentage**
Negative Impacts		
Competition with native fungi species (*)	Competition between alien macrofungi and native macrofungi.	0.1
Ecosystems (*)	Changes to biochemical properties of soil without any apparent ecological or human-related benefit.	0.1
Human health (**)	Negative consequences on human health through ingestion.	0.9
Plant disease agents (*)	Negative consequences of alien macrofungi as plant disease agents.	3.6
Ectomycorrizhal interactions with native plant species (*)	Ectomycorrhizal interactions with native plants without confirmed benefits for these and potentially weakening ectomycorrhizal interactions with native fungi.	7.9
Ectomycorrizhal interactions with alien plant species (*)	Negative ecological impacts owing to promotion of alien plant invasions.	47.8
Positive Impacts		
Food source for other species (*)	Alien macrofungi used as food source for some animal groups, hence directly contributing to the sustaining of its population.	0.1
Human food source (**)	Alien macrofungi used as a human food source.	0.2
Commercial purposes (**)	Alien macrofungi used as a product in food industries.	0.8
Forestry (**)	Establishment of ectomycorrhizal interactions with important forestry trees.	38.5

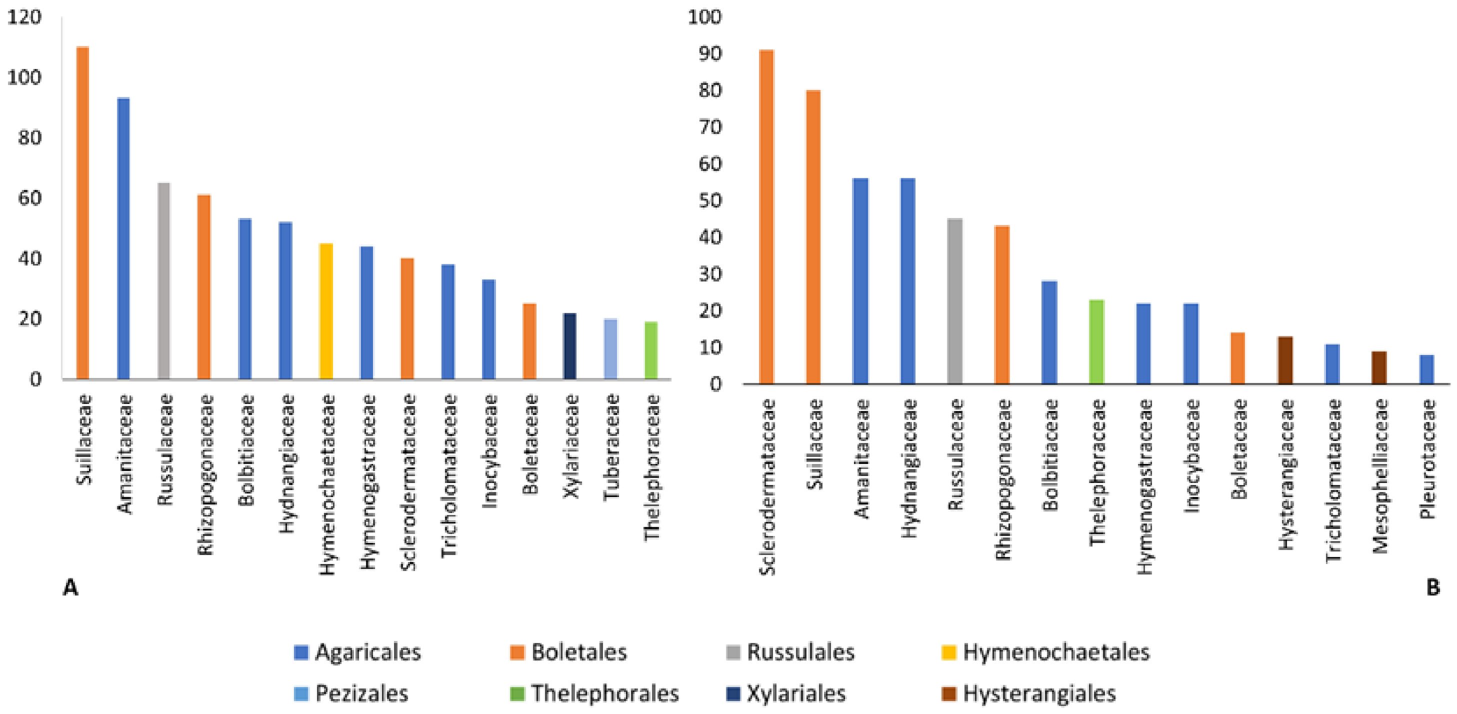

Figure 4.1 Number of the records per taxonomic family for negative (A) and positive impacts (B). Only the 15 families with most records are represented. Taxonomic orders are represented by distinct colors.

Table 4.2. Macrofungi species with the greatest diversity of impact types from both negative and positive categories. In the table 'X' represents the type of impacts that the species was recorded to cause in alien regions.

	Negative impacts				**Positive impacts**				**Total number of different impacts**
Species	**Human health**	**Ecosystems**	**Ectomycorrhizal interactions with native species**	**Ectomycorrhizal interactions with non-native species**	**Human food source**	**Forestry**	**Food source for other species**	**Commercial purposes**	
Suillus luteus (L.) Roussel		X	X	X	X	X		X	6
Amanita pantherina (DC.) Krombh.	X		X	X		X			4
Amanita phalloides (Vaill. ex Fr.) Link	X		X	X		X			4

	Negative impacts				**Positive impacts**				**Total number of different impacts**
Species	**Human health**	**Ecosystems**	**Ectomycorrhizal interactions with native species**	**Ectomycorrhizal interactions with non-native species**	**Human food source**	**Forestry**	**Food source for other species**	**Commercial purposes**	
Amanita muscaria (L.) Lam.			X	X		X	X		4
Boletus edulis Bull.			X	X	X	X			4
Suillus bovinus (L.) Roussel			X	X		X		X	4
Suillus granulatus (L.) Roussel			X	X		X		X	4
Amanita gemmata (Fr.) Bertill.	X			X		X			3

	Negative impacts				**Positive impacts**				**Total number of different impacts**
Species	**Human health**	**Ecosystems**	**Ectomycorrhizal interactions with native species**	**Ectomycorrhizal interactions with non-native species**	**Human food source**	**Forestry**	**Food source for other species**	**Commercial purposes**	
Chalciporus piperatus (Bull.) Bataille			X	X		X			3
Descolea alba (Klotzsch) Kuhar, Nouhra & M.E.Sm.				X		X			3
Hydnangium carneum Wallr.			X	X		X			3
Hysterangium inflatum Rodway			X	X		X			3

	Negative impacts				**Positive impacts**				**Total number of different impacts**
Species	**Human health**	**Ecosystems**	**Ectomycorrhizal interactions with native species**	**Ectomycorrhizal interactions with non-native species**	**Human food source**	**Forestry**	**Food source for other species**	**Commercial purposes**	
Laccaria fraterna (Sacc.) Pegler			X	X		X			3
Russula sardonia Fr.			X	X		X			3
Scleroderma flavidum Ellis & Everh.			X	X		X			3
Scleroderma verrucosum (Bull.) Pers.			X	X		X			3
Suillus brevipes (Peck) Kuntze			X	X		X			3

	Negative impacts				**Positive impacts**				**Total number of different impacts**
Species	**Human health**	**Ecosystems**	**Ectomycorrhizal interactions with native species**	**Ectomycorrhizal interactions with non-native species**	**Human food source**	**Forestry**	**Food source for other species**	**Commercial purposes**	
Suillus spraguei (Berk. & M.A.Curtis) Kuntze			X	X		X			3
Tricholoma saponaceum (Fr.) P.Kumm.			X	X		X			3

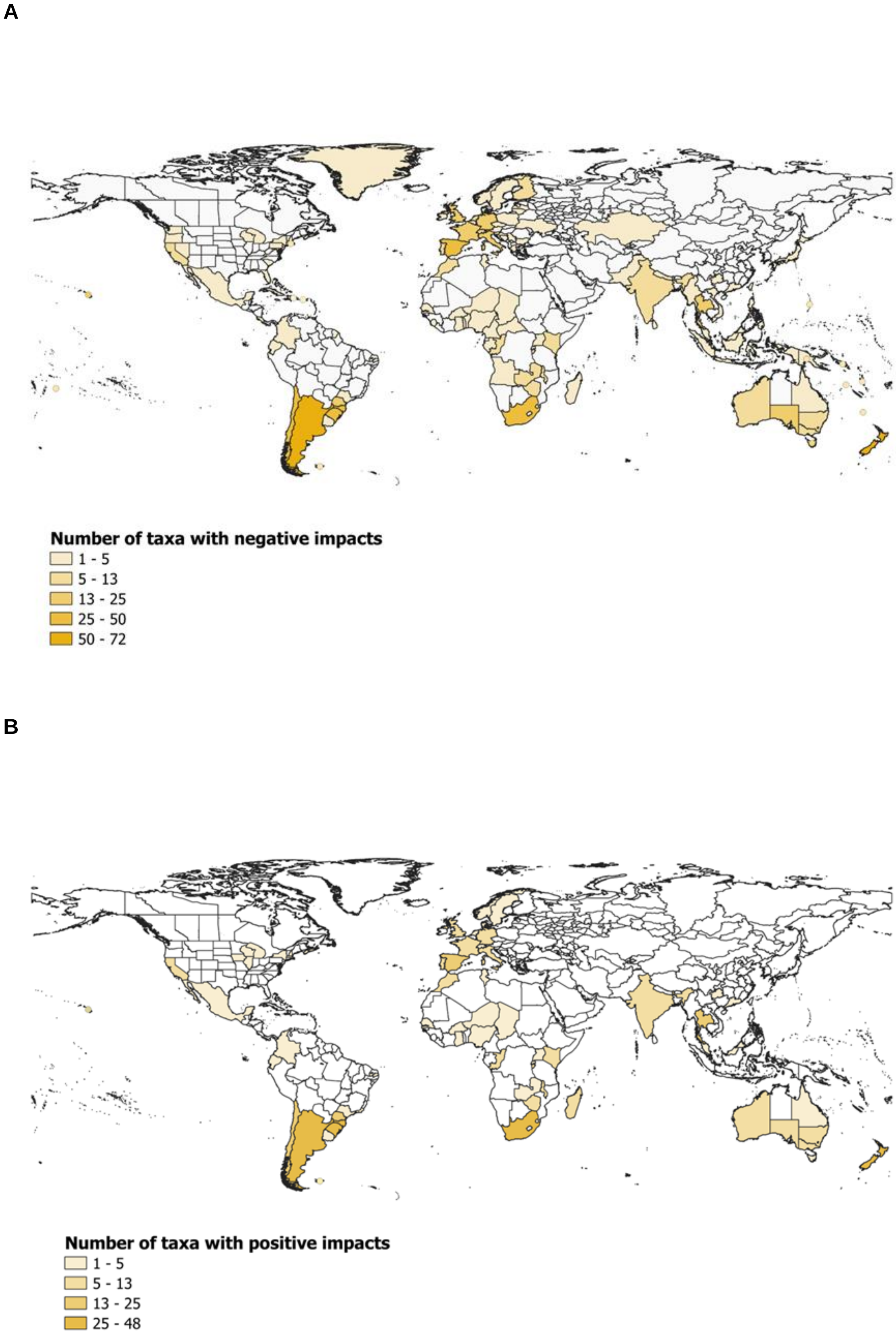

Figure 4.2 Global distribution of negative (A) and positive (B) impacts of alien macrofungi. The colors gradient represents the total number of number of species with recorded impacts.

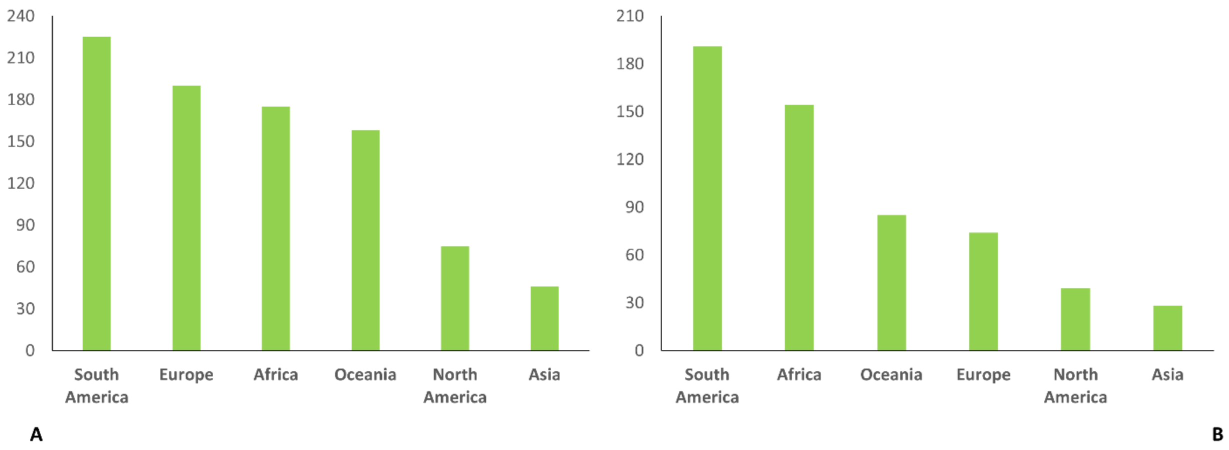

Figure 4.3 Total number of negative (A) and positive impact (B) records per continent.

4.5 Discussion

This study allowed identifying a high number and diversity of impacts of alien macrofungi in many regions of the world, including negative and positive effects on humans, native and alien plant taxa, other fungi and animal species and soil biochemistry.

Notwithstanding this variety, interactions of EM macrofungi with alien plants were the most common impacts recorded. EM species are important mutualists for plants, by providing nutrients from the soil in return for photosynthetically derived carbon (Begum et al. 2019). Therefore, they can have strong indirect effects by facilitating plant invasions, including pines (Dickie et al. 2010) eucalyptus (Santolamazza-Carbone et al. 2019), Douglas fir trees (*Pseudotsuga*; Moeller et al. 2015), willows (*Salix*; McInerney and Rees 2017) and alders (*Alnus*; Bogar et al. 2015). Examples of EM fungus species with a high number of plant interactions are *Suillus granulatus* (L.) Roussel and *Suillus luteus* (L.) Roussel as well as *Amanita muscaria* (L.) Lam., *Descolea alba* (Klotzsch) Kuhar, Nouhra & M.E.Sm. and *Rhizopogon roseolus* (Corda) Th.Fr. Despite these impacts, some of these species can also provide great benefits for economically important trees, by facilitating their establishment in novel environments (e.g. species from the *Suilloid* genus are always associated with invasive pines, particularly at early invasion, when invasive trees are most vulnerable; Policelli et al. 2019)). For those reasons, introduction of EM fungi can not only contribute to the thriving of their plant hosts, an impact viewed as positive for agroforestry activities, but to their spread beyond plantation areas, i.e., facilitating biological invasions. As a result, co-invasion with plants is the most geographically widespread impact of introduced EM fungi. In fact, the prevalence of this kind of impact may be related to the fact that is easier to assume that ectomycorrhizal fungus found only on non-native trees are likely to be invasive as well in the same areas, while determining the origin of many alien pathogens or saprotrophs is harder and usually requires extensive efforts (Rizzo 2005; Tedersoo et al. 2014).

The direct impacts of fungal introductions on native plant communities are also important to consider. Several studies have shown that alien EM fungi are highly persistent in their novel environments and can form novel associations with native host plants (Orlovich and Cairney 2004). For example, *Laccaria bicolor* (Maire) P.D.Orton isolates from North America were detected in Douglas fir (*Pseudotsuga menziesii*) plantations in Europe ten years after inoculation of out-planted seedlings, and were also found to colonize nearby uninoculated trees (Selosse and Le Tacon 1998). Similarly, isolates of *Amanita muscaria* (L.) Lam. have survived for > 36 years in *Pinus radiata* plantations in Australia (Sawyer et al. 2001). Besides, it is now associated with *Nothofagus* forests in Tasmania and New Zealand, presumably as a consequence of its introduction with pines (Fuhrer and Robinson 1992). Therefore, these alien EM fungi may establish on native hosts where they could start to alter ecosystem functions by being pathogenic to the native plants (Johnson et al 1997) or by changing ecosystem properties (e.g. changing a systems dominated by arbuscular mycorrhizal fungi to one dominated by EM fungi (Bai and Cotrufo 2022)). Also, these fungi can change the abundance and distribution of native EM fungi throughout time (Loo 2008).

Some species of macrofungi could also cause negative effects on native plants by causing diseases. The main pathogens in our database were root rotting fungi such as *Pyrrhoderma noxium* (Corner) L.W.Zhou & Y.C.Dai and *Heterobasidion annosum* (Fr.) Bref. The former species (*P. noxium)* is responsible for causing the brown root rot disease on more than 200 plant species (Sahashi et al. 2014) and is frequently cited for its damage to forest and hardwood plantations, as well as fruit orchards (Sahashi et al. 2012). Currently, it has a widespread non-native range among countries in Southeast Asia, Africa, Oceania, South America, Europe and the Caribbean (Ann et al. 2002). Mahogany, rubber, hoop pine, and cocoa plantings have been seriously affected by this species (Akiba et al. 2015). The second species H*eterobasidon annosum* (Fr.) Bref is responsible for causing butt and rot root in conifer trees and it is reported to be invasive in Asia and Oceania (Asiegbu et al. 2005). In native regions, such as North America, this species is a well-known problem being responsible for the loss of an estimated cost of $US 1 billion dollars annually (Smith 1990).

In terms of human health, most reported impacts were related to the consumption of some species. The most reported of these impacts is the poisoning caused by the ingestion, by mistake, of the dead cap (*Amanita phalloides* (Vaill. ex Fr.) Link) (French et al. 2011). This fungus contains the deadliest toxin of all poisonous mushrooms, with a reported mortality rate from 25% to 50% (Jander et al. 2000). It is one of the few alien macro-organisms that regularly causes human deaths and its high frequency in urban parks and similar settings increases the risk of accidental poisonings (Page and Westcott 2014). Most of the reported cases were from the United States, likely reflecting the widespread distribution of the species in some states (Wolfe et al. 2010), but also a popular interest in gathering and eating wild mushrooms and the existence of a network of support services for this kind of poisoning situations (McPartland et al. 1997; Brandenburg and Ward 2018). A good example of these services is the American Association of Poison Control Centers composed of 55 poison centers, who provide expert treatment advice and referral in case of exposure to poisonous or toxic substances (American Association of Poison Control Centers 2022). There were also reports of human poisoning from Africa, South America and Oceania. Besides, other introduced species like *Psilocybe mexicana* R.Heim had a lower number of cases reported in Europe, probably because they are not as widespread as *Amanita phalloides* in its alien range. At last, other species of macrofungi like *Psilocybe mexicana* R.Heim (Johnston and Buchanan 1995) or *Amanita muscaria* (L.) Lam (Shepard 2005) were used as recreational drugs in New Zealand.

Other less known negative impacts, with just a few records, refer to the introduction of alien radiata pines (*Pinus radiata*) and accompanying EM fungi *Amanita phalloides*, leading to observed changes in soil, including the release of recalcitrant nutrients, a loss of up to 30 % of soil carbon and increased bacterial dominance (Chapela et al. 2001). Another example of impacts with low frequency includes competition, for example between the introduced Chinese truffles *Tuber indicum* Cooke and Massee and *Tuber brumale* Vitt. and the native and less aggressive Perigord truffle (*Tuber melanosporum* Vittad.) in plantations in Italy (Murat et al. 2008). On the contrary, some positive impacts that only had a few records include the case in New Zealand where mycophagous native insects like *Mycetophila fagi*, *Mycetophila filicornis, Zedura curtisi* use fungal tissues of

Amanita muscaria (L.) Lam. to feed their larvae (Osawa et al. 2011). Besides, other less represented impacts include the use of the introduced *Suillus luteus* (L.) Roussel in Patagonian (Argentina) cuisine (Dickie et al 2016), the use of *Suillus granulatus* (L.) Roussel and *Suillus bovinus* (L.) Roussel in the canning industry in Madagascar (Buyck 2008) and the cultivation of *Pleurotus citronipeliatus* in some USA states of as a commercial food product (Bruce 2018). Although the scope of this paper was global, some regions are clearly underrepresented, even despite our efforts to search for literature in a variety of languages other than English (Nuñez and Amano 2021). This could be due to real absence of impacts by macrofungi on those areas, or more likely due to lack of research or studies accessible to our search engines (Nuñez et al. 2022). In fact, when compared with other taxa as birds (Martin-Albarracin et al. 2015, Evans et al. 2016), mammals (Volery et al. 2021, Allmert et al. 2022) or amphians (Kumschick et al. 2017) this taxonomic group has been far less studied than the others as a result of being complex organisms with a lack of knowledge regarding their ecology, biology or even taxonomy. Although, unlike in some of the previous studies (Martin-Albarracin et al. 2015, Allmert et al. 2022) we cannot clearly state that the number of impacts increased in wealthier regions, because there was no relationship between that impact number and per capita GDP. For both negative and positive impacts, the Spearman correlation (r_s) was close to zero and for that reason any correlations were found. That is probably related with the massive plantation of exotic pines species in the Southern Hemisphere during the last centuries and consequently the introduction of associated alien macrofungi species. Therefore, even despite European countries, New Zealand and Australia are in general better represented in terms of the total number of impact records in our database some countries of South America and Africa have also very high record numbers (e.g. Brazil, Argentina, Chile and South Africa).

Despite the overall availability of impact records and some recent advances regarding the identification of alien fungi (Vellinga et al. 2009, Desprez-Loustau et al. 2007,2010; Monteiro et al. 2020,2022), we believe our work touches only the surface of the impacts being caused by alien macrofungi worldwide. While the impacts of fungi that form symbiotic associations with alien trees have received a relevant amount of attention, either because they facilitate the establishment of invasive species or of species of economic interest (Dickie et al. 2016), many other effects of these interactions with native taxa are likely underreported (Hui et al. 2020). For example, the EM fungus *Amanita muscaria* (L.) Lam. has been established on native Nothofagus forests in New Zealand and Australia but the consequences on plant hosts remain unknown (Osawa et al. 2011; Dunk et al. 2012). Besides, very little knowledge also appears to exist regarding other types of ecological change, including impacts on taxonomic diversity. Concerning this later aspect, aboveground effects of plant invasions frequently include a substantial decline in local-scale diversity of plant communities (Wardle and Peltzer 2017). By analogy, we should expect that introduced macrofungi could cause a similar loss of belowground diversity of native fungi, however there is currently mixed evidence of how this loss actually occurs (Dickie et al. 2017). Additionally, introduced fungi can also become a food source for native animals, including a large number of insects, but there is not much evidence of how invasive fungi influence wildlife (Nuñez and Dickie 2014). Therefore, there is still a huge lack of information on this field and more survey efforts are needed to fill the presumably wide knowledge gaps about these impacts.

Finally, there are now well-defined frameworks for classifying and ranking the impacts of non-native species. For example, IUCN EICAT (IUCN 2020, Volery et al. 2020) allows assessing negative environmental impacts of alien species, SEICAT (Bacher et al. 2018) negative socioeconomic impacts, EICAT+ (Vimercati et al. 2022) positive environmental impacts, and the GISS (Nentwig et al. 2010) negative environmental and socio-economic impacts simultaneously. Certainly, the capacity to apply this sort of framework for classifying and ranking the impacts of alien macrofungi would ease the comparison of impacts with other taxonomic groups. However, to our knowledge there is no framework that considers positive socioeconomic impacts, which comprise a very substantial portion of the records of impacts in our data (39.7%). For this reason, we have developed and applied a framework appropriate to the specificities of our data, which allowed us to specify through which mechanism the impacts took place. Though, this framework could not measure impact magnitude or confidence. Nevertheless, we provide the data set of impact records we have compiled together with this work, and if a more general framework becomes available in the near future, its application to this taxonomic group will become facilitated. We also expect that our findings will incentivize the construction of a comprehensive framework that encompasses more of the negative and positive impacts of biological invasions.

4.6 Conclusions

By compiling and analyzing recorded impacts of alien macrofungi, we demonstrated the highly frequent and diverse types of effects that these taxa have on recipient ecosystems, economic activities and human well-being. Besides identifying mutualistic interactions with plant species as the most frequent (either negative or positive) impact recorded, we also showed that these and other impacts have a wide taxonomic and geographical distribution, underscoring the need for transnational cooperation strategies in managing the spread of alien species beyond single-species prevention efforts (Capinha et al., 2023). Moreover, many types of impacts are likely strongly under-recorded (e.g., changes caused to local biodiversity and trophic chains) and more research is necessary to uncover their true magnitude. Related to this, although there is no relation between the existing data on impacts and their higher frequency in wealthier regions, efforts to expand the geographical scope of these assessments are still required, specially in not so well studied countries. Despite the limitation of available data, our work provides a first step towards the integrated analysis of the impacts of alien macrofungi. Our hope is that a greater focus on macrofungi in alien and invasion-related assessment will progressively help to understand the full depth of impacts caused by these taxa in non-native regions.

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4.9 Supplementary materials

Supplementary material 1

Appendix 1. Negative impacts of alien macrofungi

Authors: Miguel Monteiro

File format: Microsoft Comma Separated Values File (.csv).Data type: Ocurrences

Explanation note: File containing the records of negative impacts of alien macrofungi worldwide.

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Link: https://doi.org/10.3897/neobiota.85.101770.suppl1

Supplementary material 2

Appendix 2. Positive impacts of alien macrofungi

Authors: Miguel Monteiro

File format: Microsoft Comma Separated Values File (.csv).Data type: Ocurrences

Explanation note: File containing the records of positive impacts of alien macrofungi worldwide.

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Link: https://doi.org/10.3897/neobiota.85.101770.suppl2

Chapter 5

General Discussion and Conclusions

5.1 General Discussion and Conclusions

We have conducted complementary studies related to the current status of macrofungi species introductions around the world. These studies focused on understanding the global distribution, the main socio-economic and environmental variables that contribute to their invasibility and the impacts that they can potentially cause in the regions where they have been already established. In this chapter, we will summarize the previous achievements and discuss our results in light of current theories regarding biological invasions.

5.2 The availability of alien macrofungi distribution data

The under-representation of macrofungi in studies of broad-scale invasion patterns reflects a lack of readily available synthesized information about their distribution in the world (Desprez-Loustau et al. 2010). This could be because most macrofungi are saprotrophic or ectomycorrhizal and the ecological changes and impacts they cause are less obvious than those of pathogenic fungi (Vizzini et al, 2009). For that reason, they have been excluded from alien species databases and many records regarding their introductions were dispersed in ‘grey’ literature (Vellinga et al. 2009). Besides, the alien status of many macrofungi species is often ambiguous, with many species being considered as ‘‘cryptogenic’’, that is of unsure origin (but suspected to be alien) (Essl et al. 2018). This often occurs because mycological inventories usually list species but do not address their native or alien status (Courtecuisse 2001). Hence, when mycologists report a ‘‘first record’’ they usually do not analyze the novelty of the record (new record and/or new taxon) or discuss its relevance in terms of biological invasion (Desprez-Loustau et al. 2009). Plus, taxonomic confusions, by pooling different species together, are another source of uncertainty for the presence and distribution of several species (Manawasinghe et al. 2021).

Hence, in Chapter 1 we present “The Global Alien Macrofungi Database “a consolidated list of 1986 records of introduced macrofungi taxa collected worldwide. Although certainly incomplete, this database represents the largest inventory of these introduced species to date and can be considered as a relevant step towards a more comprehensive knowledge regarding one of the least known groups of alien taxa. This global dataset, compiled from heterogeneous sources, was constructed with the aim of enabling analyses of fungal invasions, by using a standardized search procedure assuring a comparable data retrieval for all species and countries. For that reason, we believe that our database is quite representative of the global distribution of introduced macrofungi, allowing us to draw robust conclusions on some key invasion patterns in fungi.

5.3 The relevance of globalization on global alien macrofungi distributions

For macrofungi, most introductions are non intentional and are the result of biological contamination associated with various commodities (Wood 2017). Higher levels of imports are therefore likely to increase the probability of introduction of macrofungi and the propagule pressure, which is an important determinant of introduction success (Sikes et al. 2018; Hulme 2021). Globalization, especially international trade, is in fact a major driver of biological invasions across taxa and regions (Desprez-Loustau et al. 2007; Reino et al. 2017, Meyerson et al. 2022; Capinha et al., 2023). Hence, increasing trade volumes is one of the most important factors contributing to the exponential increase in the number of alien fungi (Panzavolta et al. 2021). Besides, countries and regions with larger populations are more likely to have high levels of transcontinental and terrestrial exchanges, due to the presence of airports and/or harbors, dense road networks, and active economies (Potgieter et al. 2021). As a result, our results on fungi are in line with many previous studies showing that globalization, especially international trade, is a major driver of biological invasions across taxa and regions (Delavaux et al. 2019; Sardain et al. 2019; Hulme 2021).

In Chapter 2, we identified a positive relationship between per capita GDP and richness of non-native species showing that economic and commercial activities are a main driver of colonization pressure by non-native macrofungi (Santini et al. 2018). Thus, the aggregated effect of importation of multiple potential vector commodities, such as ornamental and forestry plants, their seeds, non-living plant material, wood, and other materials are important drivers of the introduction of macrofungi taxa (Desprez-Loustau & Rizzo, 2011). As a result, there should be a higher richness of non-native macrofungi in wealthier regions (Clubbe et al. 2020). Besides, most populated countries are also likely to have a higher level of environmental disturbance, which may favor invasibility (With 2002). Urban forests and gardens have been shown to be areas especially affected by invasions and sources of alien species for adjacent areas (Guo et al. 2019). Finally, another possible factor linked to the ‘‘GDP” which might explain the selection of this variable to explain introduction success, is the effort dedicated to survey, detect and investigate these species that is greater in areas with more resources and infrastructures (Lodge 2006).

We also verified that the distribution of alien macrofungi is negatively related with latitude, suggesting a consistently higher richness of non-native macrofungi in the Southern Hemisphere. This is probably explained by the fact that the use of non-native tree species is much more prevalent in forestry of many countries in this hemisphere, especially pines, which were extensively planted here through the last centuries. (FAO 2015) Besides, it could justify why there is an observed higher number of non-native ectomycorrhizal fungi in these regions. On the other hand, in many important timber producing countries of the Northern Hemisphere (e.g., the USA, Canada), tree crops are mainly composed of native taxa (MacDicken 2015). Hence, the trade of exotic plants for commercial purposes can also be reflected in the negative relationship we identified for latitude and number of introduced macrofungi.

5.4 Uncovering the impacts of alien macrofungi in non-native regions

Although ectomycorrhizal fungi are increasingly recognized as invasive species their impacts were still not well recognized in most regions. Thus, in Chapter 3 we collected a total of 1420 records of alien macrofungi impacts from a vast literature search. These impacts ranged from macrofungi being toxic to humans, enabling the co-invasion of exotic plants, facilitating plantation forestry and, in some cases, becoming an important source of food. Besides, we also observed that in many cases the same species represented in the dataset could cause both negative and positive impacts.

Therefore, when studying these introduced species, we need to consider that they can be seen simultaneously as beneficial or harmful. For instance, co-invasion with plants was the most recorded and geographically widespread effect of invasive ectomycorrhizal fungi and potentially the most damaging by enhancing plant invasion success (Delavaux et al. 2019). In fact, the presence of mutualists represents one of the main hypotheses explaining the establishment of introduced tree species (e.g., pines and eucalyptus) as they are believed to rely on association with co-introduced ectomycorrhizal fungi from their native distribution range (Vellinga et al. 2009; Vlk et al. 2020). Although, we noticed that this same effect could also be portrayed as positive because plantation forestry in many countries can also rely on the same alien trees and their associated alien ectomycorrhizal fungi (Nuñez et al. 2017). For that reason, alien mutualistic fungi can also be valued for improving timber production which may create conflicts over invasive species removal (Thakur et al. 2019). Another similar case was related to the impacts that macrofungi have on the human population. We could observe that some alien species were toxic through human consumption in non-native regions outside the

European continent like *Amanita phalloides* (Domina 2021). Even though other introduced species from the suilloid group can be sold as a high value food in some countries of Africa and South America (Barroetaveña et al. 2008; Buyck 2008). As a result, the way you see an impact will depend on the studied area, monetary interests or even the alien fungal species that is being studied.

Hence, the removal of an alien macrofungal species cannot rely only on scientific knowledge but also has to be a decision based on policy and financial restrictions. This implies that a species cannot be extracted simply by being introduced, as its presence can be beneficial. Therefore, scientists and land owners need to work together in order to achieve the best solutions. Even though, at present there are only a few studies with available strategies for their management and none are based on robust scientific evidence (Dickie et al. 2016; Panzavolta et al. 2021). Besides, it is hard to get funding to research new methods in the absence of any active attempts to deal with this kind of invasions. Thus, we propose that the only way to move ahead is to integrate both management and scientific research methods in order to prevent future problems.

5.5 Final considerations regarding the status of the research of alien macrofungi

With this work we could understand that there is still a huge lack of knowledge regarding alien macrofungi species. The geographic ranges of most macrofungi are poorly documented, and the lack of natural history data can cause confusion over what is native or introduced (Pringle & Vellinga, 2006). Besides, we still know little about the potential effects of these introductions, either on the diversity of native communities or on ecosystem functioning. Hence, to understand the magnitude of macrofungal introductions it is imperative to develop global geospatial databases in order to visualize the ranges of their introductions as well as catalog the different types of impacts that they can have in non-native regions. With that, we tried to increase the availability of data regarding their introduction to raise awareness of the fungal dimension of invasions and of the need to intensify research in fungal ecology to address issues of future introductions.

To finalize, we highlight that the fungal dimension of biological invasions can be extremely relevant because new developments in fungal ecology can provide advanced approaches to deal with common issues of biological invasions. In fact, the more we begin to understand fungal ecology in general, the better we will be able to predict the ecological trajectories of future introductions. We advocate better connections between scientific fields, especially ecology, mycology and plant pathology, to exchange knowledge, cross fertilize concepts and eventually make progress in the understanding and control of biological invasions. Overall, it is necessary to increase the available literature regarding these introduced species in order to raise awareness of the fungal dimension of invasions and of the need to intensify research in fungal ecology to address issues of future introductions.

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