Received: 12 December 2022 | Revised: 18 August 2023 | Accepted: 23 October 2023

DOI: 10.1111/jbi.14755

RESEARCH ARTICLE

Journal of Biogeography WILEY

Biogeography and global flows of 100 major alien fungal and fungus-like oomycete pathogens

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Funding information
Austrian Science Fund; BiodivScen ERA-net; Czech Academy of Sciences; Czech Science Foundation; Deutsche Forschungsgemeinschaft; Fundação para a Ciência e a Tecnologia; German Federal Ministry of Education and Research; LOEWE initiative of the government of Hessen in the framework of the Centre for Translational Biodiversity Genomics (TBG); Strategic Science Investment Fund NZ; Tertiary Education Commission

Abstract

Aim: Spreading infectious diseases associated with introduced pathogens can have devastating effects on native biota and human livelihoods. We analyse the global distribution of 100 major alien fungal and oomycete pathogens with substantial socio-economic and environmental impacts and examine their taxonomy, ecological characteristics, temporal accumulation trajectories, regional hot- and coldspots of taxon richness and taxon flows between continents.

Location: Global.

Taxon: Alien/cryptogenic fungi and fungus-like oomycetes, pathogenic to plants or animals.

Methods: To identify over/underrepresented classes and phyla, we performed Chi^2 tests of independence. To describe spatial patterns, we calculated the region-wise richness and identified hot- and coldspots, defined as residuals after correcting taxon richness for region area and sampling effort via a quasi-Poisson regression. We examined the relationship with environmental and socio-economic drivers with a multiple linear regression and evaluated a potential island effect. Regional first records were pooled over 20-year periods, and for global flows the links between the native range to the alien regions were mapped.

Results: Peronosporomycetes (Oomycota) were overrepresented among taxa and regional taxon richness was positively correlated with area and sampling effort. While no island effect was found, likely due to host limitations, hotspots were correlated with human modification of terrestrial land, per capita gross domestic product, temperate and tropical forest biomes, and orobiomes. Regional first records have increased steeply in recent decades. While Europe and Northern America were major recipients, about half of the taxa originate from Asia.

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Main Conclusions: We highlight the putative importance of anthropogenic drivers, such as land use providing a conducive environment, contact opportunities and susceptible hosts, as well as economic wealth likely increasing colonisation pressure. While most taxa were associated with socio-economic impacts, possibly partly due to a bias in research focus, about a third show substantial impacts to both socio-economy and the environment, underscoring the importance of maintaining a wholescale perspective across natural and managed systems.

KEYWORDS
biological invasions, emerging infectious disease, eumycota, invasive alien species, oomycetes, parasites

1 | INTRODUCTION

Fungi, defined here in an ecological sense, that is, encompassing the true fungi (Eumycota) and the fungus-like oomycetes (Oomycota, Straminipila), which have a similar lifestyle and were historically considered fungi, are a key component of biological diversity (Antonelli et al., 2020; Hawksworth & Lücking, 2017). They are hyperdiverse and perform a wide range of vital ecological roles, providing many ecosystem functions and services (Spatafora et al., 2017; Willis, 2018). Saprobic fungi are crucial for the decomposition of dead organic matter and nutrient cycling. Symbionts engage in a continuum of interspecific relationships from mutualistic associations, such as different types of mycorrhizae, to antagonistic associations, such as pathogens causing diseases when infecting hosts (Perotto et al., 2013; Termorshuizen, 2016; Zeilinger et al., 2016). In natural ecosystems, pathogens have important regulatory roles that can alter interactions such as competition or predator–prey dynamics, and cause cascading effects in ecological communities (Hatcher & Dunn, 2011). Importantly, the establishment and severity of fungal diseases depend not only on the presence and abundance of a virulent pathogen but also of a susceptible host and suitable environmental conditions for disease emergence, conceptualised in the 'disease triangle' (Scholthof, 2007; Termorshuizen, 2016).

Biological invasions, that is the human-mediated introduction of organisms beyond their native range, can lead to changes in the key factors of the disease triangle. For example, they can enable new associations between pathogens and naïve hosts, and consequently result in emerging infectious diseases (EID) (Anderson et al., 2004; Ogden et al., 2019; Wingfield et al., 2010). Besides being caused by *invasive alien taxa* (i.e. those introduced taxa that establish, spread and cause negative impacts in new environments; sensu Blackburn et al., 2011), EIDs can also result from evolutionary changes in pathogens and hosts, such as new pathogen strains, hybridisation events, host switches, the introduction of new host breeds, changes to the surrounding environment (including climate change) and intensified cultivation practices or natural long-distance dispersal events, for example through extreme weather (Bebber, 2015; Ghelardini et al., 2016; Thines, 2019). It is not always straightforward to identify the underlying cause and, additionally, these processes are often intertwined; for example, the introduction of taxa can lead to hybridisation or horizontal gene transfer between previously allopatric pathogens (Fisher et al., 2012; Fones et al., 2020; Ghelardini et al., 2016). However, while the introduction of invasive alien taxa is only one of multiple possible causes, EIDs typically exhibit many features classical of biological invasion processes (Ogden et al., 2019; Paap et al., 2022; Slingenbergh et al., 2010; Vilà et al., 2021).

Invasive alien fungal pathogens can cause severe economic losses and damage to biodiversity and humans (Fisher et al., 2012; Fones et al., 2020). When encountering naïve hosts that lack a co-evolutionary history with the pathogen, high rates of host mortality can occur (Fisher et al., 2009, 2012; Hansen et al., 2012). Prominent examples include the causal agents of chestnut blight (*Cryphonectria parasitica* [Rigling & Prospero, 2018]), myrtle rust (*Austropuccinia psidii* [Carnegie & Pegg, 2018]), Phythopthora dieback (*Phytophthora cinnamomi* [Cahill et al., 2008]), Dutch elm disease (*Ophiostoma ulmi/novo-ulmi* species complex [Brasier & Buck, 2001]) and ash dieback (*Hymenoscyphus fraxineus* [Gross et al., 2014])—all of which resulted in widespread massive population declines in their primary hosts, leading to major changes in forest composition (Thakur et al., 2019). Although most fungal pathogens infect plants (Sexton & Howlett, 2006), alien zoopathogenic fungi are capable of causing rapid decline in animal populations too. Important examples include the chytrid fungi *Batrachochytrium dendrobatidis* and *B. salamandrivorans* threatening amphibians, and the white nose syndrome of bats caused by *Pseudogymnascus destructans* (Fisher et al., 2009; Frick et al., 2010; Spitzen-van der Sluijs et al., 2016). In addition, invasive alien fungal pathogens threaten economies and human well-being (Bebber et al., 2014; Fones et al., 2020; Ogden et al., 2019). In many parts of the world, newly established invasive alien fungal pathogens in forestry systems have increased markedly (Burgess & Wingfield, 2017; Santini et al., 2013) and there is a long history of pathogens following crops around the world, sometimes causing devastating epidemics (Santini et al., 2018). Especially when staple crops are concerned, this leads not only to economic losses but can also threaten food security (Fones et al., 2020). Consequently, microbial invasions were identified as one of the pressing issues in invasion science (Paap et al., 2022).

Indeed, whereas invasion science has long focused on large or conspicuous organisms such as vascular plants and vertebrates (Pyšek et al., 2008; Troudet et al., 2017; Vilà et al., 2021), the importance of alien fungi has been more widely recognised in recent decades (Desprez-Loustau et al., 2007; Dickie et al., 2017; Gladieux et al., 2015; Roy et al., 2017; Thakur et al., 2019). The elusive lifestyle, small size and challenging taxonomy of fungi have hampered efforts to describe their distribution and biology (Desprez-Loustau et al., 2007; Paap et al., 2022). It has long been assumed that microbial biogeography is characterised by a lack of dispersal limitation, and therefore cosmopolitan occurrence, but more recently this paradigm changed (Rout & Callaway, 2012). Advances in molecular ecology and taxonomic practice have led to considerable progress in clarifying the identification and evolutionary relationships among fungi (Crous et al., 2021), resulting in a better understanding of fungal biogeography (Lumbsch et al., 2008), and invasions, through phylogeographic studies that infer native and alien ranges (Gladieux et al., 2015). These studies have shown that regional endemism is common among fungi (Talbot et al., 2014) and only few ascomycete species are dominant cosmopolitans (Egidi et al., 2019), while many species are endemic at least to a single continent (Peay et al., 2016). A global analysis of soil fungi revealed that their overall richness increased toward the equator, especially for plant and animal pathogens (Tedersoo et al., 2014), and that the tropics are centres of endemicity (Tedersoo et al., 2022), while distributional ranges increased with latitude (Dickey et al., 2021). Alien richness hotspots of macrofungal (i.e. of those that form visible fruiting bodies) saprobes and ectomycorrhiza were found in Europe, the Americas and Oceania (Monteiro et al., 2020, 2022). However, biogeographic patterns of fungal guilds can differ substantially (Põlme et al., 2020; Tedersoo et al., 2014) and a similar global analysis for alien fungal pathogens is missing to date, despite their environmental and socio-economic impacts.

In this study, we examine the biogeography of 100 invasive alien fungal pathogens that cause major negative impacts to the environment and/or human livelihoods. We compiled information on the regional distribution, first records, ecological characteristics and the native biogeographic regions. We focus on alien fungi (neomycetes sensu Kreisel & Scholler, 1994; that is taxa introduced after 1492, the onset of the Columbian Exchange [Crosby, 2003]) and cryptogenic fungi (likely alien, sensu Essl et al., 2018) in a physiological/ecological sense (kingdom Fungi and phylum Oomycota, Straminipila) that infect a host and cause disease at some point in their life cycle (excluding human pathogens). Given the strong information bias in favour of better-studied high-impact fungal taxa, we focus on taxa with major environmental or socioeconomic impacts (for more information on species selection see Methods). Here, we (i) investigate their taxonomy and ecological characteristics (i.e. ecofunctional guild, host range, host group and affected part), (ii) analyse their distribution, identifying global hot- and coldspots of alien taxon richness while controlling for sampling effort and area and relate those hot- and coldspots to potential predictors, (iii) reconstruct temporal accumulation trajectories and (iv) analyse the global flows between continents.

While we expect that the global distribution of major alien fungal pathogens is related to the different environmental and socio-economic characteristics of regions, patterns may be different from those of other groups because a suitable host organism is required for establishment, introducing an additional barrier to the invasion process (Monteiro et al., 2022; Paap et al., 2022). Hotspots of alien animals and plants are found on islands and in coastal mainland regions (Dawson et al., 2017), but interestingly no positive island effect was found for alien macrofungi (Monteiro et al., 2022), potentially highlighting the dependence on a suitable host for alien symbiotic species (Delavaux et al., 2019). Therefore, we expect a similar pattern for pathogens.

Additionally, fungal pathogens are often not detected in areas of introduction until they cause severe disease outbreaks, often promoted through reduced ecosystem resilience (e.g. habitat deterioration) and intensively managed systems. Modern agricultural and plantation-forestry systems are particularly prone to disease outbreaks because they are usually based on a few genetically uniform crops, which are cultivated over large areas at high density, providing highly susceptible host populations (Bebber et al., 2014). An extreme case is global commercial banana production, which currently relies almost exclusively on one clonal line (Cavendish) and is threatened by banana wilt (Panama disease) caused by the invasive *Fusarium oxysporum cubense* Tropical race 4 (Ploetz, 2015) (recently proposed as a new species, *Fusarium odoratissimum* [Maryani et al., 2019], but see [Torres Bedoya et al., 2021]). Therefore, high-impact alien fungal pathogens can be expected in regions that are characterised by intensive land use, which, indeed, is also considered a likely major driver of plant pathogen richness (Makiola et al., 2019). Furthermore, suitable climatic conditions will likely drive successful establishment, although it was shown that pathogenic fungi probably have broader climatic tolerance than mycorrhizal fungi (Větrovský et al., 2019).

As with plants and animals (Dawson et al., 2017), a positive relationship between socio-economic drivers and the richness and spread of alien fungal species has been demonstrated (Desprez-Loustau et al., 2010; Monteiro et al., 2022; Scott et al., 2019; Sikes et al., 2018). Fungal pathogens are almost exclusively introduced by accident, e.g. as contaminants of goods (Hulme et al., 2008), and therefore we expect them to be closely linked to trade and economic wealth (e.g. expressed by per capita gross domestic product; GDP*pc*), as indicators of propagule pressure. While the link between economic wealth and trade has been made regularly, it may be confounded with observational capacity, i.e. richer countries are more likely to be able to detect and monitor the introduction and spread of alien taxa (Bebber et al., 2014; Waage et al., 2008). Global trade has increased strongly in recent years, and so have known alien taxon richness and first records globally, as found across various taxonomic groups (Monteiro et al., 2022; Seebens et al., 2017). This is also likely to be the case for alien fungal pathogens, where regional studies show an exponential increase (e.g. Desprez-Loustau et al., 2010; Santini et al., 2013).

Some taxonomic and functional groups may be more successful than other invasive alien species. In fact, several taxa were consistently overrepresented in regional alien fungal species lists, such as Erysiphales (Ascomycota) and Peronosporales (Oomycota) (Beenken & Senn-Irlet, 2016; Desprez-Loustau et al., 2010; Voglmayr et al., 2023). Ascomycetes, followed by oomycetes, are the most common group causing emerging forest diseases in Europe (Santini et al., 2013). Egidi et al. (2019) found that ascomycete genomes could be better equipped to cope with environmental stress and resource use, making them more competitive and enabling more generalist behaviour, attributes that can favour successful invasion (Philibert et al., 2011). Generalist behaviour is also common in oomycetes, such as *Phytophthora* spp. (Scott et al., 2019). Guild-shifting fungal pathogens such as those with a facultative parasitic lifestyle and saprotrophic or endophytic stages (Zanne et al., 2020) are thought to have an advantage during initial invasion stages compared to obligate biotrophic parasites. Finally, we expect that alien fungal pathogens, which are introduced mainly as contaminants of their animal or plant hosts or associated soils (Hulme et al., 2008; Santini et al., 2013), will consequently show similar continental global flows and distributions as their hosts (Bebber et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Data compilation

This work considers pathogenic fungi, that is those that infect and cause disease in one or more hosts at some point in their life cycle, in (semi-)natural or managed (agro-)ecosystems. We do not consider other ecofunctional guilds such as mycorrhizal fungi and pure saprotrophs. While acknowledging the global burden of fungal disease in humans (Konopka et al., 2019; Rokas, 2022), we have excluded primarily human-pathogenic fungi and zoonotic diseases from this work, which we consider a special case due to the artificial environment and immense global interconnectedness of the host, and where invasion-focused studies are largely lacking (for further literature on human fungal pathogens and human EIDs, see e.g. Konopka et al., 2019; Seyedmousavi et al., 2015, 2018; Vilà et al., 2021). Causal agents of EIDs, whose origins are unknown but are likely to be alien, were classified as cryptogenic (sensu Essl et al. (2018)) and were therefore included. The taxonomic scope of this study encompasses fungi, that is of the kingdom Fungi (Eumycota), and oomycetes (Straminipila), which are traditionally studied by mycologists and plant pathologists, due to their similar lifestyle, morphology and behaviour, and their historical classification as fungi. Considering those in an epidemiological and invasion context, for the purpose of this work we decided to include oomycetes in spite of their phylogenetic distance. The taxonomic units considered are referred to as taxa, including both species and lower taxonomic levels such as subspecies, *formae specialis*, pathotypes or hybrids. This is a practical approach in the light of heterogeneous sources and data limitations, and we acknowledge that the species level may not always be the most appropriate taxonomic level, as it might mask patterns of invasive lineages or strains.

This list of 100 major alien fungal pathogens (Table S1) focuses on taxa that show substantial negative impacts in their introduced range (as reported in scientific literature). For taxon selection, we consulted various sources: alien species compendia and online resources (e.g. GISD, EASIN, CABI ISC, EPPO lists and Pest Risk Assessments), as well as scientific literature. A preliminary taxon list was sent to experts in fungal ecology and invasion biology for feedback that was considered when compiling the final taxon list (see acknowledgements). As we included alien pathogenic fungi with environmental and/or socio-economic impacts, we considered criteria for both impact categories (Table S4). Those criteria were adapted from the EICAT (Environmental Impact Classification for Alien Taxa) and SEICAT (Socio-Economic Impact Classification for Alien Taxa) frameworks (Bacher et al., 2018; IUCN, 2020). Note, however, that we did not perform comprehensive EICAT/SEICAT assessments. The documented impact (environmental or socio-economic) was classified based on available literature. Impacts of an introduced pathogen are context-dependent and influenced by the interplay of species attributes, invasion history and characteristics of the recipient environment (IUCN, 2020). Thus, impacts may vary considerably in different parts of the alien range, across space, time, and habitats. The assigned impact therefore represents a general classification from a global perspective. As no standardised global assessment on the impacts of alien pathogenic fungi is currently available, and as data on impacts are patchy, applying the selection criteria (Table S4) was not always straightforward and uncertainties are substantial in some cases. Reports on economic losses and impacts are seldom quantified, often using vague terms like 'severe' or 'destructive' (Latombe et al., 2019). Furthermore, the classification of the predominant impact type is not always clear, as whether a host is economically important may vary from region to region. Economic impacts are also more easily detected and therefore more likely to be reported (Diagne et al., 2021), while environmental impacts tend to remain under-reported. Indirect costs of invasive alien species are often hard to measure and therefore tend to be under-reported as well (Haubrock et al., 2021). Finally, due to language restrictions of the authors (despite the extensive use of translation engines) some sources might have been missed. While we acknowledge that such listings will vary to a certain degree when compiled by different groups, reflecting geographic and taxonomic biases, we are confident that the selection of these 100 major alien pathogenic fungi includes those fungal pathogens with known substantial deleterious impacts and is robust as it is based on the exhaustive use of available information.

Our dataset is built upon a wide range of sources including national and subnational inventories, alien taxa compendia (e.g. CAB International, 2021; Pagad et al., 2018; Seebens et al., 2017), datasets provided by other researchers (e.g. Barwell et al., 2020; Bufford et al., 2016 and an updated version of Santini et al., 2013) and databases not specifically targeting alien taxa (e.g. Farr & Rossman, 2021; GBIF.org, 2021; MyCoPortal, 2021). Further, we extracted data from scientific publications, books and reports found via general and scientific search engines (i.e. Google, Google Scholar, Web of Science). Following best practice recommendations for the standardisation and integration of alien distribution data (Seebens et al., 2020), we utilised translation tables for invasion related vocabulary and a comprehensive global gazetteer to standardise locality descriptions. Scientific names were standardised and synonyms resolved using Species Fungorum (RBG KEW et al., 2021) via 'taxize' (Chamberlain et al., 2020) as the primary source, and MycoBank (Crous et al., 2004), the USDA taxonomic repository (Farr & Rossman, 2021) or IDPhy (Abad et al., 2022), if names could not be resolved via Species Fungorum or were known to be outdated. Information on ecofunctional lifestyle, host taxonomic group and the part of the host that is infected, as well as host range was collected using compendia (e.g. CAB International, 2021; Põlme et al., 2020) and targeted searches in published and grey literature using the scientific taxon name and the respective ecological characteristics. Ecological characteristics consistent within a higher rank taxonomic group were inferred for lower rank taxa (e.g. a solely parasitic lifestyle within the Pucciniales, rust fungi). For the spatial distribution, we used the Level 4 Regions of the Biodiversity Information Standard scheme (TDWG; [Brummitt, 2001]) as baseline, considering countries and subnational administrative units for large countries (i.e. United States, Canada, China, Australia, Russia, Brazil) and islands/archipelagos. Occurrence data that were lacking an interpretation of the taxon's biogeographic status were checked and a status was assigned where possible. This was done by comparing the biogeographic continental region (Level 1 Regions, TDWG [Brummitt, 2001]) of the occurrence and the native region information of the taxon, or by manual assignment (see Supplementary Information 2). Occurrences with the status 'absent' or 'intercepted' were excluded. We focused on neomycete occurrences (i.e. introduction events that likely happened after 1492), while excluding earlier ones (archeomycete occurrences; introduced before 1492; sensu Kreisel & Scholler, 1994). We included the neomycete occurrences of several prominent crop pathogens that fall into both categories but excluded those crop pathogens, which are archeomycetes in their alien range globally or for which taxonomic boundaries are unclear. Crop pathogens were also included if they reside in agroecosystems only and do not invade natural ecosystems, as we also considered the socio-economic aspect of fungal invasions. Regional records which were unlikely to reflect true established occurrences were excluded (e.g. occurrences based on soil or timber samples from Antarctica). The final dataset encompassed (i) taxon-specific information: main impact, native range, higher taxonomic ranks, ecological characteristics (Tables S1 and S3), and (ii) distribution information: presence in a region, biogeographic status (cryptogenic or alien), and if available the year of first record. After curation and completion, it contained 5398 taxon x region combinations of the 100 pathogens in 355 non-overlapping regions (284 mainland regions and 71 islands/archipelagos) worldwide.

2.2 | Analysis and visualisation

To investigate the distribution of major taxa across taxonomic groups, we constructed a cladogram on class level, with the width of each tip (presented as triangle in Figure 1) representing the proportional richness of the whole class (including all ecofunctional guilds). Information on total species numbers per clade was extracted from the Catalogue of Life (Kirk, 2020) (accessed 2021-01-21). To provide a complete overview of fungal diversity, we lumped all remaining classes that did not contain major taxa as faded tips within the respective phylum. The resulting cladogram was built with the R packages 'ggTree' (Yu et al., 2017) and 'ggTreeExtra' (Xu et al., 2021). We performed a Chi^2 test of independence to investigate whether the observed number of taxa per class and phylum differed significantly from expected distributions based on the total species numbers in each group to identify over- or underrepresented groups.

To describe global spatial distribution patterns, we calculated the total region-wise richness and the richness per impact category. Taxa that were classified as having both substantial environmental and socio-economic impacts were counted for both categories. To allow comparisons between the regions, we used a Mollweide equal-area projection. Further, we identified hot- and coldspots by correcting for regional area and sampling effort. To account for overdispersion in our count data (Overdispersion test $p < 0.001$; dispersion parameter $\phi = 6.7$), we ran a quasi-Poisson regression, with the number of taxa per region as the dependent variable and the mean sampling effort across the region, region's area and the interaction between them as predictors (richness ~ sampling effort × area). Area was log-transformed and both predictors were scaled to ensure comparability between them. As no global estimates of sampling effort for alien pathogenic fungi are available, we used estimates for plants and vertebrates (amphibians, mammals, and birds) as a proxy (Meyer et al., 2015, 2016). These datasets (equal-area grid cells, with ~110 × 110 km resolution at the equator) estimate the percentage completeness of species occurrences provided by GBIF and were here used as a proxy for the completeness of biodiversity information (Dawson et al., 2017). As the selected taxonomic groups are potential fungal hosts and as regional differences in sampling effort are strongly correlated across taxa (Meyer et al., 2015, 2016), this measure likely is a sufficient indicator for alien fungal pathogens as well. Although GBIF is biased towards specific regions of the world (Hughes et al., 2021), to our knowledge better bias correction methods are not available. We calculated the mean completeness across all grid cells per region for each taxonomic group and then took the mean across all taxonomic groups for each region (Figure S1).

The remaining unexplained variance (deviance residuals) per region was binned into quantiles and plotted to show hot- and coldspots of unexplained major pathogen richness. To test for a potential island effect, we used a Mann–Whitney-*U*-test to investigate whether mainland and island residuals were significantly different. Further, we ran a multiple linear regression to test whether there was a significant relationship between unexplained variance and the mean index of human modification of terrestrial lands (HM; Kennedy

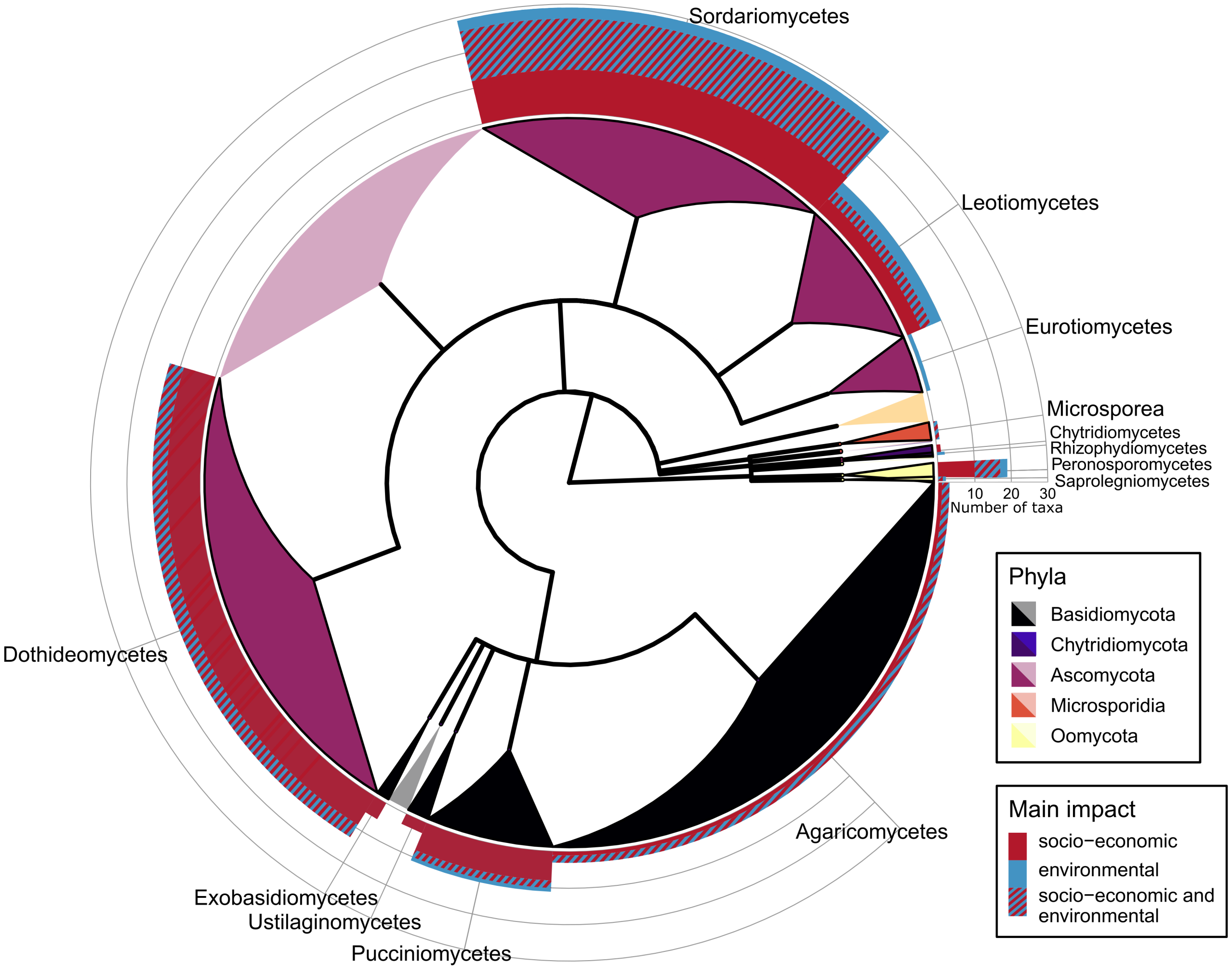

FIGURE 1 Cladogram with circular barplot, showing the taxonomic distribution of 100 major alien fungal and oomycete pathogens across classes of fungi and oomycetes. Classes that include at least one taxon are presented as triangle tips, outlined in black and coloured by phylum, and their width corresponds to the known number of species, extracted from the Catalogue of Life (Kirk, 2020). All other classes of the respective phyla are summarised in one triangle tip and displayed in light colour without black outline (e.g. all other Ascomycota in light purple). Note that within the Straminipila only the phylum Oomycota was considered, due to their historical consideration as fungi and their similar lifestyle. Classes are followed by bars, with their height corresponding to the total number of selected taxa in the respective class (red = socio-economic, blue = environmental). Taxa with notable impacts in both categories were attributed to both (blue-red striped).

et al., 2019), the mean gross domestic product per capita (GDP*pc*; Kummu et al., 2018), and bioclimatic factors expressed as the presence/absence of a certain biome in a region (Figure S2). HM is a cumulative measure of 13 anthropogenic stressors (e.g. settlements, agriculture, transportation) that quantifies the degree of land modification (Kennedy et al., 2019). GDP*pc* as proxy for wealth was found to be a better predictor of pest presence than total GDP, and while it is thought to be representative for colonisation/propagule pressure, e.g. as indicator of trade, it is likely also in part associated with sampling effort/capacity (Bebber et al., 2014), an aspect we account for beforehand in our correction model. GDP*pc* (log-transformed) and HM were centred to their means and scaled to their standard deviations. Biome presence/absence is based on a map of nine terrestrial climate-derived biomes (Loidi et al., 2022, 2023). The mountainous subbiomes were considered separately, summarised under 'orobiome'. Biomes are determined by regional climate, dominant vegetation forms and other ecological factors such as soil characteristics and disturbance (Loidi et al., 2022), all factors that likely influence environmental suitability for fungi (Větrovský et al., 2019). We did not include bioclimatic variables such as temperature and precipitation to the model due to circularity, because the biomes represent different climatic conditions already (Loidi et al., 2022). Note that 12 regions had to be excluded from the regression because data were not available for all variables due to the regions' small sizes.

Temporal invasion trends were analysed by pooling regional first records over 20-year time periods between 1800 and 2020 and calculating the total number of first records per period. To illustrate global flows between continental biogeographic regions, we mapped the links between the native biogeographic range of taxa to the biogeographic regions of their alien range(s). Taxa with native ranges covering multiple continents were counted for each corresponding continent as 1/number of continents to which the taxon is native (e.g. if a taxon was classified as native to two continents it would be counted as 0.5 for each). Flows were unidirectional for taxa with an 'unknown' native range and for hybrids.

All analyses and graphics were done using R. 3.6.0 (R Core Team, 2020) and R Studio (RStudio Team, 2021). Flow diagrams were created using the R package 'circlize' (Gu et al., 2014). All maps were produced using 'ggplot2' (Wickham, 2016).

3 | RESULTS

3.1 | Taxonomic and functional composition

Of the 100 major alien fungal pathogens (Table S1), approximately half have primarily socio-economic impacts (53 taxa), 13 taxa exhibit primarily environmental impacts, and 34 taxa have substantial impacts in both sectors (Table S2). The taxa belong to the phyla Ascomycota (53 taxa), Basidiomycota (22 taxa), Chytridiomycota (3 taxa) and Microsporidia (1 taxon), and to the phylum Oomycota (Straminipila, 21 taxa), and are distributed across 13 classes and 43 families (Figure 1, Table S2). A chi^2-test revealed significant differences between the observed taxon numbers and expected distribution of taxonomic groups at the level of phylum ($X^2_{(df=4, N=100)}=359.86$, $p<0.001$) and class ($X^2_{(df=12, N=100)}=407.49$, $p<0.001$). Especially the Peronosporomycetes (Oomycota) were over-represented, whereas the Agaricomycetes (Basidiomycota) were under-represented among the major alien fungal pathogens (Figure S3).

Although fungi can infect a wide range of species, they are especially prevalent as plant pathogens (Fisher et al., 2020; Wang & Wang, 2017). This is reflected in our dataset, where 93 of the 100 fungal pathogens infect plants, primarily angiosperms (69 fungal taxa; Table S3), while only ten taxa solely infect gymnosperms and 14 taxa infect both groups. Seven were zoopathogenic, on either vertebrates (five taxa) or invertebrates (two taxa). No pathogens of ferns, mosses or lichens were listed. Some of the plant pathogens also cause disease in humans; for example, *Cryptostroma corticale* causes respiratory disease (Braun et al., 2021), *Fusarium graminearum* produces mycotoxins harmful to domesticated animals and humans (van der Lee et al., 2015), and the sorghum ergot (*Claviceps africana*) can cause intoxications of humans and livestock through alkaloid production (Shimshoni et al., 2017). While most plant pathogens infect the aboveground organs of plants (66 taxa) and 20 infect above- and belowground plant parts, only six taxa are classified as exclusively belowground pathogens. Most animal pathogens in our dataset cause infections of the skin and only one causes infections in other parts of the body. Obligate parasites and those that are also capable of a saprotrophic lifestyle were equally represented, with 47 taxa belonging to the former and 53 taxa belonging to the latter group. Notably, nearly half of the taxa were classified as specialists that primarily infect one host genus per life stage (48 taxa). A further 36 taxa were classified as wide generalists that attack hosts across families, and 16 taxa are moderate generalists that mainly attack hosts within a family.

3.2 | Global distribution patterns

Temperate, Mediterranean and (sub)tropical regions of both hemispheres harbour many of the 100 major alien fungal pathogens (Figure 2); especially in Europe, South Africa, New Zealand, and several regions in the Americas. The top five regions were Italy (61 taxa), Germany (56), United Kingdom (56), Switzerland (54) and France (53). The richness of taxa that cause socio-economic impacts was moderately positively correlated with that of taxa causing environmental impacts (Spearman's rho = 0.55 when excluding taxa that fall into both categories; $p<0.001$).

Accounting for a region's area and average sampling effort, we identified hot- and coldspots of major alien fungal pathogen richness (Figure 3), by plotting the residuals of the quasi-Poisson regression model. The model explained 39.3% of deviance in the data and both predictors showed a strong positive correlation with major alien fungal pathogen richness ($p<0.001$), while the interaction term showed a weak negative effect ($p=0.045$) (Table S5). After accounting for both, area and sampling effort, mainland regions were not significantly different to islands (Mann–Whitney *U*-test, $n_{\mathrm{mainland}}=284$, $n_{\mathrm{island}}=71$, $W=9878$, $p=0.79$) (Figure S4). Regions with fewer pathogens reported than expected (the lower 10% of the value range, i.e. negative residuals), include cold environments such as the Arctic, Tundra and desert regions like the South-western United States, South-eastern- and Central Australia, the Sahel Zone and Namibia, whereas hotspots of pathogen richness, i.e. regions harbouring greater richness than predicted by the model (the upper 10% of the value range), include regions in Southern and Eastern Europe, New Zealand, India, Japan, Hawai'i, some Caribbean islands, southern and northern South America, and the East Coast of the United States, as well as South Africa and Kenya. The results of the multiple linear regression revealed a significant positive relationship between major alien fungal pathogen hotspots and human modification of terrestrial lands (HM), the mean per capita gross domestic product (GDP*pc* [log-transformed]), the presence of orobiomes (mountaineous regions), and temperate and tropical forests (biomes 3 and 9), while the relationship with boreal forests (biome 2) was negative (for details on effect sizes, errors, *p*-values and model diagnostics see Table S6, Figures S5, S6). No significant relationship was found for the presence of other forest types, Tundra, Mediterranean, steppe and semi−/desert biomes. The whole model explained 34% of the variance ($R^2=0.3432$).

3.3 | Temporal accumulation patterns

The first records indicate the earliest date a taxon was documented in a country or region. The earliest record in our dataset was 1817; since then, the number of first records per 20-year period increased distinctly over the past two centuries, particularly at the turn of the

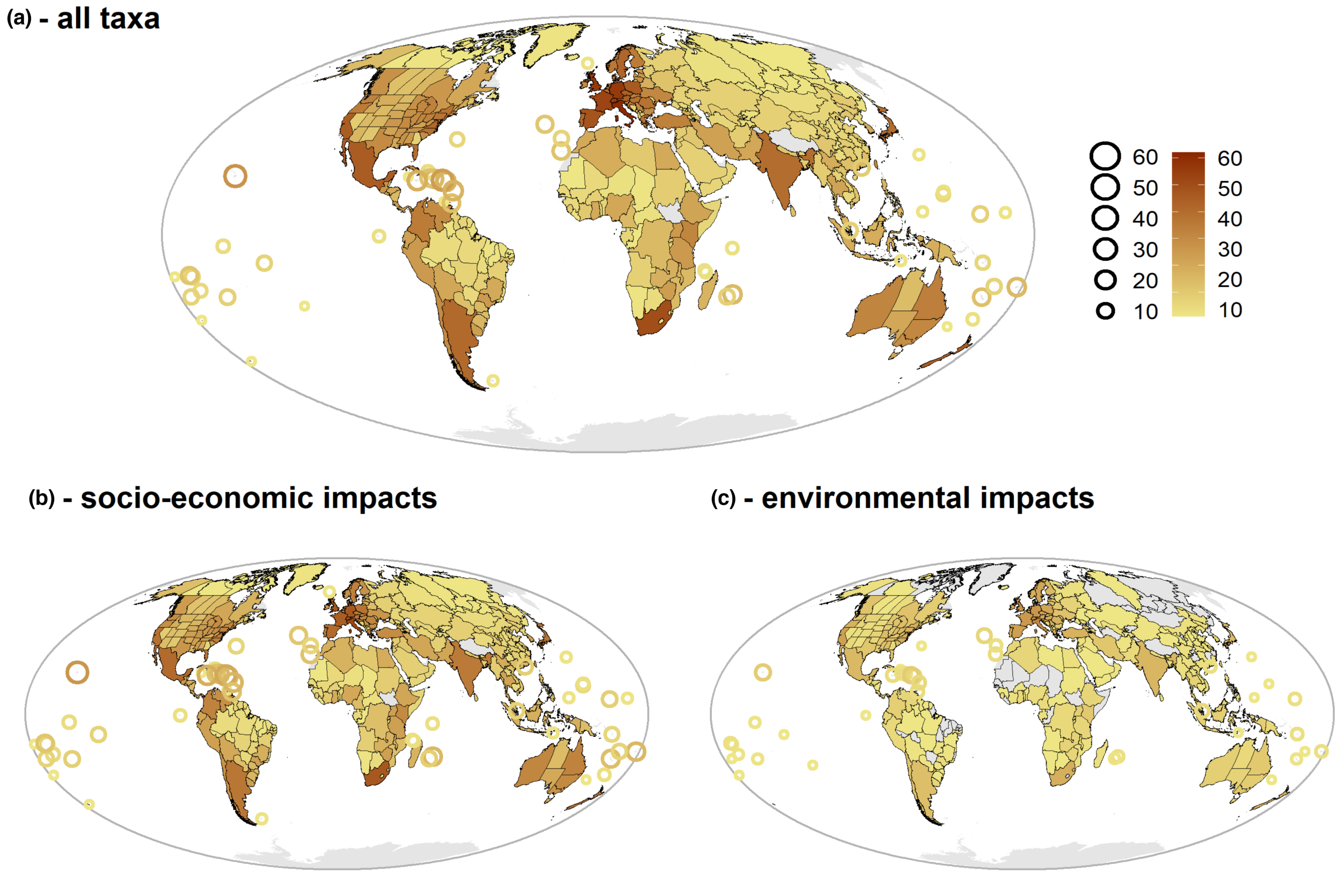

FIGURE 2 Global known richness patterns of 100 major alien fungal and oomycete pathogens; 5398 taxon x region combinations across 355 non-overlapping regions of the world. Colours correspond to the number of alien taxa per region, as does circle size for islands. Grey areas represent regions with no data on established alien or cryptogenic occurrences of the considered taxa. The maps show the absolute richness of alien and cryptogenic occurrences of (a) all 100 pathogens, (b) pathogens with substantial socio-economic impacts (*n* = 83 taxa) and (c) pathogens with environmental impacts (*n* = 47 taxa). Pathogens with both socio-economic and environmental impacts are included in both (b) and (c).

millennium (Figure 4). Although the mid-latitudes of the Northern Hemisphere are consistently most represented over the whole period, the number of first records per region increased across all latitudes in recent decades, most markedly so in Europe and Northern America (Figure S7b). Among host groups, new records associated with vertebrates showed the most pronounced increase in the past decades (Figure S7d). In the past two decades, 60 out of the 100 taxa were recorded in a new region at least once, indicating ongoing spread. Taxa with ongoing spread are mainly members of the Ascomycota (33 taxa) and Oomycota (16 taxa), with the latter group showing a dramatic increase in first record numbers in the current millennium (Figure S7a). Notably, while both groups show similar numbers of new records in the past two decades, the number of taxa associated with those new records is much lower for Oomycota, indicating that members of this group spread farther on average across regions.

3.4 | Origins and global flows among continents

Asia and North America represented the most important source regions of major alien fungal pathogens; 33 and 24 taxa are considered native to Temperate and Tropical Asia, respectively (Figure 5b). The native range of 10 taxa remains unknown, even among these better studied impactful taxa. Interestingly, none of these 100 taxa are considered native to the Pacific Islands, making this continental region a recipient only. Northern America not only acts as an important donor (19 taxa) but together with Europe is also one of the top recipients (Figure 5a). While flow patterns of the impact groups were similar, due to the large number of taxa included in both groups, the flows differ between phyla. Whereas Ascomycota and Oomycota show a considerable number of taxa having unknown origins (unidirectional flows), this is not the case for Basidiomycota, for which Temperate Asia is by far the most important donor. Europe is only a recipient of major alien fungal basidiomycete and oomycete pathogens and likewise Northern America is almost exclusively a recipient of Basidiomycota.

4 | DISCUSSION

We present a comprehensive global overview of the biogeography of 100 major alien fungal pathogens by investigating their taxonomic

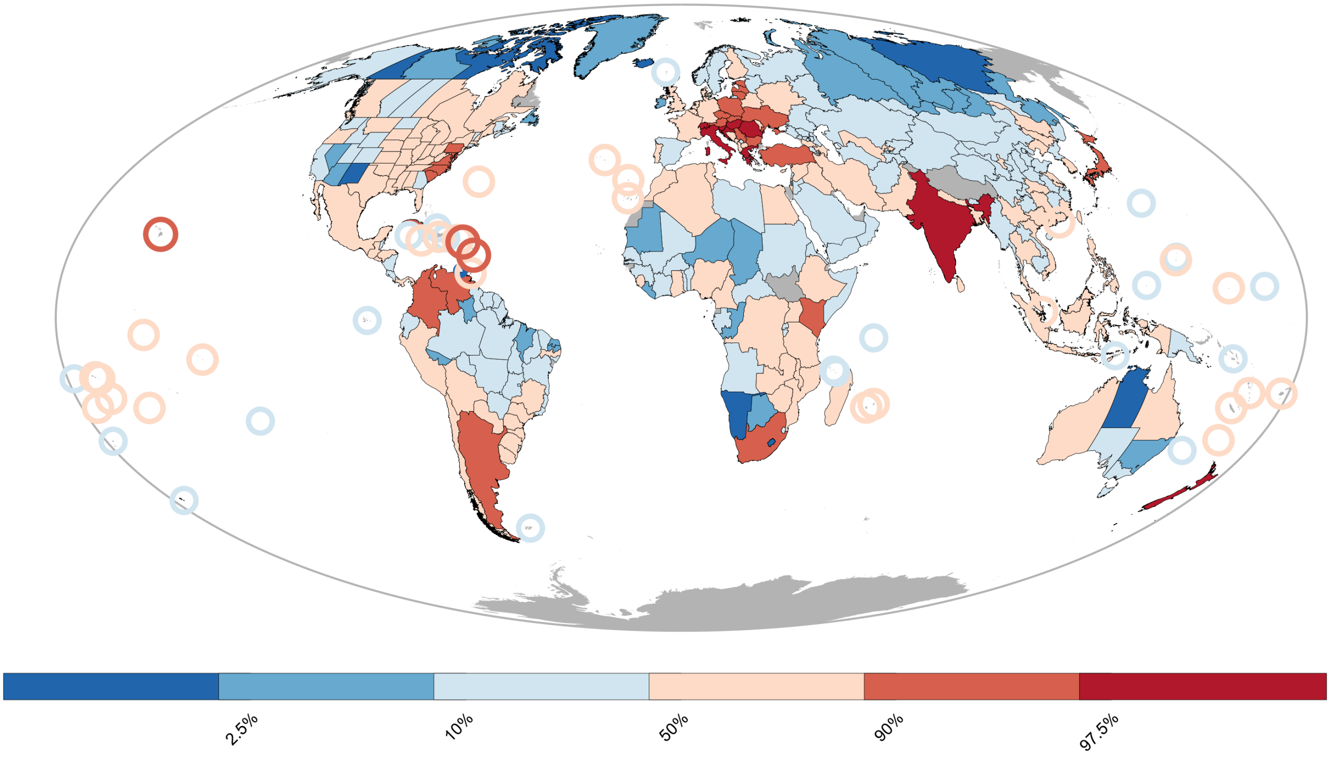

FIGURE 3 Hotspot and coldspot regions of global 100 major alien fungal and oomycete pathogen richness, accounting for area and sampling effort. Depicted are quantiles of the residuals of a quasi-Poisson regression (richness ~ average sampling effort [%] × area [km^2] (log-transformed)), with red colour indicating regions with higher pathogen numbers than expected after correction for area and sampling effort and blue colours indicating lower numbers than expected. Note the non-linear scale of the colour legend.

composition, ecological characteristics, geographic and temporal patterns, and reconstruct their origins and flows between continents. We found that mesic and wet regions, regions with high anthropogenic modification of terrestrial lands, and regions with high GDP*pc* are more likely to host impactful alien pathogens, which are disproportionately oomycetes and from Asia and North America, but otherwise show no strong trends in ecological characteristics.

We have shown high richness in temperate, Mediterranean and (sub)tropical regions, largely consistent with the general cross-taxonomic patterns of alien richness reported for other organism groups (Dawson et al., 2017; Monteiro et al., 2020). Contrary to alien plants and animals, where islands have been identified as hotspots of established alien species richness (Dawson et al., 2017; Essl et al., 2019), and in line with Monteiro et al. (2022), we found no positive island effect after correcting for sampling effort and region size. This could be, first due to the combined effect of lower richness and higher phylogenetic distinctiveness of native host group assemblages due to isolation (Moser et al., 2018), making it harder for alien fungi to colonise new species, and second, due to limited available area for agriculture and forestry. Interestingly, contrary to island theory, there was also no negative island effect found for soil fungal communities in general, a phenomenon the authors of the study attribute to a lack of dispersal limitation (Tedersoo et al., 2022).

Hotspots were associated with temperate and tropical forest biomes and the presence of orobiomes, probably because they increase habitat heterogeneity within a region (Rahbek et al., 2019). Coldspots were found in the Arctic and boreal regions, cold deserts, and the hot arid zones of the United States, Australia and Africa, likely attributable to a mix of less conducive climate and simultaneously, less anthropogenic activities, including land cover changes and trade. Nevertheless, the associated biomes did not show a significant relationship with hot- and coldspots, probably because regions that harbour such biomes still can be suitable if another conducive biome is present. While both, temperate and tropical forests, provide a conducive climate and are particularly affected by human modification of lands (Kennedy et al., 2019), the former biome additionally coincides with many high-income areas, therefore its strong positive influence in the model could also be partly an artefact of sampling effort, that we may not have been able to fully account for (e.g. in Japan, New Zealand and the US East coast). Tropical areas exhibit warm and moist conditions, particularly suitable for many fungal pathogens (García-Guzmán & Heil, 2014). Furthermore, tropical areas have been identified as fungal pathogen centres of diversity and endemism (Tedersoo et al., 2014, 2022), so the source pool of potential invaders is likely higher than for other biomes. (Sub)tropical forests and savannahs were identified as those biomes, most affected by fragmentation with up to 70% of minimally modified lands within 5 km of modified areas (Kennedy et al., 2019). Landscape configuration can be an important factor for disease emergence, where habitat fragmentation and disturbance are increasing the risk of EIDs

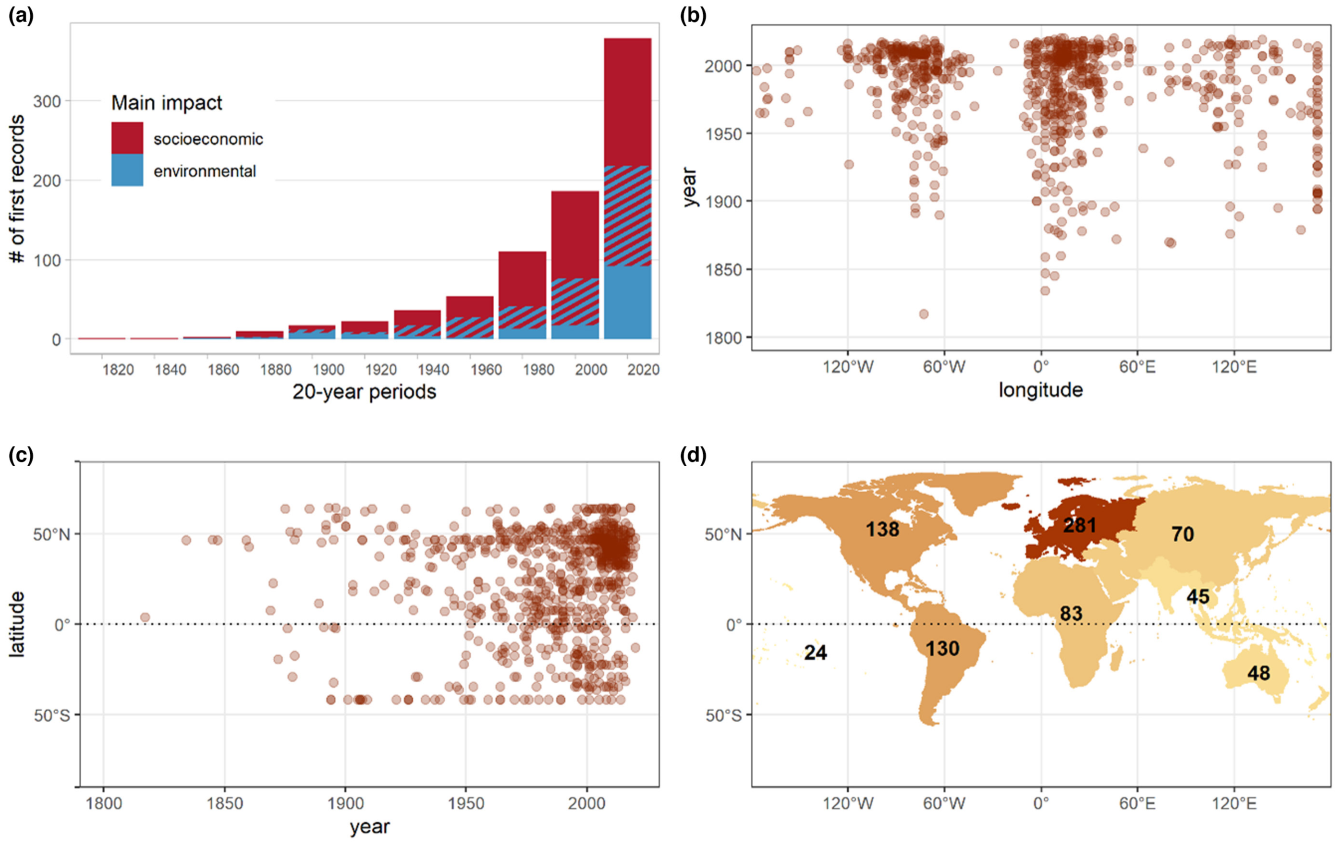

FIGURE 4 Temporal development of first records of major alien fungal and oomycete pathogens globally between 1800 and 2020 ($n = 819$). First records (the earliest date when a taxon was reported in a region) were aggregated to 20-year periods, thus indicating the number of taxon x region x time period combinations (note that a taxon can therefore be counted multiple times per period). a) Number of first records per 20-year time period coloured by impact, and temporal development of longitude (b) and latitude (c) of first records (given as centroids of the recipient regions). (d) Total number of first records per continental region; dark colours indicate high numbers of first records and light colours low numbers of first records.

in both, managed and natural ecosystems, through increased organismic exchange at the landscape-level which promote spill-over to novel naïve hosts (Guégan et al., 2023). In line with this, major alien fungal pathogen hotspots show a significant positive relationship with human modification of terrestrial lands, which considers the extent of agricultural land use, settlements and other anthropogenic stressors (Kennedy et al., 2019), and several hotspots regions exhibit high levels of cropland cover (e.g. India, Eastern Europe, southern Brasil [FAO, 2013]). This finding supports the view that heavily degraded anthropogenic systems (e.g. intensive agricultural systems, forestry plantations) may contribute to the invasion of fungal pathogens. Indeed, Makiola et al. (2019) found that land-use may drive plant pathogen richness, which was higher in agricultural systems, such as perennial cropland, productive grassland and planted forests. Alarmingly, the global area of plantation forests, primarily monocultures, has drastically increased in the recent decades (Guégan et al., 2023).

As a measure of economic wealth, GDP*pc* (Kummu et al., 2018) is correlated with research effort (Bebber et al., 2014), which we tried to account for by using biodiversity inventory completeness estimates (Meyer et al., 2015, 2016). Nevertheless, a significant positive relationship with major alien fungal pathogen hotspots persists, indicating the importance of propagule pressure, e.g. trough international trade (Dawson et al., 2017). It is widely recognised that import volumes correlate with alien fungal richness (Desprez-Loustau et al., 2010; Santini et al., 2013; Sikes et al., 2018) reflecting that trade of commodities (especially plants for planting) is a major pathway for alien pests and pathogens (Burgess & Wingfield, 2017; Ghelardini et al., 2022). For example, Asia is the main importer of live plants to Europe (Ghelardini et al., 2022), which is consistent with our findings that Asia is also the main donor of major alien fungal pathogens. Also, many major alien fungal pathogens were associated with major forestry trees (e.g. pines, eucalypts) or staple crops (e.g. rice, maize, wheat and potato), as they were moved with plants and seeds used to establish plantations (Cleary et al., 2019; Wingfield et al., 2015), often as asymptomatic endophytic infections (Slippers & Wingfield, 2007), with timber, wood products and insects associated with these products (Ploetz et al., 2013), and also machinery and soil. The long history of crop cultivation has led to the globally widespread occurrence of many pathogens, not only as neomycetes, but also as old human-mediated introductions, that is archeomycetes; introduced pre-1492, (Crosby, 2003; Santini et al., 2018). Such

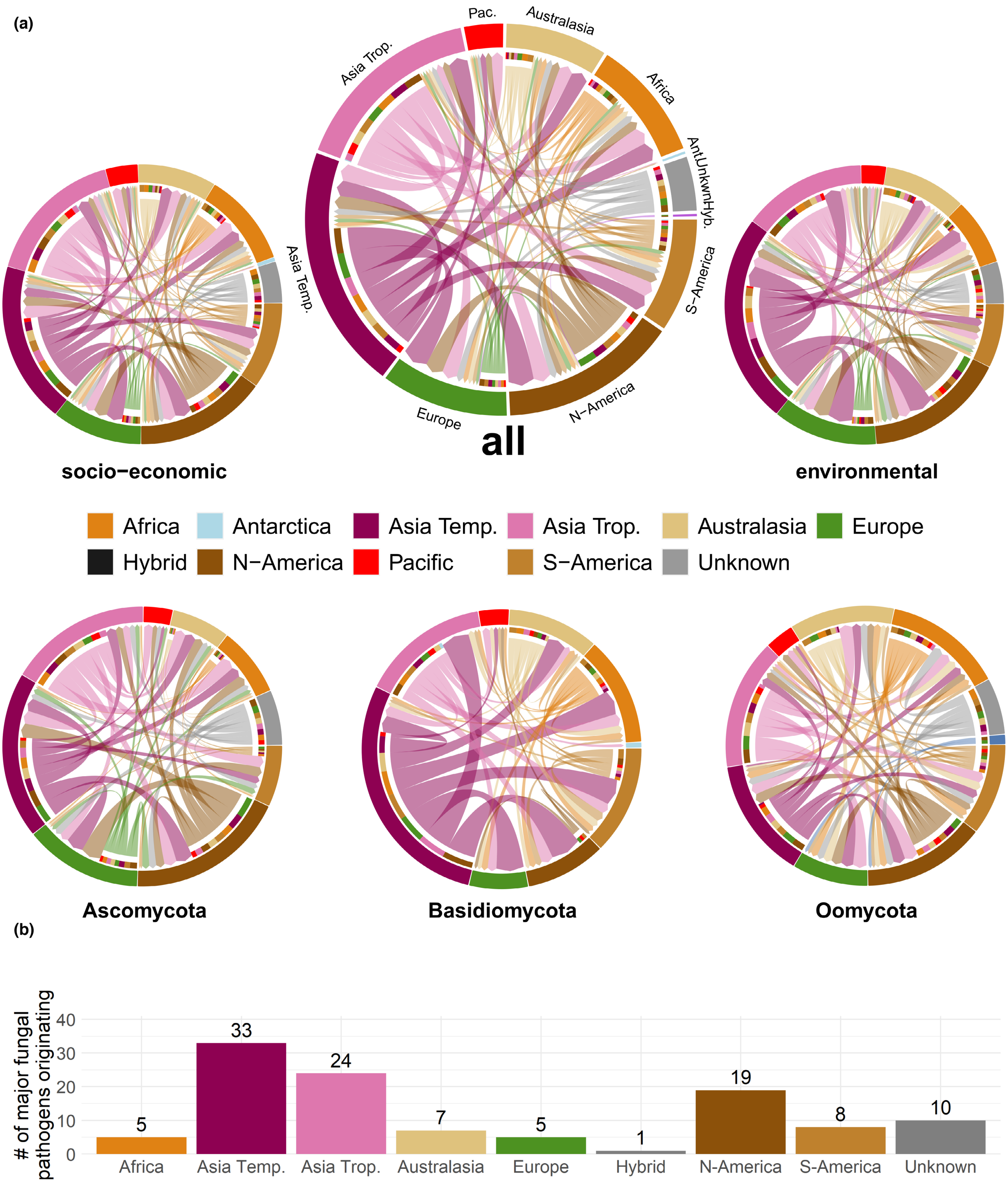

FIGURE 5 (a) Global flows between continents shown as the number of taxa introduced to another region within the same or another continent for all taxa ($n=100$), for each impact category (socio-economic [$n=83$], environmental [$n=47$]) and for the major phyla (Ascomycota [$n=53$ taxa], Basidiomycota [$n=22$ taxa], Oomycota [$n=21$ taxa]). Taxa of unknown or hybrid origin were included as unidirectional flows towards recipient regions. Taxa with native ranges that could not be assigned to a single continent were counted as $1/n_{\text{continents}}$, for example, if a taxon is considered native to two continents it was counted as 0.5 for each. Flow direction of the arcs is indicated by the arrows and the colour. Outer ring and arc colour represents the donating continent or unknown/hybrid origin, while the coloured inner ring indicates the recipient continent (e.g. for Northern America (dark brown outer ring) associated brown arcs indicate the taxa given to another region in the same or another continent, while arcs on the left side represent taxa received from other continents). Antarctica includes sub-Antarctic islands. (b) Distribution of taxon origins. Taxa with native ranges that could not be assigned to a single continent were counted separately for each.

archeomycete occurrences are by definition not represented in our data which might lower the expected bias towards crop pathogens in some regions. Despite the long presence of some species within a region, newly emerging or introduced pathogen strains still lead to significant agricultural losses (e.g. the UG99 strain of the wheat pathogen *Puccinia graminis* [Gautam et al., 2013]).

An analysis of alien plant species richness revealed that economically important plants originating in temperate Asia are disproportionately over-represented in naturalised floras (Van Kleunen et al., 2020). This could partly explain the high numbers of major alien fungal pathogens native to Asia that are alien elsewhere, as it may indicate a cascade effect, where economic use also facilitates pathogens and pests following their hosts (Burgess & Wingfield, 2017; Wingfield et al., 2015). However, this finding could reflect a reporting bias towards pathogens with socio-economic impacts (Bebber et al., 2014). Our data represented a selection of the most important taxa with well-established impacts, and pathogens associated with important economically used hosts are typically better documented, because their impacts are more obvious and substantial to humans compared to purely environmental pathogens. Not surprisingly the vast majority of research reports on plant diseases is focused on annual crops (García-Guzmán & Heil, 2014; Sexton & Howlett, 2006).

The taxonomic composition of the major alien fungal pathogens is largely consistent with general fungal diversity patterns. The Ascomycota represent the largest fungal phylum in terms of species numbers (~93,000 known species globally; [Kirk, 2020]), and it also accounts for the largest share within the major fungal alien pathogens (53 taxa), whereas only 23 taxa are included in Basidiomycota (ca. 50,000 spp.). Within both phyla a similar proportion of genera has a potentially pathogenic lifestyle (Põlme et al., 2020), but pathogenicity is not evenly distributed among classes (Berbee, 2001). A pathogenic lifestyle is more common in Oomycota (currently about 1700 spp. [Kirk, 2020]) that, in terms of species numbers, are significantly over-represented in our list (21 taxa, Figure S3). Peronosporales (Oomycota) that host many severe plant pathogens (e.g. *Phytophthora* spp.) were shown to be over-represented in Europe as well (Desprez-Loustau et al., 2010). Thus, from an ecofunctional guild perspective, those numbers seem plausible. As many of the major fungal pathogens have impacts on both, the economy and the environment, this is consistent across both impact classes. Further studies that integrate a larger sample of species could reveal if found patterns hold true for alien fungal pathogens in general.

We did not detect an overarching trend in ecological characteristics among our taxa, indicating that severe impacts of alien fungal pathogens are highly context-dependent and influenced by many factors. Contrary to expectations, facultative pathogens and generalists did not dominate the picture. Indeed, nearly half of the taxa were classified as specialists of a particular host genus. As shown for *Phytophthora*, generalist pathogens might emerge as successful cosmopolitan high-impact species, but specialists of agricultural crops can also cause major impacts and spread widely, often driven by agricultural intensification (Scott et al., 2019). In this regard, opposing life history strategies may both be beneficial in the invasion process. However, it is noteworthy that the vast majority of plant pathogens in the dataset infected aboveground organs (at least in part). This could be because those are easier to observe, but also due to more efficient spread (e.g. mildews and rusts) (Desprez-Loustau et al., 2010). While globally approximately 8000 fungal species are notable agents of plant diseases (Jayawardena et al., 2021), only 625 fungal species are currently known to cause disease in vertebrates (Fisher et al., 2020) and those proportions are reflected in our results (about 95% plant pathogens). In general, fungal diversity is lower in animals compared to plants (Peay et al., 2016). Importantly, this might be also partly due to a bias in research, as many more plant hosts than animal hosts are economically important (Sexton & Howlett, 2006). Of the seven animal pathogens only five infect—mostly poikilothermic—vertebrates (fish, amphibians, reptiles or the endothermic bats). Indeed, few fungal pathogens are able to cope with mammalian body temperature and infections are often opportunistic, reflecting weakened immune systems and therefore seldom reaching epidemic levels (Konopka et al., 2019; Robert & Casadevall, 2009). Although bacteria and viruses are usually more relevant in this context and there are relatively few animal EIDs associated with fungi, those often cause high mortality and show generalist behaviour threatening multiple taxa. Amphibians seem to be particularly vulnerable and the greatest documented biodiversity loss attributed to a single disease is caused by *B. dendrobatidis* in frogs (Hof et al., 2011; Robert & Casadevall, 2009).

Suboptimal environmental conditions can trigger opportunistic infections of stressed hosts by facultative pathogens, therefore the opportunity for new EIDs and outbreaks will likely accelerate under climate change (Blumenstein et al., 2022; Ghelardini et al., 2016; Konopka et al., 2019). In European forests natural disturbances are increasing, especially insect outbreaks which are largely driven by widespread and significant rise in temperature (Forzieri et al., 2021). Several severe outbreaks of fungal pathogens are linked to climate extremes too, for example *Cryptostroma corticale* (Sooty Bark Disease) benefits from drought and heat waves (Muller et al., 2023). Further studies, including alien fungal pathogens that have not (yet) exhibited major impacts can help to gain additional insights to the underlying factors driving the emergence of these EIDs.

The currently known invasive alien fungi are likely only the tip of the iceberg of a huge number of yet unrecognised or unreported invaders (Bebber et al., 2014). Given the huge fungal diversity to be described and understood, many more potentially high-impact fungal pathogens are likely to emerge in the future, including 'sleeper populations', that is taxa that are present in a region but not yet reported (Bebber et al., 2019; Spear et al., 2021). A global biogeographic study of the prominent oomycete plant pathogen genus *Phytophthora* found two-thirds of countries are likely under-sampled, therefore posing a potential biosecurity risk (Scott et al., 2019). Importantly sampling intensity can not only vary in time but also space and can have very region-specific histories (Waage et al., 2008). For example, sampling effort in New Zealand did not constantly increase over time, but had a peak in survey effort in the 1960s to 1980s, with a subsequent decline due to restructuring of research institutes and shifts in priorities (Sikes et al., 2018). Unfortunately, the specific trajectories of change of sampling effort are often poorly known for individual countries. Rigorous biosecurity measures in certain economic sectors (e.g. crops) have been found to coincide with decreasing plant pathogen arrival rates (Sikes et al., 2018). However, the implementation of effective biosecurity in many countries remains absent or at best ineffectively applied (Burgess & Wingfield, 2017; Early et al., 2016). This is despite the growing opportunities to improve quarantine measures by applying molecular genetic technologies (Crous et al., 2016; McTaggart et al., 2016). Also, as records purely based on morphology or symptoms can be misleading for several taxa, molecular data are a useful way to verify uncertain records in reported regions of introductions. Besides increasing data availability for phylogeographic studies, public sequence repositories—despite several pitfalls (Crous et al., 2021; Hofstetter et al., 2019)—might help to refine alien fungal pathogen distributions in future studies.

Our study shows that improved knowledge of the global biodiversity of pathogenic fungi, their biogeographic distribution, as well as the associated spatial biases in sampling intensity and observation effort should be a future research priority (Guégan et al., 2023; Konopka et al., 2019). First record rates increased particularly strongly during the past 20 years. This is likely in part attributable to increased sampling intensity (Bebber et al., 2014; Waage et al., 2008) and advances in molecular tools, leading to the identification of new species, for example, within the Oomycetes (Scott et al., 2019), and improving the ability to accurately identify fungi. Nevertheless, this trend was found across multiple taxonomic groups (Seebens et al., 2017), and, considering the lag effect that often occurs between introduction and detection (i.e. invasion debt; (Essl et al., 2011), many new invasions are to be detected. This is emphasised by the rising levels of global trade and travel and increasing incidence of epidemics in the past decades (Fisher et al., 2020). There is an urgent need to substantially advance our understanding of fungal invasions and to develop effective measures and a global strategy to mitigate this growing threat (Wingfield et al., 2015).

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ACKNOWLEDGEMENTS

AS, BL, SD and FE acknowledge funding by the Austrian Science Foundation FWF (grants I 3757-B29 and P 34688). PP and JP were supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). MvK acknowledges funding by the German Research Foundation DFG (grant 264740629). CC acknowledges funding from Fundação para a Ciência e a Tecnologia (CEECIND/02037/2017 and UIDB/00295/2020). LR was funded through the FCT contract 'CEECIND/00445/2017' under the 'Stimulus of Scientific Employment—Individual Support' and by FCT 'UNRAVEL' project (PTDC/BIA-ECO/0207/2020). HS received funding through the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, and with the funding organisation German Federal Ministry of Education and Research (BMBF; grant 16LC1807A). MT is supported by the LOEWE initiative of the government of Hessen in the framework of the Centre for Translational Biodiversity Genomics (TBG). JLB was supported by the Tertiary Education Commission through a Centre of Research Excellence grant to the Bio-Protection Research Centre and data sourced from NZFungi2 were funded through the Strategic Science Investment Fund.

We thank Dan Bebber, Treena Burgess, Pedro Crous, Pierre Gladieux, Thomas Jung for their helpful comments on the preliminary taxon list and offer our sincere gratitude to all colleagues that provided data for this study.

We appreciate the helpful comments of two anonymous reviewers and the handling editor, Lucie Zinger.

No fieldwork was conducted during this study.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during this study are available in the supplementary material.

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BIOSKETCH

Anna Schertler is interested in the distribution and ecology of species, particularly the patterns and underlying processes of biological invasions. This work is part of her PhD studies at the Department of Botany and Biodiversity Research at the University of Vienna in the Division of BioInvasions, Global Change & Macroecology. The group conducts multifaceted research centred at the crossroads of invasion science, macroecology, biogeography and conservation biology (https://bioinvasions.univie.ac.at/), and is heavily involved in the GloNAF project, a living global database about naturalized alien plants (https://glonaf.org/).

Author contribution: Anna Schertler, Bernd Lenzner, Stefan Dullinger, Dietmar Moser and Franz Essl conceived the ideas; Anna Schertler collected the data, with additional data provided by collaborators (Jennifer L. Bufford, Alberto Santini, Luisa Ghelardini, Hanno Seebens) and specific input to the list from Alberto Santini, Luisa Ghelardini, Jennifer L. Bufford, Marco Thines and Michael J. Wingfield; Anna Schertler analysed the data with assistance from Bernd Lenzner, Stefan Dullinger, Dietmar Moser and Franz Essl; Anna Schertler led the writing with contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Schertler, A., Lenzner, B., Dullinger, S., Moser, D., Bufford, J., Ghelardini, L., Santini, A., Capinha, C., Monteiro, M., Reino, L., Wingfield, M. J., Seebens, H., Thines, M., Dawson, W., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P. … Essl, F. (2024). Biogeography and global flows of 100 major alien fungal and fungus-like oomycete pathogens. *Journal of Biogeography*, *51*, 599–617. https://doi.org/10.1111/jbi.14755