CZECH MYCOLOGY 78(1): 69–108, MAY 22, 2026 (ONLINE VERSION, ISSN 1805-1421)

Alien fungi and oomycetes in the Czech Republic

ZUZANA HAŇÁČKOVÁ[1]*, MARKÉTA HRABĚTOVÁ[1], LUCIE ZÍBAROVÁ[2], IVANA ŠAFRÁNKOVÁ[3], MICHAELA SEDLÁŘOVÁ[4], EVA BERGOVÁ[5], VERONIKA DUMALASOVÁ[6], ALENA HANZALOVÁ[6], FRANTIŠEK LORENC[7], JANA PALICOVÁ[6], DAVID NOVOTNÝ[6], IVETA SVOBODOVÁ[5], MARKÉTA ŠANDOVÁ[8], DANIEL ZAHRADNÍK[1], KAREL ČERNÝ[1]*

[1] Landscape Research Institute, p.r.i., Květnové nám. 391, CZ-252 43 Průhonice, Czech Republic
[2] Resslova 26, CZ-400 01 Ústí nad Labem, Czech Republic
[3] Department of Crop Science, Breeding and Plant Medicine, Faculty of AgriSciences, Mendel University in Brno, Zemědělská 1665/1, CZ-613 00 Brno, Czech Republic
[4] Department of Botany, Faculty of Science, Palacký University Olomouc, Šlechtitelů 27, CZ-779 00 Olomouc-Holice, Czech Republic
[5] Central Institute for Supervising and Testing in Agriculture, Šlechtitelů 23/773, CZ-779 00 Olomouc 9, Czech Republic
[6] Czech Agrifood Research Center, Drnovská 507/73, CZ-161 00 Praha 6, Czech Republic
[7] Forestry and Game Management Research Institute, p.r.i., Strnady 136, CZ-252 02 Jíloviště, Czech Republic
[8] Mycological Department, National Museum, Cirkusová 1740, CZ-193 00 Praha 9, Czech Republic
*corresponding authors: karel.cerny@vuk.gov.cz, zuzana.hanackova@vsuo.cz

Haňáčková Z., Hrabětová M., Zíbarová L., Šafránková I., Sedlářová M., Bergová E., Dumalasová V., Hanzalová A., Lorenc F., Palicová J., Novotný D., Svobodová I., Šandová M., Zahradník D., Černý K. (2026): Alien fungi and oomycetes in the Czech Republic. – Czech Mycol. 78(1): 69–108.

Although transfers and invasions of alien fungi and oomycetes to new environments have ecological and economic impacts comparable to those of plants and animals, their importance has so far been underestimated. Here, we compile accessible records of alien species from these two groups. Extensive research of data across literature, on-line databases, herbaria, and institutional and personal collections has resulted in the first list of alien and cryptogenic fungi and oomycetes for the present-day area of the Czech Republic.

A total number of 352 alien taxa recorded in the period 1813–2022 includes 38 archaeomycetes (i.e. species introduced into Europe before 1492), 310 neomycetes, and 4 unranked species. The highest proportion of alien fungi and oomycetes originated from North America, Europe, and temperate Asia. From the taxonomic point of view, ascomycetes represent the highest proportion of alien species, while at the class level, *Peronosporomycetes*, *Dothideomycetes*, *Leotiomycetes*, *Pucciniomycetes*, *Sordariomycetes*, and *Agaricomycetes* are the most frequent. Plant parasites prevail, whereas saprotrophic fungi are less numerous and other ecological groups are rare: six mycorrhizal fungi and two wild animal parasite species have been recorded in the Czech Republic. An assessment of potential risk indicated that numerous species impact (in order of frequency) horticulture, agriculture, and forestry. We identified 56 casually introduced species, 156 naturalised taxa, and 72 invasive species. Significant ecosystem damage may be expected for 36 introduced species, six of which can be classified as transformers. Five species were classified as eradicated.

The terminology used in invasive plant and animal biology was adopted, with minor modifications to reflect the specificity of fungi and oomycetes. Natural and geopolitical conditions are discussed and taken into account in the proposed general scheme of invasions of fungi and oomycetes

representing an integral part of neobiota and sharing invasion principles and rules with alien macroorganisms.

Key words: biological invasions, framework of fungal invasions, neofunga, neomycetes, plant parasites, soil ecology, trading.

Article history: received 22 October 2025, revised 16 March 2026, accepted 20 March 2026, published online 22 May 2026 (including Electronic Supplement).

DOI: https://doi.org/10.33585/cmy.78106

Haňáčková Z., Hrabětová M., Zíbarová L., Šafránková I., Sedlářová M., Bergová E., Dumalasová V., Hanzalová A., Lorenc F., Palicová J., Novotný D., Svobodová I., Šandová M., Zahradník D., Černý K. (2026): Nepůvodní houby a oomycety České republiky. – Czech Mycol. 78(1): 69–108.

Přestože mají přenosy a invaze nepůvodních hub a oomycet do nových prostředí srovnatelné ekonomické a ekologické dopady s těmi u rostlin nebo živočichů, jejich význam byl dosud podceňován. Tato studie přináší souhrn dostupných záznamů o druzích z těchto skupin organismů. Rozsáhlý výzkum údajů z odborné literatury, online databází, herbářů a institucionálních i osobních sbírek vedl k sestavení prvního seznamu nepůvodních a kryptogenních hub a oomycet pro území dnešní České republiky.

Celkem bylo za období 1813–2022 zaznamenáno 352 nepůvodních taxonů, z toho 38 archeomycet (tj. druhů zavlečených do Evropy před rokem 1492), 310 neomycet a 4 druhy bez zařazení. Největší podíl těchto druhů pochází ze Severní Ameriky, Evropy a temperátní Asie. Z taxonomického hlediska představují největší část nepůvodních druhů askomycety, zatímco na úrovni tříd jsou nejčastější *Peronosporomycetes*, *Dothideomycetes*, *Leotiomycetes*, *Pucciniomycetes*, *Sordariomycetes* a *Agaricomycetes*. Převládají parazitické houby napadající rostliny, zatímco saprotrofní houby jsou méně početné a ostatní ekologické skupiny jsou vzácné – v České republice bylo zaznamenáno šest druhů mykorhizních hub a dva druhy parazitující na volně žijících živočiších. Hodnocení potenciálního rizika ukázalo, že značný počet druhů ovlivňuje zahradnictví, zemědělství a lesnictví. Celkově bylo zaznamenáno 56 příležitostně zavlečených, 156 naturalizovaných a 72 invazních druhů. U 36 zavlečených druhů lze očekávat významné poškození ekosystémů; šest druhů lze považovat za transformery. Pět druhů bylo klasifikováno jako eradikované.

Terminologie používaná v biologii invazí rostlin a živočichů byla převzata pouze s drobnými úpravami, které zohledňují specifika hub a oomycet. Přírodní a geopolitické podmínky jsou diskutovány s ohledem na navržené obecné schéma invazí hub a oomycet, které představují nedílnou součást neobioty a sdílejí principy a pravidla invazí s nepůvodními makroorganismy.

INTRODUCTION

The centuries-old and ever-accelerating process of introduction and spread of non-native organisms is an important part of global environmental change. Biological invasions often lead to significant economic losses, disruption of biodiversity, and ecosystem stability, and also pose a threat to human health (Wittenberg & Cock 2001, Seebens et al. 2017, Pyšek et al. 2020). Research in ecology and invasion biology has primarily focused on plants and animals (Pyšek

et al. 2020), while microorganisms remain poorly explored. These organisms include two groups of fungi *sensu lato*, i.e. true fungi (Fungi) and oomycetes (Stramenopiles). For the purpose of this study, we will refer to this ecological group as fungi (see also Schertler et al. 2024 for similar usage). Although these groups are phylogenetically distinct, their convergent evolution has led to the development of similar morphology and enzymatic pathways, enabling them to share the same ecological roles as parasites (biotrophs, necrotrophs, or hemibiotrophs) and also saprotrophs. Nevertheless, true fungi exhibit a substantially greater ecological amplitude than oomycetes, encompassing broader physiological requirements and environmental tolerances, whereas oomycetes are constrained to a narrower ecological range, being strongly dependent on moist and aquatic environments (Laevens et al. 2024, Rodenburg et al. 2024, Masigol et al. 2025). These two groups of organisms have remained marginal due to many reasons, e.g. their cryptic lifestyle, small size, constantly evolving taxonomy, biogeographical uncertainties, etc. (Desprez-Loustau et al. 2007, Gladieux et al. 2015). Another reason why fungi have been neglected may have been the widely accepted but erroneous assumption of their cosmopolitan species distribution, which has been rejected only recently (for more details, see Gladieux et al. 2015). The assumed absence of endemism in fungi probably reflected a rather incorrect assessment of complexes of allopatric and phylogenetically different taxa hidden within one morphological species. Molecular approaches have revealed that these organisms possess distinct biogeographic ranges (Taylor et al. 2006, Gross et al. 2021). Many alien species were introduced before they were scientifically described or their possible significance was revealed (Palm 2001, Rizzo 2005). Subsequent identification (only after establishment in the new area) therefore causes uncertainty about the alien species origin.

A clear proof of the underestimation of the importance of fungi among invasive organisms is the fact that only three species of true fungi and two species of oomycetes are listed among the world's 100 worst invasive alien species (Lowe et al. 2000, Luque et al. 2014, IUCN on-line) and only six species are on a similar European list (Nentwig et al. 2018). The most recent example is the list of invasive alien species of EU concern (European Union 2022), from which, despite three updates, microorganisms are still missing (cf. Paap et al. 2020). Despite this fact, fungi have come to the forefront of interest in recent years due to significant progress in their study through molecular methods (Crous et al. 2021). Recently, the significance of these organisms in global change is no longer doubted (Gladieux et al. 2015) and the number of fungal invasions is expected to exceed that of plants and animals (Desprez-Loustau et al. 2007, Gladieux et al. 2015).

Ecological groups and impact of alien fungi. Life strategies of fungi and oomycetes range from parasitism to mutualism to saprotrophy. The

most important group among introduced fungi and oomycetes are parasites, which represent the majority (approx. 60–80%) of this part of the neobiota (Desprez-Loustau et al. 2010, Voglmayr et al. 2023). Here, we distinguish between parasites and pathogens: while the term *parasite* is commonly used in ecological contexts for organisms living at the expense of a host, *pathogen* refers more specifically to organisms which cause disease and is more frequently used in zoo- and phytopathology. Outbreaks of microscopic pathogens are challenging to recognise and could therefore harm ecosystems irreversibly. Past introductions with catastrophic consequences include many oomycete phytopathogens such as *Phytophthora infestans*, the cause of potato late blight, initiating the Great Irish Famine in the mid-19th century (Bourke 1964, Turner 2005), *P. cinnamomi*, responsible for dieback of eucalyptus trees in Australia and due to its wide host range posing a threat to local biodiversity and entire ecosystems in over 70 countries (Cahill et al. 2008), *P. agathidicida*, responsible for the dieback of kauri in New Zealand (Bradshaw et al. 2020), *P. ramorum*, responsible for the sudden oak dieback on the West Coast of the USA (Hansen et al. 2008). In addition, outbreak of European ascomycete *Pseudogymnoascus destructans* threatens the North American population of bats with white-nose syndrome (Frick et al. 2016, Drees et al. 2017). Examples of significant invasions taking place in Europe include *Ophiostoma novo-ulmi*, *Hymenoscyphus fraxineus*, and *Phytophthora ×alni*, responsible for large-scale damage to populations of their tree hosts and therefore forest stands (Brasier et al. 2004, Brasier & Kirk 2010, Gross et al. 2014), *Batrachochytrium dendrobatidis* and *B. salamandrivorans* (e.g. Fisher et al. 2009, Martel et al. 2013), posing a serious risk to amphibian biodiversity, and *Aphanomyces astaci*, causing crayfish plague (Holdich et al. 2009).

In general, the most intensively studied invasive species have been parasites due to their deleterious effects on diseased hosts. Parasites are generally the best studied group of introduced fungi due to their often visible impact on economically important hosts (Desprez-Loustau et al. 2007, Thakur et al. 2019). There is much less information about other groups of introduced fungi – mutualists, saprotrophs, and endophytes, whose proportion in neomycobiota might be underestimated (Desprez-Loustau 2009). The trade of plant material is an important route through which non-native plant pathogens are introduced (Brasier 2008), so it can be expected that also other plant-associated species, endophytic and mycorrhizal fungi, are transferred and thus their actual share in neomycobiota might be significantly higher (Pietras 2024). As their introduction does not usually impact the economy nor the natural environment, their presence in new areas is documented insufficiently. Therefore, the introductions of conspicuous saprotrophic and mycorrhizal species (*Aureoboletus projectellus*, *Clathrus archeri*, *Favolaschia calocera*), mycorrhizal poisonous species *(Amanita muscaria*, *A. phalloides*), and edible mushrooms (*Agaricus bisporus*, *Lentinula edodes*,

Pleurotus citrinopileatus) are recorded, but their influence on local ecosystems is generally poorly studied (Voglmayr & Krisai-Greilhuber 2002, Desprez-Loustau et al. 2007, Dickie et al. 2016, Pietras 2024), although negative impact has been documented (Veerabahu et al. 2025). Some groups of fungal organisms are practically not represented among the invasive ones at all – e.g. lichenised representatives of *Lecanorales* or microscopic insect parasites of the *Laboulbeniales* order, very likely due to insufficient research (Desprez-Loustau et al. 2010, but see Tragust et al. 2015).

Introduction pathways. Fungi are usually introduced inadvertently to new localities as unwanted contaminants of soil and substrates, plants (including seeds) and animals, wood biomass, packaging material, etc. (Brasier & Buck 2001, Wingfield et al. 2001, Ocasio-Morales et al. 2007, Brasier 2008, Sikes et al. 2018). For many saprotrophs, organic materials, e.g. wood chips, appear to be the main routes of introduction (Desprez-Loustau 2009). Also people represent relevant vectors; some introductions may be caused by tourism, agricultural and horticultural activities, and even by intentional introduction into the wild (Viljanen-Rollinson & Cromey 2002, Veerabahu et al. 2025). Finally, wind-borne spore transfer across continents cannot be ruled out in some cases (Brown & Hovmøller 2002). At present, the main cause of the spread of alien fungi is trade in plant material, which significantly increases the risk of introduction. This is largely because a considerable proportion of imported material is represented by living, containerised ornamental plants (with substrates acting as a significant source of neobiota; see above) and because regulatory measures aimed at limiting the introduction of harmful agents are failing (Brasier 2008). The number of recorded alien fungi (esp. tree pathogens) has increased exponentially in Europe over the last 200 years, which relates to globalisation (Desprez-Loustau 2009, Santini et al. 2013). The frequency of invasions depends on several geographical, climatic, and socio-economic factors, including population size, economic activity, and trade volume, as well as geographical location, precipitation, temperature, presence of susceptible hosts or their phylogenetically related species, and others (Desprez-Loustau 2009, Desprez-Loustau et al. 2010).

European national lists of alien fungi. National lists of alien fungi and oomycetes have already been published in a number of European countries – e.g. Germany (Kreisel & Scholler 1994, Karasch et al. 2021), the United Kingdom (Hill et al. 2005, Roy et al. 2012), France (Desprez-Loustau et al. 2010), Poland (Mułenko et al. 2010), Norway (Gederaas et al. 2012, Sandvik et al. 2019, 2020), Switzerland (Beenken & Senn-Irlet 2016), Lithuania (Motiejūnaitė et al. 2017), and Austria (Voglmayr et al. 2023). These include from about 80 on the Norwegian to 375 species on the Austrian list (Sandvik et al. 2020, Voglmayr et al. 2023). The European list of alien fungi dates back to 2009 (Desprez-Loustau et al. 2009)

and includes a total of 688 species considered non-native in at least some European countries. Recently, 3 fungi and 3 oomycetes are ranked among the worst alien organisms in Europe (Nentwig et al. 2018).

Conceptual model of fungal invasion. In order to adequately classify individual species according to their stage of invasion, we had to adapt the general conceptual model of species introductions developed by botanists and zoologists (Blackburn et al. 2011) to fungi and oomycetes. However, its application has proven challenging for several important reasons.

The first and most important problem that invasion mycology has to deal with is the lack of standardised terminology. The obvious reason is the persistent dichotomy in the study of invasions, which has historically been studied in various scientific disciplines, whose representatives have communicated with each other only to a limited extent. Until recently, many mycologists, especially plant pathologists, remained isolated from the mainstream of ecology and, reciprocally, scant attention was paid to fungi by ecologists (Desprez-Loustau et al. 2007). In the case of fungal invasions, where parasites account for the majority of this neobiota in Europe (about 80%; Desprez-Loustau et al. 2010), research was logically conducted primarily in applied agricultural sciences and forest pathology was characterised by a mechanistic approach inherited from the broader discipline of phytopathology (Paap et al. 2020). Studies dealing with alien pathogens of woody plants (or invasive forest pathogens) were often carried out without any links to biological invasions and sometimes did not reflect invasion sciences at all.

For example, the term *invasive species* is often used in a broad, non-specific sense and not to describe the exact stage of invasion (Santini et al. 2013) or is replaced by the superior term *established* (= *naturalised*) species (e.g. Desprez-Loustau et al. 2010, Motiejūnaitė et al. 2017, Voglmayr et al. 2023, and many others). Sometimes similar expressions are used which could easily be substituted by already established terms. For example, 'ephemerous' and 'spreading' instead of *casual*, 'established' instead of *naturalised*, and the hybrid term 'established invasive species' are used (Beenken & Senn-Irlet 2016).

When the term *invasive species* is used in mycology or forest pathology, it is usually defined with the attributes naturally used in invasion biology as non-nativeness and introduction. In addition, it often includes the attribute of impact (environmental, economic, or human harm), caused or potentially caused by a species (e.g. Santini et al. 2013, Beenken & Senn-Irlet 2016, Iannone et al. 2020, Voglmayr et al. 2023, etc.). Even the IUCN uses a similar definition (IUCN online). However, invasion science does not consider 'impact' to be part of the definition (Richardson et al. 2000, Colautti & MacIsaac 2004, Ricciardi & Cohen 2007, Blackburn et al. 2011, Soto et al. 2024). While a certain proportion of invasive species can indeed cause environmental or other damage, this depends on taxonomic

group and habitat (Jeschke & Pyšek 2018). In some cases, the habitat or substrate of an introduced species is neither specified – whether anthropogenic/non-native or natural/native. As a result, lists of invasive species sometimes include taxa which cannot be invasive in nature, as they occur on introduced hosts only, e.g. *Kabatina thujae* and *Phloeospora robiniae* (Santini et al. 2013).

Recently, there have been calls for closer interdisciplinary collaboration and possibilities for harmonisation are being explored (Wingfield et al. 2017, Paap et al. 2020). Invasive science terminology has even partially been adopted (e.g. Voglmayr et al. 2023), but significant differences remain. A conceptual framework for forest tree pathogens was developed by Paap et al. (2022) who used the concept by Blackburn et al. (2011). Unfortunately, this pertains exclusively to forest tree pathogens, which constitute just a small fraction of neofunga. A weakness of this framework is the problematic sequencing of certain steps in the invasion process and the imprecise use of the term 'invasive organism'. Therefore, in this work we aim to follow the approach used in invasion sciences as closely as possible and seek to develop it for the entire group of fungi and oomycetes, including saprotrophic and mycorrhizal fungi, as well as parasites of other plant hosts and even some animal species. On the other hand, it must be admitted that adoption of the conceptual model by Blackburn et al. (2011) has brought considerable difficulties, mainly due to the specific biology and level of knowledge concerning fungi and oomycetes. Some principles, barriers, and categories were easily transferable to mycology, others proved to be less important, while certain aspects proved to be more important and had to be incorporated into the scheme (Fig. 1). Selected points are discussed below.

Aims of the study. The study was conducted to prepare an annotated list of fungi and oomycetes considered to be alien and cryptogenic in the Czech Republic for the first time, based on a preliminary list (Haňáčková et al. 2023), which was substantially expanded, supplemented, and critically processed. Species were divided into archaeomycetes and neomycetes (introduced into Europe before/after 1492), similarly to Beenken & Senn-Irlet (2016) and in the same sense as non-native plants are classified in Europe (Richardson et al. 2000). Additional taxonomic, nomenclatural and ecological data were attached and analysed, including the most important substrates and hosts, disease and affected organs (in the case of parasites), area of main impact, and first known sources of occurrence in the Czech Republic. Finally, individual fungal and oomycete taxa were assigned to stages of invasion according to the proposed conceptual framework of the invasion process and analysed.

METHODS

Data collection. The list of fungi (Opisthokonta, Amorphea) and oomycetes (Stramenopiles, TSAR) alien in the Czech Republic was composed based on a thorough study of literary resources, collections in the Czech institutional and private herbaria (especially National Museum, Prague), online databases concerning fungi (MyCoPortal, https://www.mycoportal.org/portal/; JACQ, https://www.jacq.org/; GBIF, https://www.gbif.org/) and plant pathogens (CABI, https://www.cabidigitallibrary.org/; EPPO, https://www.eppo.int/; ÚKZÚZ, https://ukzuz.gov.cz/public/portal/ukzuz), databases of alien species (DAISIE, Roy et al. 2020; EASIN, https://easin.jrc.ec.europa.eu/; GISD, http://www.iucngisd.org/gisd/; USDA Fungal Databases, https://fungi.ars.usda.gov/), and extensive discussions by the authors. Data collection took place between 2020 and 2023. In our concept we omit some 'fungus-like' organisms such as slime moulds (Amoebozoa, Amorphea) and plasmodiophores (Rhizaria, TSAR), lichenised fungi, obligate human and domestic animal pathogens, species maintained solely in culture, and DNA sequences. To be included, an organism had to be classified as: (1) non-native (in the sense of Essl et al. 2018), spread outside its native range by human activity, whether intentionally or not; (2) cryptogenic species, i.e. considered non-native but without definite supporting evidence (Paap et al. 2020); or (3) species of uncertain biogeographic status (Essl et al. 2018), whose origin in the area of interest cannot be ruled out. The list contains organisms which have spread as a direct result of human action (i.e. transmission of the organism itself) or indirectly (i.e. creation of new biotopes or transformation of existing habitats). Conversely, species with natural occurrence in Central Europe, whose area is currently expanding but cannot be unequivocally attributed to human influence, were excluded.

Only a small number of cryptogenic taxa have been included in the list. These are taxa of particular importance in the Czech Republic whose original range is unknown and whose distribution is usually worldwide. In case their genetic diversity is higher in Europe, it is related to intensive cultivation of their hosts, such as with *Verticillium dahliae* (Atallah et al. 2010; Short et al. 2015). Its current distribution appears to be the result of dissemination from one or more centres in relatively recent times (Short et al. 2015). Originally, the species had a much more restricted range, which has greatly expanded as a result of human activity (Subbarao 2020). The presented list comprises both neomycetes (species introduced into Europe after 1492; Kreisel & Scholler 1994), as well as archaeomycetes (introduced before 1492) whose origin outside the Czech Republic cannot be disputed. The list includes only species whose occurrence within the current boundaries of the territory of the Czech Republic is clearly documented.

Evaluation of particular taxa. For each taxon (see Electronic Supplement), the list provides its currently accepted name (in accordance with Index Fungorum, https://indexfungorum.org/ or recent publications), its taxonomic position (class, order, family), date and citation of its first record in the Czech Republic, area of origin based on the World Geographic Scheme for Recording the Distribution of Plants (Brummitt 2001; where for taxa spread in several areas the closer one was always used for evaluation; e.g. Europe for species with a Mediterranean distribution), and invasive status in the Czech territory, with categories based on the concept of invasion ecology (e.g. Richardson et al. 2000, Blackburn et al. 2011).

The main principles have been retained but the adopted category definitions (Tab. 1, Fig. 1) are in accordance with the biology of fungi and oomycetes (especially parasites), replacing ambiguous or misleading categories previously used in phytopathology and mycology.

Tab. 1. Terminology used in classification of alien fungal and fungus-like taxa (according to Richardson et al. 2000, Blackburn et al. 2011, Pyšek & Richardson 2012, Essl et al. 2018).

Category	Definition
Alien	Alien taxa in a given area whose presence there is (or is assumed to be) due to intentional or accidental introduction as a result of human activity.
Casual	Alien taxa which may temporarily flourish and even reproduce occasionally in an area, characteristically in human-made habitats, but which do not form long-term surviving self-replacing populations.
Cryptogenic	Taxa of unknown biogeographic origin which cannot be categorised as native or alien, but indirect evidence indicates alien origin.
Invasive	Naturalised taxa with reproductive particles often produced in very large numbers and having the potential to spread over a considerable area. Characteristically spread to natural or semi-natural habitats and to native hosts. Organisms which have occupied all suitable habitats should still be considered invasive, since the possibility of their re-invasion cannot be excluded.
Naturalised	Alien taxa which reproduce consistently and sustain populations over many life cycles without direct intervention by humans. They do not necessarily invade natural or semi-natural ecosystems. They can spread expansively in anthropogenic habitats and in introduced ornamental, forest tree or crop host species.
Transformer	A subset of invasive species which change the character, condition, form, or nature of native ecosystems over a substantial area relative to the extent of that ecosystem.

Furthermore, the list includes life strategies of species, area of main potential importance in the Czech Republic (in the case of parasites), substrate, and, in the case of parasites, main or typical hosts, and hosts known in the Czech Republic, infected organ, and disease caused. Finally, the source of information on the first identification of the species in the territory of present-day Czech Republic is given. In the case of collections, herbaria and databases, the number of a specific item or preserved isolate or a link is given, and as the last, a list of selected synonyms is presented. Unfortunately, some information can only be provided with some degree of uncertainty, which is highlighted in the overview with a question mark. Most species were evaluated based on the opinion of two experts.

The statistical significance of differences in the intensity of new alien fungus and oomycete occurrence was evaluated using chi-square goodness-of-fit tests. Holm's correction was applied for multiple comparisons of more than two time periods. The results are presented in the form of homogeneous groups at a significance level of 0.05. All statistical analyses were performed using R statistical software, version 4.4.3 (R Core Team 2021).

FUNGI IN A GENERALISED INVASION SCHEME

The invasion process model (Blackburn et al. 2011), applied on plants and animals in invasion ecology, was modified to create a generalised scheme of fungal/oomycete invasion (Fig. 1).

The diagram shows four stages of invasion: transport, introduction, population establishment, and spread, which are separated by main barriers which the invaders must overcome during the invasion process: geographical, quarantine, survival at the points of introduction, reproduction, dispersal, environment, and substrate (jump to a native host). Several well-known examples of alien fungi and oomycetes are presented to illustrate their classification within the proposed scheme based on their current state of invasion in the Czech Republic.

In the first invasion stage – stage of transport – the alien fungal species is moved beyond the limits of its original distribution range by human action (Blackburn et al. 2011). For plant parasites in general, the most common way is unintentional introduction together with a living host –

via asymptomatic plant material and less frequently through seeds, wood biomass, substrates, and other plant-associated materials (Bérubé & Nicolas 2015, Vettraino et al. 2015, Franić et al. 2019). In this stage, a species spreading spontaneously in Europe but not detected in the Czech Republic yet can be identified. Particularly, species such as *Geosmithia morbida* causing thousand cankers disease of walnut, *Gibberella circinata* (pitch canker), *Neonectria neomacrospora* (fir canker), and *Phytophthora kernoviae* (beech bleeding canker) should be mentioned. There is no doubt that some of them (for instance *N. neomacrospora*) will be detected in the Czech Republic in the near future.

After overcoming the **geographical barrier**, the introduction stage follows. The main barrier preventing successful completion of the introduction phase, especially of some economically important and dangerous taxa, is the **quarantine barrier**. It consists of a series of external and internal quarantine and phytosanitary measures (European Union 2016). Quarantine measures are legally established (in the Czech Republic by e.g. Act No. 326/2004 Coll. on Phytosanitary Care and Decree No. 215/2008 Coll. on Measures against the Introduction and Spread of Harmful Organisms of Plants and Plant Products, based on the EU phytosanitary regulation – Council Directive 2000/29/EC). Strict measures are applied against quarantine pests, and risk analyses are prepared for non-quarantine alien pests to guide further interventions. Very likely, the measures have been effective, and thus for instance *Phytophthora ramorum* (rhododendron dieback, sudden oak death, sudden larch death) and *Cryphonectria parasitica* (chestnut blight) can be considered eradicated in the Czech Republic (https://www.eppo.int/). However, the question is to what extent this barrier is effective and to what extent the measures are applied against organisms outside the visible tip of the iceberg. There is usually considerable scepticism among experts in this regard (e.g. Brasier 2008) and a large proportion of unintentionally introduced species – not only fungi – easily overcome this barrier (Blackburn et al. 2011).

The quarantine barrier has been overcome by species such as *Seiridium cardinale* (cypress canker). This species was introduced into a private garden with *Cupressocyparis leylandii* in Central Bohemia around the year 2000 and probably persisted several years at the locality (where it was detected in 2003, Landscape Research Institute herbarium – Mrázková PS 2619). However, spread of the parasite at the locality or its surroundings was later not confirmed. Given the limited occurrence of suitable hosts in the country, the parasite apparently failed to overcome the dispersal barrier and should now be considered locally extinct or eradicated. Another example is *Phytophthora nemorosa*, a polyphagous parasite causing root rot of deciduous trees and shrubs. The species was identified in 2022 on *Buxus sempervirens* plants imported from the Netherlands and sold in a network of garden centres (Hrabětová, pers. comm.). Although no other occurrences have been detected so far, its broad host range suggests that it may successfully overcome the reproduction and dispersal barriers and will eventually become naturalised in the country.

In our model, the quarantine barrier precedes or corresponds to the captivity and cultivation barrier described by Blackburn et al. (2011), although the captivity or cultivation barrier per se can in fungi directly concern only limited numbers of cultivated species, most others are not affected or at most indirectly, therefore we have not included it as essential in the scheme (Fig. 1).

In the third phase of the invasion – stage of establishment of the population – the invading organism must overcome additional barriers at the point of escape into the environment. The first **survival barrier** and second **reproduction barrier** are both generally less important for fungi (especially parasites) than for plants (their hosts), because the main environment of the parasite is its host, to which it is already adapted. In addition, the parasite is most often introduced with its host to places that are suitable for the host (and therefore usually also for the parasite) or are deliberately modified to make them suit for e.g. various horticulture or nursery premises. Abiotic factors which can have a significant impact on the survival of the invading organism strictly bound to the host (i.e. parasite, mycorrhizal fungus, endophyte) are most often humidity and temperature, along with other factors such as soil type (Marçais et al. 2004, Ireland et al. 2013, Burgess et al. 2017). The reproduction barrier is also relatively unimportant for many fungi and particularly plant parasites, because most species of interest are characterised by massive production of some kind of

propagules, at least simple asexual spores, which are usually very easily dispersed (cf. Fontaine et al. 2013, Hietala et al. 2018). However, the barrier can be critical in sexually reproducing fungi if only one mating type is introduced and only primary mycelium is formed, or in heteroecious rusts, where the other host may not be present. It may be important in species with a low reproductive rate (e.g. those forming fruitbodies and basidiospores only several years after somatogamy or forming closed sporocarps; Schwartz et al. 2006, Dickie et al. 2016). If a species overcomes the reproduction barrier and is able to reproduce in the new environment, it becomes naturalised and potentially passes on to the last stage of invasion – spread.

At the beginning of the fourth stage of invasion – stage of spread – the **dispersal barrier** stands in the way of the invading parasite. As mentioned, overcoming this barrier is relatively easy for a vast majority of introduced fungi as they typically produce enormous numbers of microscopic propagules which spread easily over long distances by water, air, or vectors (Ristaino & Gumpertz 2000, Grosdidier et al. 2018). In many species, humans act as an obvious vector, either by planting infected hosts or by transporting infested materials such as timber, wood chips, or horticultural substrates (Vannini et al. 2012, Szczepkowski et al. 2014). The dispersal barrier can theoretically be more important in, for example, species with a monocyclic disease cycle and in species whose propagule production depends on specific environmental conditions (e.g. humidity), on a certain phenological phase of the host, etc.

The reproduction and dispersal barriers have been overcome by the extremely dangerous polyphagous *Phytophthora cinnamomi* (phytophthora root and collar rot), as stable and long-term persisting outdoor occurrences are known from ornamental greenery and nurseries. Moreover, new outbreaks of the pathogen continue to be detected across the Czech Republic (Černý et al. 2020, Bačová et al. 2024). Thus, its population should be considered established, and the organism naturalised. However, *P. cinnamomi*, being a thermophilic organism, still faces strong environmental barriers, particularly low winter temperatures, which prevent its significant spread. Its occurrence in the Czech Republic is not yet known from the natural environment, and thus we cannot yet talk about overcoming the environmental barrier and about invasion. From other ecological groups, we may include here the recently recorded wood-debris inhabiting saprotroph *Queletia mirabilis* (Kříž & Zíta 2016).

The spread to areas distant from places of introduction requires overcoming the **environmental barrier**. This barrier refers to the abiotic environmental conditions in the vicinity of introduction and naturalisation sites, which are usually, although not necessarily, more or less human-altered habitats. In general, the most critical environmental factors for fungi are again humidity and temperature. A naturalised species which has probably not yet overcome this barrier in the Czech Republic is the above-mentioned thermophilic soil species *Phytophthora cinnamomi*. Only (probably often hidden) micropopulations of this species are maintained in nurseries and ornamental plantings (CCPO) here. Abiotic environmental conditions, on the other hand, probably rarely pose a major barrier for invading fungi from the temperate zone (primarily North America and temperate Asia), which is the main source of neofunga in the case of the Czech Republic. In addition, parasites are natrually strongly bound to the environment of their hosts, thus if the environmental conditions suit the host, they will usually suit its microbial crew as well.

The environmental (abiotic) barrier has been overcome by many alien fungi and oomycetes. For instance, successful naturalisation and massive distribution is known in *Apiognomonia veneta* (sycamore anthracnose; Gregorová et al. 2010), *Seifertia azaleae* (rhododendron bud rot; Landscape Research Institute herbarium – Mrázková PS 4800), and *Nothophaeocryptopus gaeumannii* (Swiss needle cast of Douglas fir; Samek et al. 2019). These parasites are commonly found in anthropogenic environments on non-native hosts in ornamental and in the last case also in forest plantations. On the other hand, they are not known to affect the native hosts – or rather, this ability has not yet been documented – and therefore cannot be considered invasive *sensu stricto*, although they meet the basic characteristics of this category (production of large quantities of reproductive particles, long-

distance dispersal, persistent and frequent occurrence). Thus, they can be seen as naturalised species. A comparable case is *Phytophthora pini*, a recently introduced parasite detected in ornamental plantings (Mrázková et al. 2025), which should also be classified as naturalised, albeit with a higher alert level due to its ability to infect native tree species (Jung et al. 2016) and its greater potential to spread into Czech natural ecosystems. This category may further include certain saprotrophic fungi such as *Bartheletia paradoxa* (saprotroph on dead *Ginkgo biloba* leaves), *Serpula lacrymans*, decaying deadwood in buildings, and mycorrhizal *Rhizopogon* species identified on *Pseudotsuga* after 2000.

A crucial condition for the successful invasion of parasites (but also mycorrhizal fungi, host-specific endophytes, saprotrophs, etc.) is the presence of a suitable substrate or sufficiently large, spatially and functionally accessible and long-term stable host population. In the absence of this condition, extinction awaits the invading organism. However, plant parasites are, as mentioned above, predominantly introduced with their host – usually also non-native and widely distributed ones. Thus, the whole pathosystem is introduced into a new environment and successful naturalisation of parasites is probably rather the rule than the exception. This naturalisation typically takes place in anthropogenic habitats (agroecosystems, nurseries, ornamental greenery, etc.). Further spread depends on the presence of other accessible hosts in the vicinity of naturalisation sites. The environmental continuum changing from the point of introduction due to spatial autocorrelation, e.g. from anthropogenic to natural (see Blackburn et al. 2011), which forms the background against which plant and many animal invasions take place, can be used in microbial invasions rather scarcely. This applies only to ecologically less specialised or polyphagous species (such as *P. cinnamomi*; Farr & Rossman 2022). From the parasite's perspective, the surrounding environment is usually highly discontinuous and the possibility of spreading is critically determined by the presence of suitable hosts. Thus, the idea that a spreading invasive population undergoes a series of successive establishment events, and this in an increasingly large range of environmental conditions (Blackburn et al. 2011), does generally not apply to parasites. In their case, the presence of a suitable host serves as an unequivocal classifier of environmental suitability, determining the introduction and survival of the invading organism in the new area. The discontinuity of the environment from the perspective of substrate-specific parasites of plants and animals, endophytes, saprotrophs, and mycorrhizal fungi goes so far that it directly determines the position in the invasion scheme which could be accessed and often strictly defines the type of environment that can be settled – agroecosystems, horticultural premises, urban ornamental greenery, non-native forest stands, etc. As an example we can mention the occasionally introduced species *Platanus* ×*hispanica* (Pyšek et al. 2022) and *Rhododendron* spp., which are only grown in ornamental plantings in the country, with their massively spreading alien and host-specific parasites *Apiognomonia veneta* and *Seifertia azaleae*, resepectively. Both parasites lack the possibility to occur anywhere else than in the anthropogenic environment. Therefore, the distribution, origin, and potentially invasion status of plant parasite hosts must be reflected in some way when describing the invasion status of their parasites.

For the reasons mentioned above, the **native host or substrate barrier** must be incorporated into the invasion scheme. This barrier may correspond to the environmental barrier in undisturbed habitats to some extent (Richardson et al. 2000). Parasites of most cultivated crops and ornamental plants most often do not even enter the natural environment through this barrier (Haňáčková et al. 2023). However, organisms which overcome this last barrier (for instance *Aphanomyces astaci*, *Cryptostroma corticale*, *Eutypella parasitica*, *Hymenoscyphus fraxineus*, *Lecanosticta acicola*, *Ophiostoma novo-ulmi*, *Phytophthora* ×*alni*, *P.* ×*cambivora*, *Sphaeropsis sapinea*) can be considered invasive in the true sense and may pose a significant risk to natural ecosystems. Only species from this group can become so-called *transformers*.

In the case of mycorrhizal and saprotrophic fungi, the principle is identical to that in parasitic species: it always involves establishing a new and sometimes merely re-establishing a previously known substrate association. Given that mycorrhizal fungi influence the surrounding ecosystem,

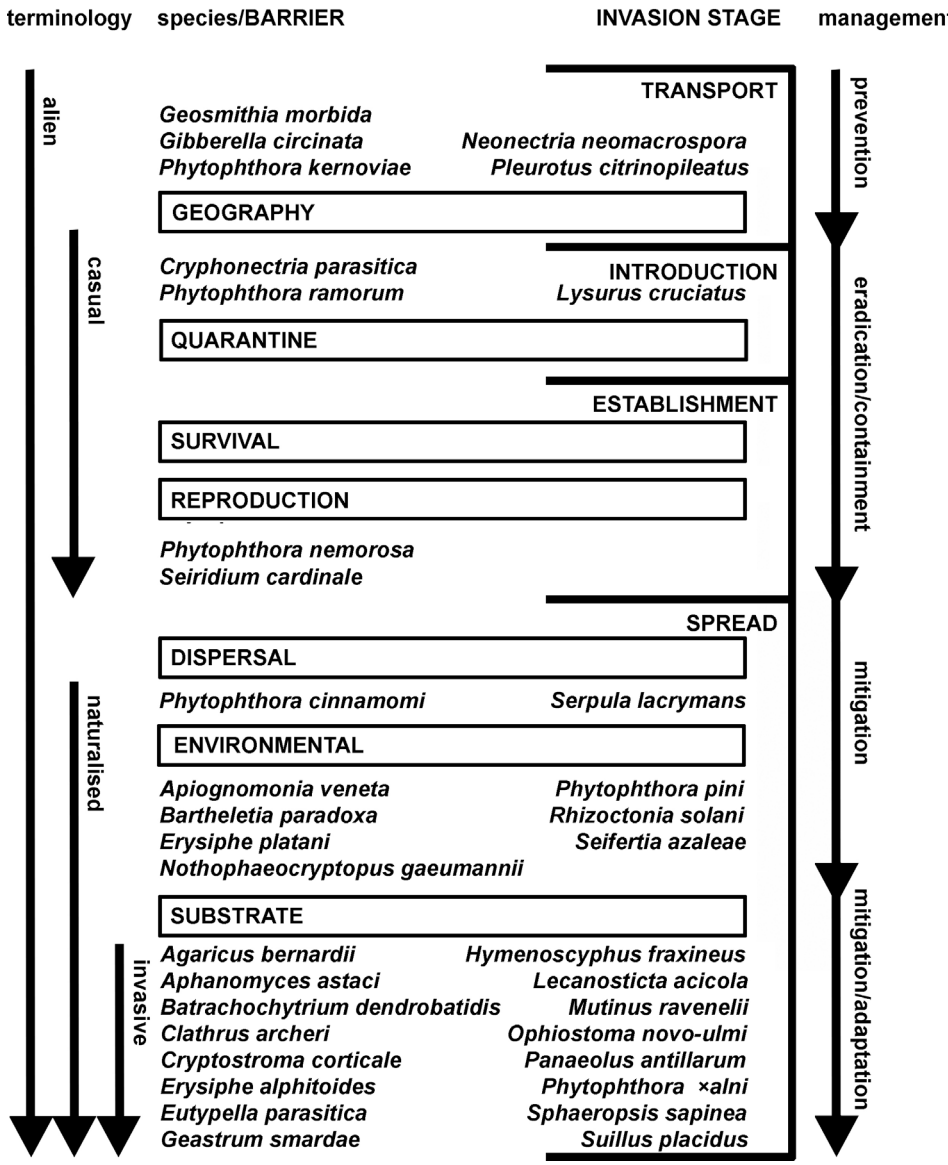

Fig. 1. Proposed generalised scheme of fungal invasion. Species examples are based on their current status in the Czech Republic.

species spreading extensively in the environment, even if exclusively in association with their original host, should likewise be identified as invasive, as in the case of *Suillus lakei* and *S. sibiricus*. Some non-native ectomycorrhizal fungi enhance the spread of non-native plants and therefore both partners are considered invasive, as shown by the famous example of *Pinaceae* from the Southern Hemisphere (Nuñez & Dickie 2014). However, in Central Europe, introduced trees such as *Pinus*

strobus and *Pseudotsuga menziesii* have here their European relatives at the genus or family level, so their ectomycorrhizal symbionts have a much greater ability to establish symbiosis with native trees (Vlk et al. 2020). Of saprotrophic fungi which spread uncontrollably in natural habitats we can mention for instance *Clathrus archeri* and *Mutinus ravenelii*.

The scheme of fungal invasion also includes types of prevailing management measures responding to particular invasion stages. Prevention can be applied only before and at the beginning of the process. Eradication and containment should be implemented as soon as new introduction occurs, while mitigation follows in the case of escape or overcoming the dispersal barrier. In the Czech Republic, a representative example is the set of methodological guidelines developed by Černý et al. (2020), aimed at reducing the occurrence and spread of non-native species of the genus *Phytophthora* in forest nurseries. In the case of widely distributed transformer pathogens, where the cultivation of susceptible native host species has already been at least partially reduced, mitigation measures may no longer be effective and should instead be replaced by adaptive management strategies. This should be applied, for example, to the invasions of *Phytophthora ×alni*, *Ophiostoma novo-ulmi*, and *Hymenoscyphus fraxineus*, where the cultivation of alders, elms, and ashes, respectively, has been locally restricted in order to prevent further damage and avoid additional unnecessary costs. Examples of adaptive management proposals include Černý et al. (2016) for ash dieback and Zýka et al. (2018) for *Gemmamyces* bud blight of spruce.

An important complementary output of predictive modelling is provided by statistical and expert-based models and their map visualisations assessing impacts of invasive pathogens at broader spatial scales (e.g. Zýka et al. 2018, Chumanová et al. 2021). The final adaptive strategy involves resistance breeding and the deployment of resistant genotypes. In the Czech Republic, the most advanced progress in this area has been achieved in the selection of resistant genotypes and subsequent breeding of *Alnus glutinosa* in relation to *Phytophthora ×alni*, a programme which was initiated more than ten years ago (Štochlová et al. 2016).

RESULTS

Diversity

At present, the list of alien species includes a total of 352 taxa of fungi and oomycetes (see Electronic Supplement). The largest groups are *Ascomycota* (173 species), followed by *Basidiomycota* (101), *Peronosporomycota* (76), and *Chytridiomycota* (2). In total, 13 classes are represented in the list (Fig. 2), the most numerous being *Peronosporomycetes* with 74 taxa (21.0%), *Dothideomycetes* with 69 species (19.6%), *Leotiomycetes* with 61 species (17.3%), *Pucciniomycetes* with 45 species (12.8%), *Sordariomycetes* with 41 species (11.6%), *Agaricomycetes* with 35 species (9.9%), and *Exobasidiomycetes* and *Ustilaginomycetes* both with 10 species (2.8%), while the numbers of taxa of other classes are limited to just a few species: *Bartheletiomycetes* (1 species), *Eurotiomycetes* (2), *Rhizophydiomycetes* (1), *Saprolegniomycetes* (2), and *Synchytriomycetes* (1).

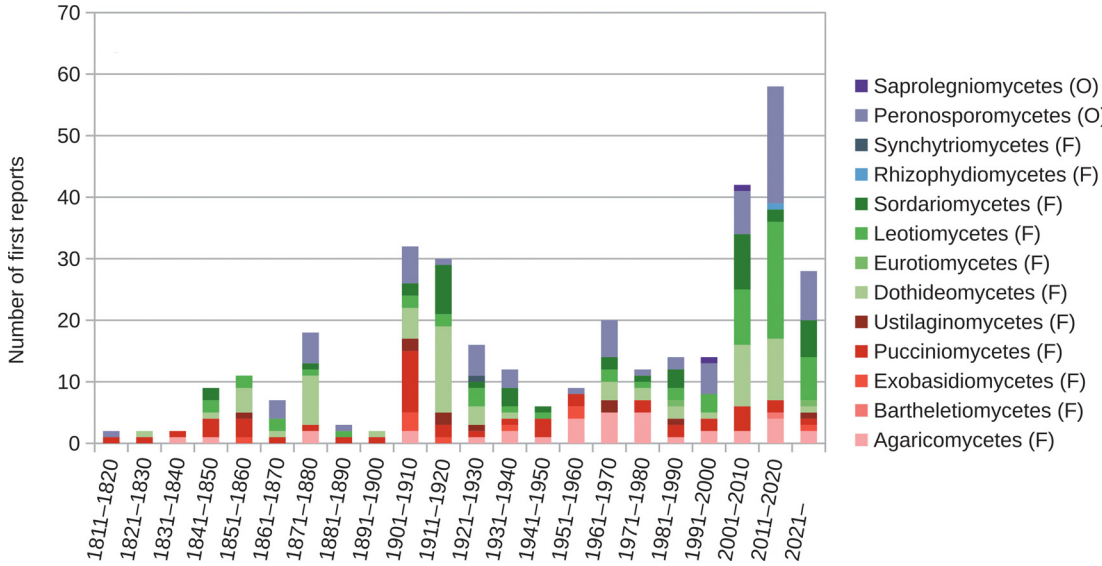

Fig. 2. Introduction of alien fungi and oomycetes at class level. F = true fungi, O = oomycetes.

History of introductions

Our inventory of alien fungal taxa documented between 1813 and 2022 encompasses 352 species, comprising 38 archaeomycetes (10.8%) and 310 neomycetes (88.1%). For four taxa it is not yet possible to decide whether they are archaeomycetes or neomycetes. Archaeomycetes and neomycetes exhibited different patterns, so due to the limited accuracy of introduction time, archaeomycetes should be dealt with separately.

Archaeomycetes are dominated by *Peronosporomycetes* (mainly *Peronosporales*) with 17 species (44.7%), while the second most numerous group is *Pucciniomycetes* with seven species (18.4%). Most archaeomycetes are of – usually southern and southeastern – European origin. Several taxa originate from Asia, North Africa, and the Middle East. Four species have an unknown original range. The majority of archaeomycetes are classified as plant parasites of aboveground plant organs with a main impact in agronomy and horticulture (see below). At the same time, they cause noticeable symptoms of damage and can be relatively easy to identify, thus their interceptions are usually older than those of neomycetes. Specifically, 28 taxa were recorded before 1938, whereas only seven species have been documented since 1989. The only ecological exception among the archaeomycetes is polyphagous species *Berkeleyomyces basicola*, which is not limited to aerial tissues but causes important root rot of crops and ornamentals.

Neomycetes are predominantly represented by members of the *Dothideomycetes* class, with *Leotiomycetes* and *Peronosporomycetes* also being highly abundant.

The exact year of first confirmed occurrence in the Czech Republic was determined for a total of 335 taxa, only the decade for another 14 taxa, and no information was available for 3 taxa. The oldest known information on the occurrence of an alien fungal organism in the Czech Republic to date comes from 1813 and relates to the collections of *Cronartium pini* by F.X. Ramisch from Prague, and of *Wilsoniana portulacae* by G. Menzel from Nové Město pod Smrkem (Liberec Region); both specimens are deposited in the State Museum of Natural History Karlsruhe (Germany). On the other hand, the latest data from 2022 add six taxa. This includes two oomycetes, *Phytophthora chlamydospora* and *P. nemorosa*, both isolated and identified by M. Hrabětová and M. Mrázková from the roots of *Buxus sempervirens* and deposited in the Czech Collection of Phytopathogenic Oomycetes (CCPO, Průhonice). Imported *Buxus* plants were sold in a shopping centre in Prague, thus these oomycetes can be classified as casually introduced. Three phytopathogenic ascomycetes were recorded: *Erysiphe pulchra* on *Cornus mas* in Plané loučky Nature Reserve near Olomouc (Sedlářová & Ondryáš 2023), *Phomopsis juniperivora* on *Juniperus sabina* cv. Tamariscifolia in Průhonice, and *Diaporthe japonica* on *Kerria japonica* in Prague-Uhříněves (both deposited by K. Černý and M. Hrabětová in the CCPO).

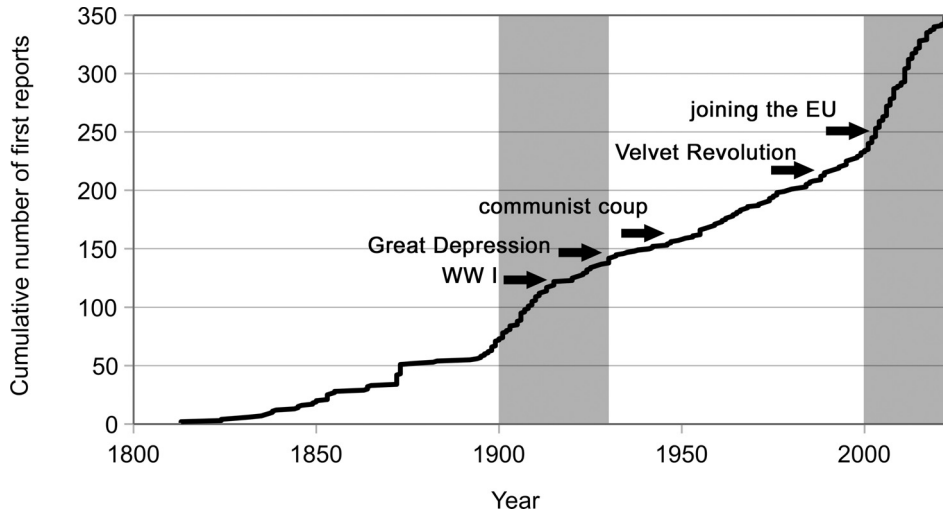

Fig. 3. Development of the cumulative number of first reports of introduced species in the Czech Republic. Main periods of introductions (grey fields) and significant socio-economic events (black arrows) highlighted.

The timeline of first records of alien fungi covers a period of more than 200 years (from 1813 to 2022; Fig. 3). The trend in the development of the numbers for first interceptions (n = 349) is characterised by considerable variability and presence of at least four different phases, but an overall gradually increasing inclination caused by a higher number of new records after 2000 is evident. The first phase, in which the curve has a gentle slope (average increase of species per year 0.81), extends into the 1890s, interrupted only by a short-term increase in the 1871–1880 decade. This is replaced by a second phase with a significantly steeper slope (avg. increase 2.30 species per year), lasting over 30 years, from the late 1890s to 1930. A third phase then follows, characterised by a long period with a slight increase in number of newly identified species (avg. increase 1.31 species per year) lasting until the end of the millennium. Finally, from 2001 onwards, it was replaced again by a curve with a very steep slope signalling a prolonged increase in the number of newly identified species (avg. increase 5.18 species per year). The existence of four different phases in the introduction curve has strong statistical support (Tab. 2).

Tab. 2. Average annual number of introduced species in different periods. Letters indicate homogeneous groups at $\alpha = 0.05$, tested with chi-square goodness-of-fit tests followed by Holm's correction for multiple comparisons.

Period	Average yearly increment
1811–1900	0.81^{a}
1901–1930	2.30^{b}
1931–2000	1.31^{ab}
2001–2022	5.18^{c}

Some taxonomic (and ecological) groups of fungi and oomycetes were more frequently introduced (or identified) in some periods than in other ones (Fig. 4). A detailed analysis shows that the peak numbers of introductions in almost all major classes fall into the first, second, or both waves of globalisation (see Figs 3, 4).

The three groups (*Ustilaginomycetes*, *Pucciniomycetes*, and *Exobasidiomycetes*) had the maximum number of interceptions at the turn of the 19th and 20th centuries. Other groups (such as *Sordariomycetes* and *Dothideomycetes*) have two local maxima – around the turn of the 19th and 20th centuries and after 2000. In contrast, *Agaricomycetes* were continuously identified during the 20th century. The other two classes (*Peronosporomycetes*, *Leotiomycetes*) have their maximum of introductions after 2000.

A significantly higher number of introductions during one or both waves of globalisation were statistically confirmed for *Dothideomycetes*, *Leotiomycetes*, *Peronosporomycetes*, and *Sordariomycetes* (Tab. 3). In some cases, these maxima

are clearly related to a higher representation of a particular group within a class, e.g. *Erysiphales* (*Leotiomycetes*) and *Pythiales* (*Peronosporomycetes*; data not shown). The only one exception to the general pattern of introductions are the *Agaricomycetes*, which were most frequently recorded during the period 1931–2022, although the difference compared to the second wave of globalisation is not conclusive.

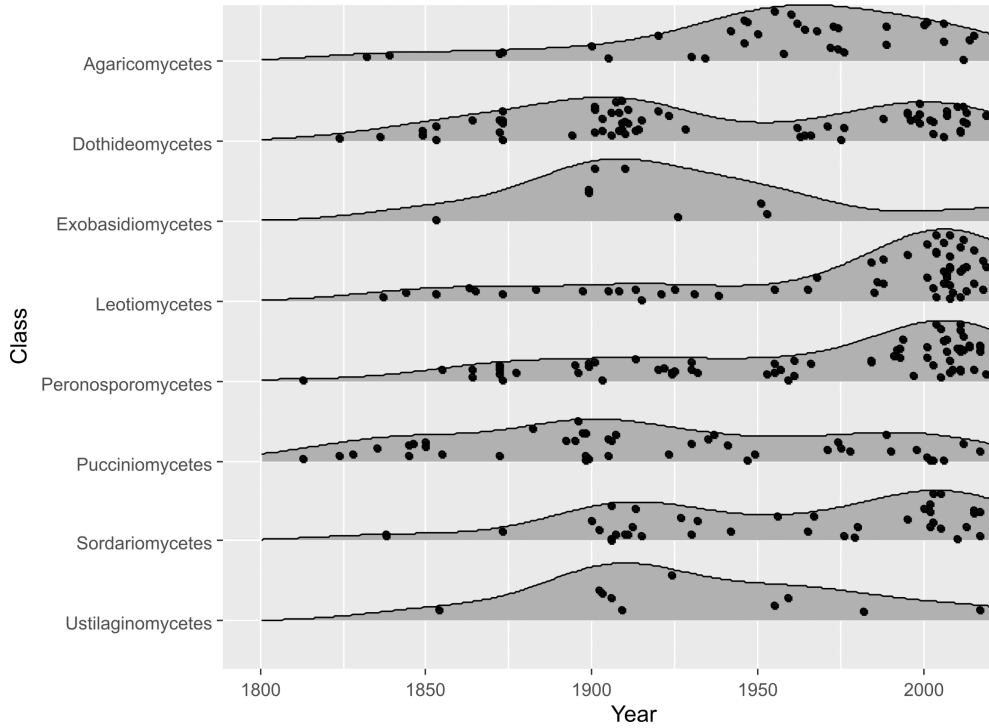

Fig. 4. Introduction of the most abundant groups of alien fungi and oomycetes at class level. Dots represent particular species introduced in a given year.

Tab. 3. Average annual number of introduced alien species of the most important classes in different periods. Letters indicate homogeneous groups at $\alpha = 0.05$, tested with chi-square goodness-of-fit tests followed by Holm's correction for multiple comparisons.

Period	*Agaricomycetes*	*Dothideomycetes*	*Leotiomycetes*	*Peronosporomycetes*	*Sordariomycetes*
1811–1900	0.06^{a}	0.18^{a}	0.10^{a}	0.16^{a}	0.04^{a}
1901–1930	0.10^{a}	0.77^{c}	0.20^{a}	0.33^{a}	0.40^{bc}
1931–2000	0.29^{a}	0.21^{ab}	0.16^{a}	0.24^{a}	0.14^{ab}
2001–2022	0.32^{a}	0.64^{bc}	1.50^{b}	1.50^{b}	0.68^{c}

Origin of alien species

A more detailed analysis of the native geographic areas of introduced fungi (Fig. 5) shows that the two largest and equal parts – 83 taxa (23.6%) – probably originate both from other parts of Europe (although nearly a half of these are archaeomycetes) and from North America. A somewhat lower number – 67 taxa (19.0%) – come from Asia, with the majority of species (61) coming from temperate Asia and only a minor part (6) from tropical Asia. The vast majority (64.5%) of introduced species thus originate from temperate regions of the northern hemisphere. Furthermore, 16 taxa (4.6%) were introduced from South America, 15 from Africa (4.3%), and 6 from Australasia (1.7%). For 82 taxa (23.3%), the area of origin could not be determined (three species from this group being cryptogenic).

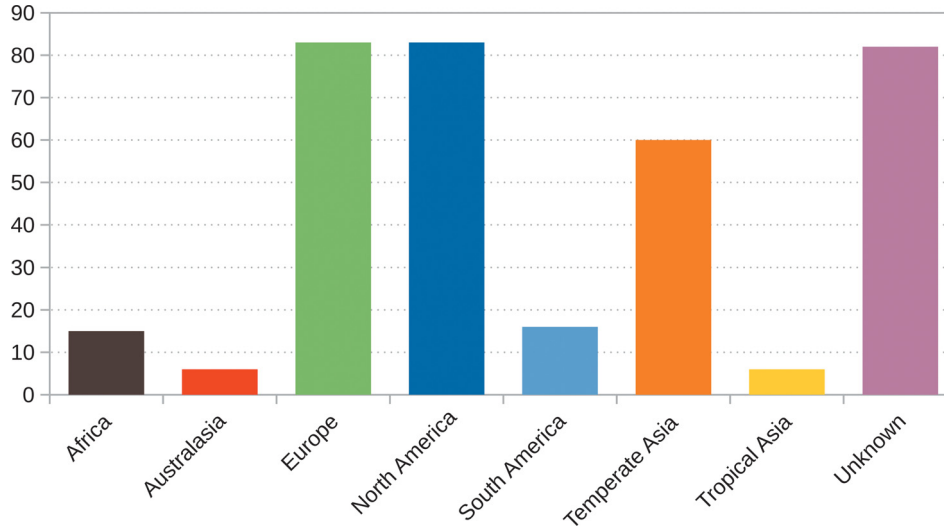

Fig. 5. Origin of alien fungi and oomycetes introduced in the Czech Republic (total number of species).

The two significant periods of introduction (1st and 2nd waves of globalisation) are important not only in terms of the timeline of fungi and oomycetes and their classification, but also in terms of native regions. Significant maxima of introductions from Europe and South America are associated with the first wave of globalisation, whereas species from North America, temperate Asia, and species with unknown native areas are mostly assigned to the second wave (Fig. 6). For these three groups of introduction according to native area, statistical support was also confirmed, indicating that North America and temperate Asia have recently played a particularly important role in terms of introductions (Tab. 4).

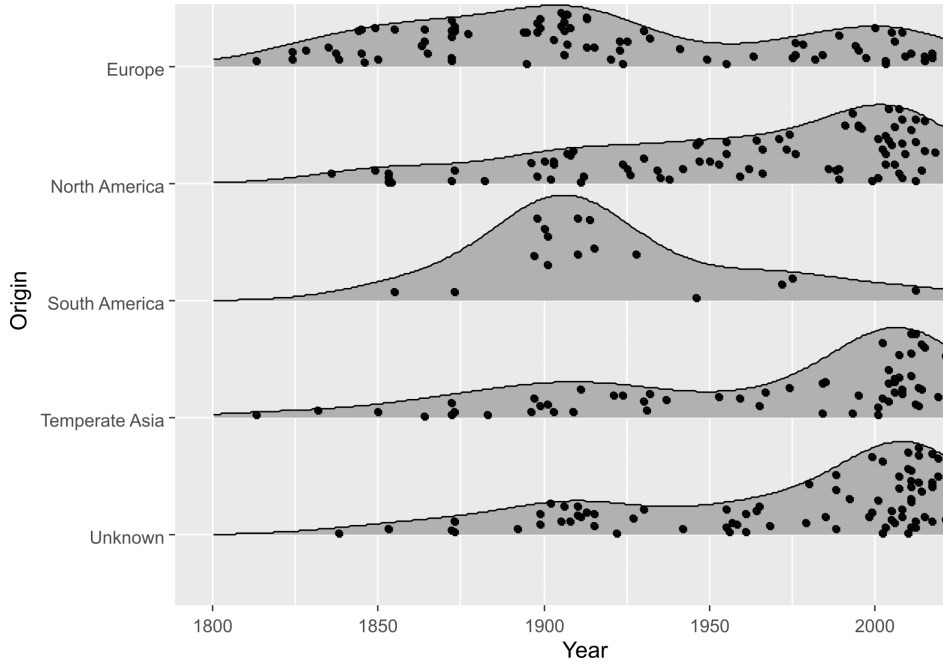

Fig. 6. Introduction of the most important alien fungi and oomycetes at the level of geographic origin (major regions only). Dots represent particular species introduced in a given year.

Tab. 4. Average annual number of introduced alien species from North America and temperate Asia by period. Letters indicate homogeneous groups at $\alpha = 0.05$, tested with chi-square goodness-of-fit tests followed by Holm's correction for multiple comparisons.

Period	North America	Temperate Asia
1811–1900	0.13^{a}	0.12^{a}
1901–1930	0.40^{a}	0.19^{a}
1931–2000	0.43^{a}	0.27^{a}
2001–2022	1.23^{b}	1.27^{b}

Life strategies and potential impact

Of the 352 alien taxa identified in the Czech Republic, 314 species (89.2%) are plant parasites or saproparasites (10 species; Fig. 7). *Ascomycota* (173 species) predominate in this group, with smaller proportions for *Peronosporomycota* (74), *Basidiomycota* (65), and exceptionally, representatives of *Chytridiomycota* appear here (2). Saprotrophic fungi are the second most important, although a significantly smaller ecological group, comprising 30 species (8.5%). This group is predominated by *Agaricomycetes* (26 species), but also includes *Bartheletia*

paradoxa (*Bartheletiomycetes*), *Ciboria americana* and *Hymenoscyphus reynoutriae* (*Leotiomycetes*), and *Hapalocystis berkeleyi* (*Sordariomycetes*). Mycorrhizal fungi are represented by six species from the *Agaricomycetes*, while finally two species, *Batrachochytrium dendrobatidis* (*Rhizophydiomycetes*) and *Aphanomyces astaci* (*Saprolegniomycetes*), are animal parasites.

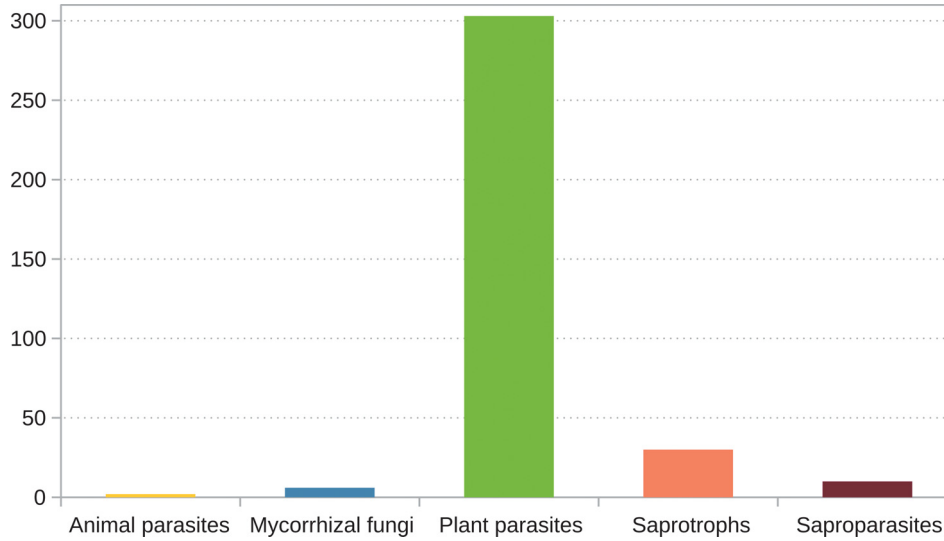

Fig. 7. Life strategies of introduced alien species (total number of species).

Negative impacts (economic, environmental; Fig. 8) have been documented or can be reasonably expected for most of the recorded species, namely 307 taxa (87.5%), with about one fifth of taxa (70) potentially having an impact in multiple areas of interest.

Most species (181) have or may have a negative effect in horticulture. Typically, representatives of genera *Blumeriella*, *Calonectria* (*C. pseudonaviculata*), *Cryptostroma* (*C. corticale*), *Didymascella*, *Dothistroma* (*D. septosporum*), *Entyloma*, *Erysiphe*, *Golovinomyces*, *Kabatina*, *Lecanosticta* (*L. acicola*), *Ophiostoma* (*O. novo-ulmi*), *Phyllosticta*, *Phytophthora* (*P. cinnamomi*, *P. citrophthora*, etc.), *Puccinia*, *Sphaeropsis* (*S. sapinea*), *Septoria*, and *Verticillium* can be mentioned. The spectrum of alien species important in horticulture overlaps with those important also in other areas as well, mostly in agriculture (42 species) and forestry (28).

A potential impact in agriculture can be expected for 144 species. Among the alien parasites with a very significant impact in agricultural production, we

can mention species of the following genera: *Colletotrichum*, *Erysiphe* (especially *E. necator* on grapevine), *Monilinia*, *Peronospora*, *Phytophthora* (*P. infestans*, etc.), *Plasmopara* (*P. viticola*, *P. halstedii*), *Pseudoperonospora*, *Ramularia*, *Rhizoctonia*, *Septoria*, *Sporisorium*, *Synchytrium* (*S. endobioticum* on eggplant), *Uromyces*, *Venturia*, *Verticillium*, and many others. The impact of these pathogens in areas other than agriculture is relatively small, relating mostly to polyphagous *Phytophthora* spp. (e.g. *P. cactorum*, *P. plurivora*). The only area sharing a larger number of pathogens with agriculture is horticulture (Fig. 8).

A potential impact in the field of forestry was determined for 44 species. Species important in Czech forestry include several dangerous pathogens causing damage to forests and nurseries in various regions of the world, especially in Europe, North America, and Australia. Typical examples include *Cronartium ribicola*, *Cryptostroma corticale*, *Dothistroma septosporum*, *Erysiphe alphitoides*, *Eutypella parasitica*, *Hymenoscyphus fraxineus*, *Lecanosticta acicola*, *Nothophaeocryptopus gaeumannii*, *Ophiostoma ulmi* and *O. novo-ulmi*, *Phytophthora* spp., *Rhabdocline pseudotsugae*, *Sphaeropsis sapinea*, and others.

At least 36 species have a significant negative impact on the natural environment. These include animal parasites such as *Batrachochytrium dendrobatidis*, which has contributed to global amphibian declines, and *Aphanomyces astaci* causing crayfish plague. Secondly, this category includes practically all species of the previous categories which are able to parasitise our native hosts. Among them are key pathogens such as *Ophiostoma novo-ulmi*, *Hymenoscyphus fraxineus*, *Lecanosticta acicola*, *Dothistroma septosporum*, and multiple species of the genus *Phytophthora*, including *Phytophthora ×alni*, *P. plurivora*, *P. cinnamomi*, and *P. ramorum*. However, all alien species able to invade the natural environment can affect communities of the invaded habitats in some way.

A total of 70 species can cause significant damage in several different areas of interest. As already mentioned, the greatest overlaps in impact can be identified especially between the areas of horticulture and agriculture or forestry. A few polyphagous parasites with extremely broad host ranges of genus *Phytophthora* (e.g. *P. cactorum*, *P. pseudocryptogea*, etc.) can cause potential damage in all specified agroecosystems and wild habitats (Fig. 8).

Several taxa also have an impact on human health (ambilateral pathogens *Cryptostroma corticale* and *Fusarium proliferatum*) and one taxon seriously damages wooden structures (*Serpula lacrymans*).

An analysis of the number of first interceptions of parasitic fungi per impact area supported the fact that massive introductions of fungi have always occurred within the waves of globalisation. In the case of parasites important in agriculture and horticulture, there were two waves 1901–1930 and 2001–2022, while the introduction of alien species with relevance to other areas of interest occurred mainly during the second wave of globalisation (Fig. 9).

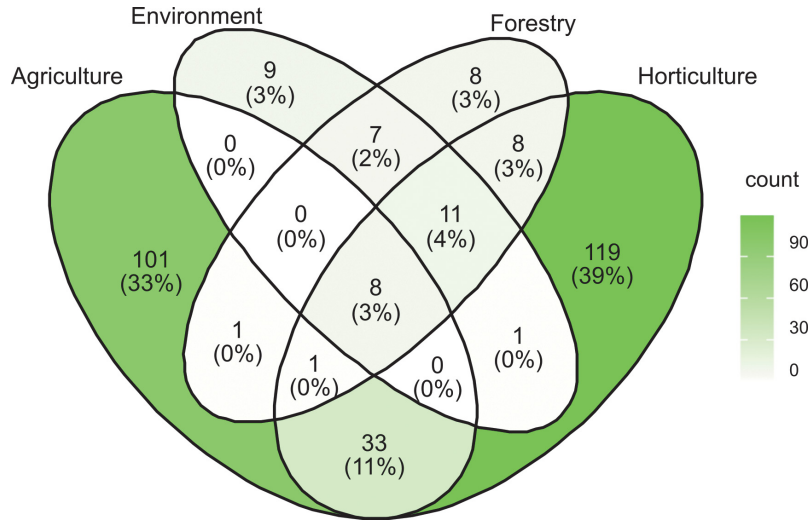

Fig. 8. Venn diagram of the distribution of potential impact of alien parasitic fungi in particular areas of interest.

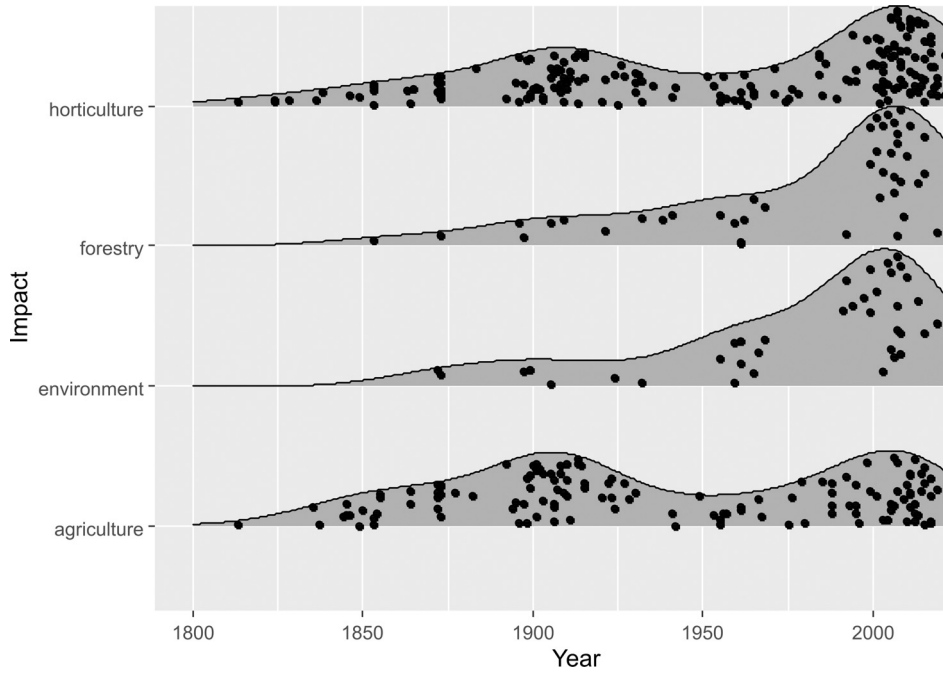

Fig. 9. Introduction of alien parasitic species according to area of impact during the time period. Dots represent particular species introduced in a given year.

DISCUSSION

This paper presents the first attempt to develop a general invasion framework for fungi *sensu lato*. The broader context explaining the proposed scheme is described in the Methods section. The paper also provides a list of alien fungi and oomycetes recorded in the Czech Republic, expanded with information on their first records, probable native ranges, and their potential impacts. The diversity, temporal trends, native ranges, ecology, and impacts of these introduced species are discussed below.

Number of species and diversity

At present, the list of alien fungal and oomycete species includes a total of 352 taxa (Electronic Supplement), of which 310 species are classified as neomycetes. This number is comparable to the results from similar recent research conducted elsewhere in Central Europe – Austria has 375 documented neomycete species (Voglmayr et al. 2023), Switzerland 283 species (Beenken & Senn-Irlet 2016). In post-communist European countries, comparable assessments have been carried out in Lithuania (Motiejūnaitė et al. 2017; 142 taxa) and Poland (Mułenko et al. 2010; 86 taxa) only.

Our list certainly cannot be considered final. At present, there is no checklist of fungi and oomycetes in the Czech Republic, which would be of great help in refining the list of alien species. Especially in macromycetes (but not exclusively), occurrence data are scattered across hundreds of small articles, unpublished final reports, and herbarium collections, which have been taken into account only to a limited extent. We can also state with certainty that other invasive organisms are still spreading in the Czech Republic, and dozens of taxa known from other parts of Europe are likely to be detected here sooner or later – e.g. *Agroathelia rolfsii* (see CABI 2025), *Aureoboletus projectellus* (Banasiak et al. 2019)[1], and *Batrachochytrium salamandrivorans* (Vojar et al. 2021). It can be reasonably assumed that some of them may already be present but have just not been detected (e.g. *Aphanomyces raphani*, *Erysiphe kenjiana* and *Neonectria neomacrospora*) or have not attracted systematic attention due to their low importance or attractiveness – probably many species of *Leotiomycetes* and *Dothideomycetes* parasitising on leaves of exotic ornamental plants.

As mentioned above, a considerable number of recent records can be attributed to advances in diagnostic and taxonomic methods. Even many non-native

[1] In 2025, a possible record of *A. projectellus* from North Bohemia (Lužické hory Mts) emerged. The evidence is based on a photograph of a basidioma of which no voucher specimen was preserved (Z. Brunner, pers. comm.). However, this record is beyond the temporal scope of the article (see Material and Methods) and is therefore not included.

species were first described in their secondary ranges, e.g. numerous *Phytophthora* species (former case of e.g. *P. ramorum*; Werres et al. 2001, Jung et al. 2020), powdery mildews (*Erysiphaceae*; Mougou et al. 2008), and macromycetes (*Marasmius teplicensis*; Antonín 1993). It is very likely that the list can be supplemented by many species from the highly diverse genus *Pythium* s.l., which has been practically ignored in terms of native area, invasiveness, and impact on ecosystems, although it contains a number of species which are now regularly identified mainly in anthropogenic habitats across the Czech Republic and Europe (Boie et al. 2024; see CCPO). Other illustrative examples are the recently found high diversity of exotic powdery mildew species in urban greenery (Mieslerová et al. 2020) and new records of saprotrophic fungi on substrates such as wood chips, compost, etc. (Kříž et al. 2015, Petrželová & Sochor 2019). It can also be assumed that the situation of many species with disputed origin will be clarified, and some of them may be transferred to the category of alien species (e.g. *Colletotrichum dematium*, etc.).

The largest group in our checklist is *Ascomycota* (49.1%), followed by *Basidiomycota* (28.7%) and *Peronosporomycota* (21.6%). Their proportions are very similar to those recently reported in Central Europe by Voglmayr et al. (2023) from Austria (56.0%, 30.1%, and 12.8%, respectively) and Beenken & Senn-Irlet (2016) from Switzerland (50.5%, 36.0%, and 12.7%, respectively). The relatively high proportion of oomycetes in our dataset may be attributed to the inclusion of archaeomycetes (with many species of *Peronosporales*), the integration of recent research on invasive *Pythiales* reflecting growing interest in this group (Brasier 1999), and the investigation of new introduction pathways (e.g. Mrázková et al. 2022, 2025). The structure of our dataset generally corresponds with that of other national and also European data (Desprez-Loustau 2009, Beenken & Senn-Irlet 2016, Voglmayr et al. 2023).

History of introductions

Archaeomycetes are fungi and oomycetes (most often parasites of agricultural crops) introduced to the Czech territory from the Mediterranean and the Middle East in the Middle Ages. Unfortunately, this group is most likely significantly underestimated in the final list for objective reasons (e.g. insufficient knowledge of biogeography). It can particularly be assumed that many agricultural crops and their weeds imported to Central Europe were accompanied by their parasites. However, many parasites of agricultural crops, e.g. parasites of anecophytes (old agricultural crops unknown from the natural environment), can to a greater or lesser extent pass on to related species which are wild or native to the Czech Republic (e.g. *Blumeria graminis* and *Puccinia striiformis*; Urban & Marková 2009, Petřeková 2018). It is therefore possible that also other species of archaeomycetes (even if

we mistakenly consider them to be native) have passed on to related species native to the Czech Republic, but without thorough population studies it is not easy to decide whether it is an original or an introduced taxon. We have consistently avoided such uncertain taxa, and the presented list does not contain them. Thus, these reasons and likely others as well explain why some works avoid this group (Beenken & Senn-Irlet 2016, Voglmayr et al. 2023). However, some other studies contain archaeomycetes at least to some extent (e.g. DAISIE, Desprez-Loustau 2009, Motiejūnaitė et al. 2017). As this is the first list of alien fungi in the Czech Republic, we have decided to include them.

The trend in number of interceptions of introduced fungi and oomycetes from the beginning of the 19th century until World War II corresponds relatively well with the development described by Voglmayr et al. (2023) for neighbouring Austria. This includes such details as accelerated introductions in the late 19th century and early 20th century, which mirror major advances in fungal taxonomy and the emergence of modern phytopathology (Köck 1935, Beran 1951, Hawksworth & Lücking 2017, Sedlářová et al. 2021) as well as the effect of the first wave of globalisation (Bonnamour et al. 2021). A certain difference is the stronger decrease in interceptions during the second decade of the 20th century (World War I) and immediate post-war period in Austria. However, the overall trend is very similar, probably due to the fact that these two countries share their history in the Austro-Hungarian Empire and later within the broader Central Europe region until the end of World War II.

A more pronounced and long-lasting rise in recorded species around the turn of the 20th century can be attributed to the mentioned methodological progress and increasing global trade. Expansion of professional and amateur mycological activity, together with the growth of herbarium collections (Dörfelt & Heklau 1998), has substantially improved the documentation of fungal diversity. This period was followed by a slowdown of introductions, corresponding to the period beginning with the Great Depression and ending with World War II. The observed trends align with similar curves describing the dynamics of alien fungal interceptions elsewhere in Europe: Desprez-Loustau (2009), Santini et al. (2013), Beenken & Seen-Irlet (2016), Motiejūnaitė et al. (2017), Voglmayr et al. (2023).

A notably different trend begins in the 1950s, when an exponential rise of new interceptions of alien fungi emerges in Europe (e.g. Santini et al. 2013, Voglmayr et al. 2023). By contrast, in the territory of today's Czech Republic, a more or less linear trend continues from the Great Depression, through World War II to the incorporation of the state into the Eastern Bloc. The deliberate interruption of economic contacts with Western Europe during this communist era (Bojňanský 1956) likely played a role in maintaining a reduced rate of introductions over the following fifty years. However, some invasive species have arrived in the Czech

Republic with the import of plant material as part of the so-called 'economic aid' (e.g. probably *Plasmopara halstedii*; Kitner et al. 2023).

Today's extreme trend of increasing numbers of newly detected species began after the turn of the new millennium and is clearly related to the reopening of the economy and the Czech Republic's accession to the European Union, similarly to Lithuania (Motiejūnaitė et al. 2017). Owing to its central location in Europe, the Czech Republic has also become an important transit hub for goods from and to other European countries. Over the subsequent two decades, the number of intercepted alien fungal species rose significantly, surpassing the growth observed during the same period in older EU member countries (Santini et al. 2013, Voglmayr et al. 2023). This reflects a gradual equalisation of invasion levels in Western Europe and post-Soviet Central Europe. The pool of non-native organisms formed in Western Europe over decades (Haubrock et al. 2023) has probably played a role in this process. The data from Lithuania (Motiejūnaitė et al. 2017) supports this trend. Another study from a post-communist European country with a similar history is very necessary to verify the trend we have found.

It is very likely that many of the newly detected species have occurred in Czech territory much longer. Such organisms undoubtedly include for example *Eutypella parasitica* (Černý et al. 2017), which must have been present for at least one or two decades according to the size of the lesions in colonised maple trunks in the Silesian region. A similar assumption can be applied to some *Phytophthora* species (e.g. *P. plurivora*, *P.* ×*cambivora*, *P. cinnamomi*; Cejp & Jechová 1962, Černý et al. 2008, 2011). More recent examples include *Phomopsis juniperivora* and *Diaporthe japonica* (see details in Results). Both taxa have almost certainly been naturalised and widely distributed in the Czech Republic for decades but overlooked so far. It can be assumed that a shorter or longer period between introduction or naturalisation and detection exists in most (especially microscopic) pathogens. This interval can be several decades long (cf. Drenkhan et al. 2014, 2017, Wylder et al. 2018) and is referred to as 'invasive debt' (Essl et al. 2011, Bonnamour et al. 2023). If such delays were considered, the invasion curve (Fig. 1) would have a significantly more gradual character. The role of careful mycofloristic research is of fundamental importance in determining the invasion process as a whole. Perhaps that is why the trends found in *Agaricomycetes* – where a disproportionately wider network of skilled field mycologists, both professional and amateur, exists in the Czech Republic – differ so fundamentally from those found in other important groups (*Peronosporomycetes*, *Leotiomycetes*, *Dothideomycetes*, etc.; Fig. 4, Tab. 3). These differences probably reflect certain mycological patterns, not only in the Czech Republic, but also in Europe as a whole.

Almost all fungi and fungus-like organisms associated with plants live at least part of their lives in plants without any symptoms. In most cases, the appearance

of symptoms on plants depends not only on the fungus (or fungus-like organism), but also on the host plant and the conditions in which the plant and fungi live at a given time. It is less likely that fungi (or fungus-like organisms) will be detected in the asymptomatic stage than in the stage when they cause symptoms on the plant. In the future, more frequent use of next-generation sequencing (and similar methods) in the study of microbial communities in environmental samples will provide more information about the occurrence of fungi at a stage when they do not produce fruitbodies, colonies, or symptoms on their hosts visible to the naked eye.

Origin of alien species

An analysis of the origin of introduced fungi (Fig. 5) showed that about 2/3 of alien species were introduced from three regions – Europe, North America and temperate Asia. Other world regions only play a minor role as native areas of introduced species. The vast majority of introduced species thus come from temperate regions of the northern hemisphere. Again, these numbers are consistent with findings of comparable studies in other European countries (Desprez-Loustau et al. 2010, Beenken & Senn-Irlet 2016, Voglmayr et al. 2023).

It was also found that the numbers of species introduced from the three main source regions are roughly the same (around 20%), but the development of introductions from them over time has a completely different character (Fig. 6). The largest proportion of species originating from Europe were found before and during the first wave of globalisation, moreover nearly a half of introduced species are archaeomycetes. Introductions from North America and temperate Asia predominate during the second wave of globalisation (after 2000). In the case of these groups of introduced fungi, statistical support was found, so we can say that North America and temperate Asia have recently been of the greatest importance in terms of recent introductions (Tab. 4). These findings coincide with the most common source areas for the world's top 100 fungal and oomycete pathogens (Schertler et al. 2024). If compared to the value of international trade (European Union 2025), to which the number of introductions relates (Santini et al. 2013), we can speculate about China and the USA as the main recent sources of introduced species. Import from China to the EU significantly increased from 7.8% in 2002 to 20.5% in 2023 (Eurostat on-line). Also the import of live plants to Europe is the largest from Asia (Ghelardini et al. 2022, Schertler et al. 2024).

For nearly 1/4 of introduced species the area of origin is unknown, similarly to other countries (for instance Desprez-Loustau et al. 2010, Voglmayr et al. 2023), and introduction of this group has the same pattern as introductions from North America and temperate Asia. Thus, we can speculate that many species with unknown origin may be native to these regions.

Life strategies and potential impact

The most frequent ecological group of introduced fungi in the Czech Republic is plant parasites and saproparasites (89.2%). Saprotrophic fungi represent the second most frequent group (8.5%), while mycorrhizal fungi contribute 1.6% to the diversity, and animal parasites less than 1.0%. A high proportion of plant parasites is a common pattern and can be identified in all surveys of non-native fungi within Europe (Beenken & Senn-Irlet 2016, Motiejūnaitė et al. 2017, Voglmayr et al. 2023). This predominance is attributable to the easy spread of pathogens as overlooked colonisers of plant material (Brasier 2008), their high economic importance, the visible manifestation of diseases, and the resulting increased attention to parasitic species (Pimentel et al. 2001, Desprez-Loustau et al. 2007, Voglmayr et al. 2023). The intense and spontaneous dispersal of some groups, such as *Erysiphales*, *Peronosporales*, and *Pucciniales*, also plays a major role due to their high production of airborne spores. Consequently, these groups tend to be overrepresented in the lists of alien fungi (Desprez-Loustau et al. 2010) similarly to the Czech data. A somewhat lower proportion of parasites was identified in France only (about 60%), which is undoubtedly due to the greater research focus on *Agaricomycetes* in that country (Desprez-Loustau et al. 2010).

The spectrum of alien species relevant to horticulture significantly overlaps with the spectrum impacting forestry and the natural environment, indicating that (1) many of these species share closely related or identical hosts in all of these areas, and (2) the introduction of non-native plant pathogens together with ornamental plant material poses a serious risk to forestry and the natural environment (Brasier 2008).

A negative economic or environmental impact is expected for 87.5% of identified species. Large numbers of these species can cause damage in agriculture and horticulture (each about 40%) and their introduction corresponds with both historical waves of globalisation. Only 12% of introduced species may pose a risk to forestry and less than 7% to the natural environment. However, these species have usually been introduced only in recent decades (Tab. 3), partly because more attention has been paid to this group of organisms. It is likely that the importance of at least some of them will grow substantially in the coming decades. This is supported by the modelling of their potential distribution, as shown for recently detected species such as *Phytophthora ramorum*, *Cryptostroma corticale*, and other species (Chumanová et al. 2021). Since many alien species have arrived as just a few individuals, they can go unnoticed for a period of time before their populations build up and reach visible levels (Richardson et al. 2000). Unfortunately, a relatively large proportion of species (22%) can have a negative effect in multiple areas, either because their hosts play an important role in more areas, or because they are highly polyphagous species which can easily spread to our

native hosts, such as many species of *Phytophthora*. This trend is worrying and may have serious consequences for human society and the environment (Brasier 2008, Philibert et al. 2011).

In the case of saprotrophic and mycorrhizal species, we can expect an effect on the composition or structure of the original microbiota (Mujic et al. 2023), while parasites may also affect species depending on infected hosts. Mycorrhizal fungi may also exert an indirect effect by facilitating the survival of non-native plants (Dickie et al. 2010).

NOTES ON SPECIES OF UNCERTAIN STATUS

Here we discuss listed species with some degree of uncertainty.

Ascochyta grossulariae – species recorded in 1872 (PRM 173134), but excluded from the list because of its uncertain species concept.

Ciboria americana – species recorded in 2016, while the National Museum in Prague holds a herbarium specimen originally identified as *Rutstroemia gallincola* from as early as 1925 (PRM 14982), which differs from *C. americana* in the ITS sequence by only a single nucleotide. Moreover, *C. americana* was described in 1902 from *Castanea sativa* in America and given the origin of the host, it may in fact represent a species introduced from Europe to America.

Ciborinia allii – species mentioned in the Czech phytopathological literature as a relatively common agent of garlic rot (Rod 1988). However, that reference lacks a herbarium specimen and a detailed morphological description.

Coleosporium telekiae – taxon listed for the Czech Republic only as a synonym of *C. tussilaginis* (Urban & Marková 2009), which was also confirmed by Helfer (2013). This species is therefore likely native to European *Asteraceae*.

Coniothyrium laburnophilum – the record of this species originates from the EASIN database (see Methods), which refers to the USDA Fungal Databases. Unfortunately, the corresponding record cannot be traced in this database. However, since the species occurs in Poland (Mułenko et al. 2008), it will probably also be present in the Czech Republic.

Corynespora cassiicola – species listed as a pathogen of mainly greenhouse cucumber in agricultural inspection reports, but the record is not supported by herbarium specimens or a more detailed description of the species.

Peronospora viciae – for confirming this species, a revision of herbarium collections would be necessary.

Phytophthora erythroseptica – the record of this species was mentioned in Czech horticultural literature based solely on disease symptoms (Krejzar & Pánková 2014). Molecular genetic or immunodiagnostic methods were not used for identification. No strain has been isolated. This record is highly questionable.

Plasmopara caucalis and *P. petroselini* – these species were described in 1951 and we are not aware of any other synonyms (Index Fungorum, see Methods). However, the records for the Czech Republic date back to 1913 and 1920, respectively (Müller & Kokeš 2008). Unfortunately, herbarium specimens were not traced, so they may be erroneous records. Two items collected after 2000 are deposited in the herbarium of the Department of Crop Science, Breeding and Plant Medicine, MENDELU.

Pluteus variabilicolor – species considered by some authors to be non-native to Europe. However, Ševčíková & Dima (2021) contradicted this and suggested it to be a rare species, native to temperate zones of Eurasia.

Pucciniastrum fuchsiae – species sometimes assigned to *P. epilobii* or *P. circaeae*. The record for the Czech Republic is derived from a record identified as *P. epilobii* on *Fuchsia* (Urban & Marková 2009).

Uromyces lupinicola – species described by Czech author Bubák (1906). It is not certain whether it is a synonym of *U. lupini* Berk. & M.A. Curtis.

Verticillium alboatrum and *V. dahliae* – the records of these species are from 1956 and 1927, respectively. However, as was recently clarified (Inderbitzin et al. 2011), at that time morphological differentiation was not sufficient for the precise identification of some *Verticillium* species. For this reason, it is also difficult to determine the original distribution area of these species. Due to their high rate of spread and serious negative impacts on their hosts, we consider these species to be cryptogenic.

Verticillium nonalfalfae – the original range of this species is uncertain for the same reasons as for the previous species.

Wilsoniana bliti – records for the Czech Republic from GBIF (https://www.gbif.org/) include the host *Amaranthus retroflexus*. However, *W. amaranthi*, which is morphologically difficult to distinguish from *W. bliti*, may also occur on *Amaranthus* spp. (Voglmayr & Riethmüller 2006) and therefore the oldest records may be questionable.

ACKNOWLEDGEMENTS

ZH, MH, DZ and KČ were supported by TA ČR project SS02030018 DivLand. MS thanks project IGA UP PrF_2026_001 for support. MŠ was financially supported by the Ministry of Culture of the Czech Republic under no. DKRVO 2024-2028/3.I.c, 00023272. The work of VD, AH, DN, and JP was funded by the Czech Ministry of Agriculture (MZE-RO0425). FL thanks the support of the Czech Ministry of Agriculture for the development of research organisations (MZE-RO0123). We gratefully acknowledge the contributions of the curators of herbarium collections Tereza Tejklová (Museum of Eastern Bohemia, Hradec Králové), Vladimír Antonín (Moravian Museum, Brno), Petr Zehnálek (National Museum, Prague), and Miroslav Beran (South Bohemian Museum, České Budějovice). We owe our gratitude to the many mycologists and phytopathologists who chose Bohemia, Moravia, and Silesia as the focus of their research; without their many years of work, this list could not have been compiled.

REFERENCES

ANTONÍN V. (1993): Studies in marasmioid fungi – VIII. *Marasmius teplicensis*, a new species of the sct. *Sicci* growing in a greenhouse. – Česká Mykologie 46: 209–212. DOI: https://doi.org/10.33585/cmy.46304

ATALLAH Z.K., MARUTHACHALAM K., DU TOIT L., KOIKE S.T., DAVIS R.M., KLOSTERMAN S.J., HAYES R.J., SUBBARAO K.V. (2010): Population analyses of the vascular plant pathogen *Verticillium dahliae* detect recombination and transcontinental gene flow. – Fungal Genetics and Biology 47: 416–422. DOI: https://doi.org/10.1016/j.fgb.2010.02.003

BAČOVÁ A. ET AL. (2024): Hidden *Phytophthora* diversity unveiled in tree nurseries of the Czech Republic with traditional and metabarcoding techniques. – European Journal of Plant Pathology 170(1): 131–156. DOI: https://doi.org/10.1007/s10658-024-02886-1

BANASIAK Ł., PIETRAS M., WRZOSEK M., OKRASIŃSKA A., GORCZAK M., KOLANOWSKA M., PAWŁOWSKA J. (2019): *Aureoboletus projectellus* (Fungi, *Boletales*) – An American bolete rapidly spreading in Europe as a new model species for studying expansion of macrofungi. – Fungal Ecology 39: 94–99. DOI: https://doi.org/10.1016/j.funeco.2018.12.006

BEENKEN L., SENN-IRLET B. (2016): Neomyceten in der Schweiz. Stand des Wissens und Abschätzung des Schadpotentials der mit Pflanzen assoziierten gebietsfremden Pilze. – WSL Berichte 50: 1–93. Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. [in German]

BERAN F. (1951): 50 Jahre österreichischer Pflanzenschutz 1901–1951. – Bundesanstalt für Pflanzenschutz, Wien. [in German]

BÉRUBÉ J.A., NICOLAS G.G. (2015): Alien fungal species on asymptomatic live woody plant material imported into Canada. – Canadian Journal of Plant Pathology 37: 67–81. DOI: https://doi.org/10.1080/07060661.2014.986526

BLACKBURN T.M., PYŠEK P., BACHER S., CARLTON J.T., DUNCAN R.P., JAROŠÍK V., WILSON J.R.U., RICHARDSON D.M. (2011): A proposed unified framework for biological invasions. – Trends in Ecology & Evolution 26: 333–339. DOI: https://doi.org/10.1016/j.tree.2011.03.023

BOIE W., SCHEMMEL M., YE W., HASLER M., GOLL M., VERREET J.A., CAI D. (2024): An assessment of the species diversity and disease potential of *Pythium* communities in Europe. – Nature Communications 15(1): 8369. DOI: https://doi.org/10.1038/s41467-024-52761-0

BOJŇANSKÝ V. (1956): Peronospóra slnečnicová [*Plasmopara halstedii* (Farlow) Berl. et de Toni] v ČSR [*Plasmopara halstedii* (Farlow) Berl. et de Toni in Czechoslovakia]. – Poľnohospodárstvo 3: 397–401. [in Slovak]

BONNAMOUR A., BLAKE R.E., LIEBHOLD A.M., NAHRUNG H.F., ROQUES A., TURNER R.M., YAMANAKA T., BERTELSMEIER C. (2023): Historical plant introductions predict current insect invasions. – Proceedings of the National Academy of Sciences 120: e2221826120. DOI: https://doi.org/10.1073/pnas.2221826120

BONNAMOUR A., GIPPET J.M.W., BERTELSMEIER C. (2021): Insect and plant invasions follow two waves of globalisation. – Ecology Letters 24: 2418–2426. DOI: https://doi.org/10.1111/ele.13863

BOURKE P.M.A. (1964): Emergence of potato blight, 1843–46. – Nature 203: 805–808. DOI: https://doi.org/10.1038/203805a0

BRADSHAW R.E. ET AL. (2020): *Phytophthora agathidicida*: research progress, cultural perspectives and knowledge gaps in the control and management of kauri dieback in New Zealand. – Plant Pathology 69: 3–16. DOI: https://doi.org/10.1111/ppa.13104

BRASIER C.M. (2008): The biosecurity threat to the UK and global environment from international trade in plants. – Plant Pathology 57: 792–808. DOI: https://doi.org/10.1111/j.1365-3059.2008.01886.x

BRASIER C.M., BUCK K.W. (2001): Rapid evolutionary changes in a globally invading fungal pathogen (Dutch elm disease). – Biological Invasions 3: 223–233. DOI: https://doi.org/10.1023/A:1015248819864

BRASIER C. M., COOKE D.E.L., DUNCAN J.M. (1999): Origin of a new *Phytophthora* pathogen through interspecific hybridization. – Proceedings of the National Academy of Sciences 96(10): 5878–5883. DOI: https://doi.org/10.1073/pnas.96.10.5878

Brasier C.M., Kirk S.A. (2010): Rapid emergence of hybrids between the two subspecies of *Ophiostoma novo-ulmi* with a high level of pathogenic fitness. – Plant Pathology 59: 186–199. DOI: https://doi.org/10.1111/j.1365-3059.2009.02157.x

Brasier C.M., Kirk S.A., Delcan J., Cooke D.E.L., Jung T., Man In't Veld W.A. (2004): *Phytophthora alni* sp. nov. and its variants: designation of emerging heteroploid hybrid pathogens spreading on *Alnus* trees. – Mycological Research 108: 1172–1184. DOI: https://doi.org/10.1017/S0953756204001005

Brown J.K.M., Hovmøller M.S. (2002): Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. – Science 297: 537–541. DOI: https://doi.org/10.1126/science.1072678

Brummitt R.K. (2001): World geographical scheme for recording plant distributions (2nd ed.). – Hunt Institute for Botanical Documentation, Pittsburgh.

Bubák F. (1906): Houby české. 1. Rezy (*Uredinales*) [Czech fungi. 1. Rust fungi (*Uredinales*)]. – Archiv pro přírodovědecké prozkoumání Čech, fasc. XIII, no. 5: 1–228. [in Czech]

Burgess T.I. et al. (2017): Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. – Global Change Biology 23: 1661–1674. DOI: https://doi.org/10.1111/gcb.13492

CABI (2025): *Athelia rolfsii* (sclerotium rot). – https://plantwiseplusknowledgebank.org/doi/10.1079/pwkb.species.49155 [accessed 30 April 2025]

Cahill D.M., Rookes J.E., Wilson B.A., Gibson L., McDougall K.L. (2008): *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. – Australasian Journal of Botany 56: 279–310. DOI: https://doi.org/10.1071/BT07159

CCPO (on-line): Czech Collection of Phytopathogenic *Oomycetes*. – https://vuk.gov.cz/sbirka-fytopatogennich-oomycetu/ [accessed 17 May 2026]

Cejp K., Jechová V. (1962): Subtropické druhy rodu *Phytophthora* de Bary dovezené k nám s jižním ovocem: *Phytophthora citrophthora* (Sm. et Sm.) Leonian a *P. citricola* Sawada [Subtropical species of the genus *Phytophthora* de Bary transported into Czechoslovakia on the fruits of southern origin: *Phytophthora citrophthora* (Sm. et Sm.) Leonian and *P. citricola* Sawada]. – Česká Mykologie 16: 198–202. [in Czech]

Chumanová E., Černý K., Brestovanská T., Haňáčková Z., Havrdová L., Zýka V. (2021): Atlas potenciální distribuce vybraných druhů invazních patogenů dřevin a jejich impaktu na lesní ekosystémy v ČR [Atlas of the potential distribution of selected invasive tree pathogens and their impact on forest ecosystems in the Czech Republic]. – Výzkumný ústav pro krajinu, Průhonice. [in Czech]

Colautti R.I., MacIsaac H.J. (2004): A neutral terminology to define 'invasive' species. – Diversity and Distributions 10: 135–141. DOI: https://doi.org/10.1111/j.1366-9516.2004.00061.x

Crous P.W., Rossman A.Y., Aime M.C., Allen W.C., Burgess T., Groenewald J.Z., Castlebury L.A. (2021): Names of phytopathogenic fungi: a practical guide. – Phytopathology 111(9): 1500–1508. DOI: https://doi.org/10.1094/PHYTO-11-20-0512-PER

Černý K., Gregorová B., Strnadová V., Tomšovský M., Holub V., Gabrielová Š. (2008): *Phytophthora cambivora* causing ink disease of sweet chestnut recorded in the Czech Republic. – Czech Mycology 60: 265–274. DOI: https://doi.org/10.33585/cmy.60210

Černý K., Havrdová L., Němec P., Hrabětová M., Mrázková M., Zahradník D., Grígel J., Šetinová D. (2020): Integrovaná ochrana sazenic v lesních školkách před patogeny z r. *Phytophthora* [Integrated management of forest nursery saplings against *Phytophthora* pathogens]. Certified Methodology 68354/2020-MZE-16222/M216. – Výzkumný ústav pro krajinu a okrasné zahradnictví, Průhonice. [in Czech]

Černý K., Havrdová L., Zlatník V., Hrabětová M. (2016): Pěstování jasanu v prostředí s výskytem *Hymenoscyphus fraxineus* [Cultivation of ash under conditions of *Hymenoscyphus fraxineus* occurrence]. – Výzkumný ústav pro krajinu a okrasné zahradnictví, Průhonice. [in Czech]

Černý K., Hrabětová M., Svobodová I., Mrázková M., Kowalski T. (2017): *Eutypella parasitica* naturalised in Bohemian and Polish Silesia. – Forest Pathology 47: e12347. DOI: https://doi.org/10.1111/efp.12347

ČERNÝ K., TOMŠOVSKÝ M., MRÁZKOVÁ M., STRNADOVÁ V. (2011): The present state of knowledge of *Phytophthor*a spp. diversity in forest and ornamental woody plants in the Czech Republic. – New Zealand Journal of Forestry 41S: S75 – S82.

DESPREZ-LOUSTAU M.L. (2009): Alien fungi of Europe. – In: Netwig W., ed., Handbook of alien species in Europe. Invading Nature – Springer Series in Invasion Ecology, Vol 3., pp. 15–28. Springer, Dordrecht.

DESPREZ-LOUSTAU M.L., COURTECUISSE R., ROBIN C., HUSSON C., MOREAU P.-A., BLANCARD D., SELOSSE M.-A., LUNG-ESCARMANT B., PIOU D., SACHE I. (2010): Species diversity and drivers of spread of alien fungi (sensu lato) in Europe with a particular focus on France. – Biological Invasions 12: 157–172. DOI: https://doi.org/10.1007/s10530-009-9439-y

DESPREZ-LOUSTAU M.L., ROBIN C., BUÉE M, COURTECUISSE R., GARBAYE J., SUFFERT F., SACHE I., RIZZO D. (2007): The fungal dimension of biological invasions. – Trends in Ecology & Evolution 22: 472–480. DOI: https://doi.org/10.1016/j.tree.2007.04.005

DICKIE I.A., BOLSTRIDGE N., COOPER J.A., PELTZER D.A. (2010): Co-invasion by *Pinus* and its mycorrhizal fungi. – New Phytologist 187: 475–484. DOI: https://doi.org/10.1111/j.1469-8137.2010.03277.x

DICKIE I.A., NUÑEZ M.A, PRINGLE A., LEBEL T., TOURTELLOT S.G., JOHNSTON P.R. (2016): Towards management of invasive ectomycorrhizal fungi. – Biological Invasions 18: 3383–3395. DOI: https://doi.org/10.1007/s10530-016-1243-x

DÖRFELT H., HEKLAU H. (1998): Die Geschichte der Mykologie. – Einhorn Verlag, Schwäbisch Gmünd. [in German]

DREES K.P. ET AL. (2017): Phylogenetics of a fungal invasion: origins and widespread dispersal of white-nose syndrome. – mBio 8: e01941-17. DOI: https://doi.org/10.1128/mbio.01941-17

DRENKHAN R., SANDER H., HANSO M. (2014): Introduction of Mandshurian ash (*Fraxinus mandshurica* Rupr.) to Estonia: Is it related to the current epidemic on European ash (*F. excelsior* L.)? – European Journal of Forest Research 133: 769–781. DOI: https://doi.org/10.1007/s10342-014-0811-9

DRENKHAN R., SOLHEIM H., BOGACHEVA A, RIIT T., ADAMSON K., DRENKHAN T., MAATEN T., HIETALA A.M. (2017): *Hymenoscyphus fraxineus* is a leaf pathogen of local *Fraxinus* species in the Russian Far East. – Plant Pathology 66: 490–500. DOI: https://doi.org/10.1111/ppa.12588

ESSL F. ET AL. (2011): Socioeconomic legacy yields an invasion debt. – Proceedings of the National Academy of Sciences 108: 203–207. DOI: https://doi.org/10.1073/pnas.1011728108

ESSL F. ET AL. (2018): Which taxa are alien? Criteria, applications, and uncertainties. – BioScience 68: 496–509. DOI: https://doi.org/10.1093/biosci/biy057

EUROPEAN UNION (2016): Regulation (EU) 2016/2031 of the European Parliament and of the Council of 26 October 2016 on protective measures against pests of plants, amending Regulations (EU) No 228/2013, (EU) No 652/2014 and (EU) No 1143/2014 of the European Parliament and of the Council and repealing Council Directives 69/464/EEC, 74/647/EEC, 93/85/EEC, 98/57/EC, 2000/29/EC, 2006/91/EC and 2007/33/EC (amended 5 January 2025). – Official Journal of the European Union L 317/4. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A32016R2031 [accessed 30 April 2025]

EUROPEAN UNION (2022): Commission Implementing Regulation (EU) 2022/1203 of 12 July 2022 amending Implementing Regulation (EU) 2016/1141 to update the list of invasive alien species of Union concern. – Official Journal of the European Union L 186/10. https://eur-lex.europa.eu/eli/reg_impl/2022/1203/oj/eng [accessed 30 April 2025]

EUROPEAN UNION (2025): International trade in goods by partners. August 2025. – https://ec.europa.eu/eurostat/statistics-explained/SEPDF/cache/65099.pdf [accessed 13 April 2026]

EUROSTAT (on-line): EU imports of goods, 2002 and 2023. – https://ec.europa.eu/eurostat/statistics-explained/images/a/a4/EU_imports_of_goods%2C_2002_and_2023.png [accessed 1 May 2025]

FARR D.F., ROSSMAN A.Y. (on-line): Fungal Databases. – Systematic Mycology and Microbiology Laboratory, ARS, USDA. https://fungi.ars.usda.gov/ [accessed 30 December 2025]

FISHER M.C., GARNER T.W.J., WALKER S.F. (2009): Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. – Annual Review of Microbiology 63: 291–310. DOI: https://doi.org/10.1146/annurev.micro.091208.073435

Fontaine M.C., Gladieux P., Hood M.E., Giraud T. (2013). History of the invasion of the anther smut pathogen on *Silene latifolia* in North America. – New Phytologist 198: 946–956. DOI: https://doi.org/10.1111/nph.12177

Franić I. et al. (2019): Are traded forest tree seeds a potential source of non-native pests? – Ecological Applications 29: e01971. DOI: https://doi.org/10.1002/eap.1971

Frick W.F., Puechmaille S.J., Willis C.K.R. (2016): White-nose syndrome in bats. – In: Voigt C.C., Kingston T., eds, Bats in the Anthropocene: Conservation of bats in a changing world. pp. 245–262. Springer, Cham.

Gederaas L., Moen T.L., Skjelseth S., Larsen L.-K., eds (2012): Alien species in Norway – with the Norwegian Black List 2012. – The Norwegian Biodiversity Information Centre, Trondheim.

Ghelardini L., Santini A., Luchi N. (2022): Globalization, invasive forest pathogen species, and forest tree health. – In: Asiegbu F.O., Kovalchuk A., eds, Forest Microbiology: Volume 2: Forest Tree Health, pp. 61–76. Elsevier. London. DOI: https://doi.org/10.1016/B978-0-323-85042-1.00035-5

GISD (on-line): Global Invasive Species Database. – http://www.iucngisd.org/gisd/ [accessed 30 April 2025]

Gladieux P., Feurtey A., Hood M.E., Snirc A., Clavel J., Dutech C., Roy M., Giraud T. (2015): The population biology of fungal invasions. – Molecular Ecology 24: 1969–1986. DOI: https://doi.org/10.1111/mec.13028

Gregorová B., Černý K., Holub V., Strnadová V. (2010): Effects of climatic factors and air pollution on damage of London plane (*Platanus hispanica* Mill.). – Horticultural Science 37: 109–117.

Grosdidier M., Ioos R., Husson C., Cael O., Scordia T., Marçais B. (2018): Tracking the invasion: dispersal of *Hymenoscyphus fraxineus* airborne inoculum at different scales. – FEMS Microbiology Ecology 94: fiy049. DOI: https://doi.org/10.1093/femsec/fiy049

Gross A., Holdenrieder O., Pautasso M., Queloz V., Sieber T.N. (2014): *Hymenoscyphus pseudoalbidus*, the causal agent of European ash dieback. – Molecular Plant Pathology 15: 5–21. DOI: https://doi.org/10.1111/mpp.12073

Gross A., Petitcollin C., Dutech C., Ly B., Massot M., Faivre d'Arcier J., Dubois L., Saint-Jean G., Desprez-Loustau M.-L. (2021): Hidden invasion and niche contraction revealed by herbaria specimens in the fungal complex causing oak powdery mildew in Europe. – Biological Invasions 23: 885–901. DOI: https://doi.org/10.1007/s10530-020-02409-z

Haňáčková Z., Hrabětová M., Zíbarová L., Šafránková I., Sedlářová M., Černý K. (2023): Seznam nepůvodních hub a houbových organismů ČR [List of non-native fungi and fungus-like organisms in the Czech Republic]. – Výzkumný ústav pro krajinu, Průhonice. [in Czech]

Hansen E.M., Kanaskie A., Prospero S., McWilliams M., Goheen E.M., Osterbauer N., Reeser P., Sutton W. (2008): Epidemiology of *Phytophthora ramorum* in Oregon tanoak forests. – Canadian Journal of Forest Research 38: 1133–1143. DOI: https://doi.org/10.1139/X07-217

Haubrock P.J., Balzani P., Macêdo R., Tarkan A.S. (2023): Is the number of non-native species in the European Union saturating? – Environmental Sciences Europe 35: 48. DOI: https://doi.org/10.1186/s12302-023-00752-1

Hawksworth D., Lücking R. (2017): Fungal diversity revisited: 2.2 to 3.8 million species. – Microbiology Spectrum 5: 1–17. DOI: https://doi.org/10.1128/microbiolspec.funk-0052-2016

Helfer S. (2013): *Coleosporium* in Europe. – Mycotaxon 124: 87–99. DOI: https://doi.org/10.5248/124.87

Hietala A.M., Børja I., Solheim H., Nagy N.E., Timmermann V. (2018): Propagule pressure build-up by the invasive *Hymenoscyphus fraxineus* following its introduction to an ash forest inhabited by the native *Hymenoscyphus albidus*. – Frontiers in Plant Science 9: 1087. DOI: https://doi.org/10.3389/fpls.2018.01087

Hill M. et al. (2005): Audit of non-native species in England for nature tomorrow. – English Nature Research Reports No. 662. English Nature, Peterborough.

Holdich D.M., Reynolds J.D., Souty-Grosset C., Sibley P.J. (2009): A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. – Knowledge and Management of Aquatic Ecosystems 2009: 394–395. DOI: https://doi.org/10.1051/kmae/2009025

HRABĚTOVÁ M., MRÁZKOVÁ M., ČERNÝ K. (2023): First report of *Phytophthora occultans* causing dieback of *Buxus sempervirens* in the Czech Republic. – Plant Disease 107: 1246. DOI: https://doi.org/10.1094/PDIS-07-22-1537-PDN

IANNONE III B.V. ET AL. (2020): Invasive species terminology: standardizing for stakeholder education. – The Journal of Extension 58(3): 27. DOI: https://doi.org/10.34068/joe.58.03.27

INDERBITZIN P., BOSTOCK R.M., DAVIS R.M., USAMI T., PLATT H.W., SUBBARAO K.V. (2011): Phylogenetics and taxonomy of the fungal vascular wilt pathogen *Verticillium*, with the descriptions of five new species. – PLOS One 6: e28341. DOI: https://doi.org/10.1371/journal.pone.0028341

IRELAND K.B., HARDY G.E.S.J., KRITICOS D.J. (2013): Combining inferential and deductive approaches to estimate the potential geographical range of the invasive plant pathogen, *Phytophthora ramorum*. – PLOS One 8: e63508. DOI: https://doi.org/10.1371/journal.pone.0063508

IUCN (on-line): Invasive alien species. – https://iucn.org/our-work/topic/invasive-alien-species [accessed 30 May 2025]

JESCHKE J.M., PYŠEK P. (2018): Tens rule. – In: Jeschke J.M., Heger T., eds, Invasion biology: Hypotheses and evidence, pp. 124–132. CAB International, Wallingford.

JUNG T. ET AL. (2016): Widespread *Phytophthora* infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of *Phytophthora* diseases. – Forest Pathology: 46: 134–163. DOI: https://doi.org/10.1111/efp.12239

JUNG T. ET AL. (2020): A survey in natural forest ecosystems of Vietnam reveals high diversity of both new and described *Phytophthora* taxa including *P. ramorum*. – Forests 11: 93. DOI: https://doi.org/10.3390/f11010093

KARASCH P., HALBWACHS H., KRUSE J., RABITSCH W., NEHRING S. (2021): Pilze. – In: Rabitsch W., Nehring S., eds, Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde terrestrische Moose, Flechten und Pilze. BfN-Skripten 603. Bundesamt für Naturschutz, Bonn. [in German]

KITNER M. ET AL. (2023): Genetic structure of *Plasmopara halstedii* populations across Europe and South Russia. – Plant Pathology 72: 361–375. DOI: https://doi.org/10.1111/ppa.13666

KÖCK G. (1935): Ludwig Hecke zum Gedächtnis. – Österreichische Botanische Zeitschrift 84: 295–301. DOI: https://doi.org/10.1007/BF01256726 [in German]

KOKEŠ P., MÜLLER J. (2004): Checklist of downy mildews, rusts and smuts of Moravia and Silesia. – Czech Mycology 56: 121–148. DOI: https://doi.org/10.33585/cmy.56109

KREISEL H., SCHOLLER M. (1994): Chronology of phytoparasitic fungi introduced to Germany and adjacent countries. – Botanica Acta 107: 387–392. DOI: https://doi.org/10.1111/j.1438-8677.1994.tb00812.x

KREJZAR V., PÁNKOVÁ I. (2014): Růžová hniloba bramboru – *Phytophthora erythroseptica* [Pink rot of potato – *Phytophthora erythroseptica*]. – Rostlinolékař 25: 14–16. [in Czech]

KŘÍŽ M., ZÍBAROVÁ L., MAROUNEK D. (2015): Zajímavé lupenaté houby v pozoruhodné mykologické lokalitě u Bechlína na Roudnicku [Some interesting species of gilled mushrooms in a remarkable mycological site near Bechlín, Roudnice area]. – Mykologický sborník 92: 63–78. [in Czech]

KŘÍŽ M., ZÍTA V. (2016): First records of gasteromycete *Queletia mirabilis* in the Czech Republic. – Czech Mycology 68: 85–95. DOI: https://doi.org/10.33585/cmy.68105

LAEVENS G.C., DOLSON W.C., DRAPEAU M.M., TELHIG S., RUFFELL S.E., ROSE D.M., GLICK B.R., STEGELMEIER A.A. (2024): The Good, the Bad, and the Fungus: Insights into the relationship between plants, fungi, and oomycetes in hydroponics. – Biology 13(12): 1014. DOI: https://doi.org/10.3390/biology13121014

LOWE S., BROWNE M., BOUDJELAS S., DE POORTER M. (2000): 100 of the world's worst invasive alien species. A selection from the Global Invasive Species Database. Updated 2004. – Invasive Species Specialist Group, Auckland.

LUQUE G.M., BELLARD C., BERTELSMEIER C., BONNAUD E., GENOVESI P., SIMBERLOFF D., COURCHAMP F. (2014): The 100th of the world's worst invasive alien species. – Biological Invasions 16: 981–985. DOI: https://doi.org/10.1007/s10530-013-0561-5

Masigol H., Solbach M.D., Pourmoghaddam M.J., Ahadi R., Mostowfizadeh-Ghalamfarsa R., Taheri S.R., Tobias-Hünefeldt S.P., Bonkowski M., Grossart H.P. (2025): A glimpse into Oomycota diversity in freshwater lakes and adjacent forests using a metabarcoding approach. – Scientific Reports 15(1): 19124. DOI: https://doi.org/10.1038/s41598-025-01727-3

Marçais B., Bergot M., Pérarnaud V., Levy A., Desprez-Loustau M.L. (2004): Prediction and mapping of the impact of winter temperature on the development of *Phytophthora cinnamomi*-induced cankers on red and pedunculate oak in France. – Phytopathology 94: 826–831. DOI: https://doi.org/10.1094/PHYTO.2004.94.8.826

Martel A. et al. (2013): *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. – Proceedings of the National Academy of Sciences 110: 15325–15329. DOI: https://doi.org/10.1073/pnas.1307356110

Mieslerová B., Sedlářová M., Michutová M., Petřeková V., Cook R., Lebeda A. (2020): Powdery mildews on trees and shrubs in botanical gardens, parks and urban green areas in the Czech Republic. – Forests 11: 967. DOI: https://doi.org/10.3390/f11090967

Motiejūnaitė J., Markovskaja S., Kutorga E., Iršėnaitė R., Kasparavičius J., Kačergius A., Lygis V. (2017): Alien fungi in Lithuania: list of species, current status and trophic structure. – Botanica Lithuanica 23: 139–152. DOI: https://doi.org/10.1515/botlit-2017-0016

Mougou A., Dutech C., Desprez-Loustau M.L. (2008): New insights into the identity and origin of the causal agent of oak powdery mildew in Europe. – Forest Pathology 38: 275–287. DOI: https://doi.org/10.1111/j.1439-0329.2008.00544.x

Mrázková M., Hrabětová M., Černý K. (2025): First report of *Phytophthora pini* causing root and collar rot of *Chamaecyparis lawsoniana* and *Taxus baccata* in the Czech Republic. – New Disease Reports: 52:e70061. DOI: https://doi.org/10.1002/ndr2.70061

Mrázková M., Hrabětová M., Šetinová D., Černý K. (2022): First report of *Phytophthora nicotianae* causing root and basal stem rot of *Rosmarinus* and *Thymus* and foliar blight of *Rhododendron* in the Czech Republic. – Plant Disease 106: 2990. DOI: https://doi.org/10.1094/PDIS-08-21-1712-PDN

Mujic A.B., Policelli N., Nuñez M.A., Truong C., Smith M.E. (2023): Co-invasive ectomycorrhizal fungi alter native soil fungal communities. – Plant and Soil 484: 547–567. DOI: https://doi.org/10.1007/s11104-022-05820-8

Mułenko W., Majewski T., Ruszkiewicz-Michalska M. (2008): A preliminary checklist of micromycetes in Poland. – W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow.

Mułenko W., Piątek M., Wołczańska A., Kozłowska M., Ruszkiewicz-Michalska M. (2010): Plant parasitic fungi introduced to Poland in modern times. Alien and invasive species. – Biological Invasions in Poland 1: 43–64.

Müller J., Kokeš P. (2008): Erweitertes Verzeichnis der Falschen Mehltaupilze Mährens und tschechisch Schlesiens. – Czech Mycology 60: 91–104. DOI: https://doi.org/10.33585/cmy.60107 [in German]

Nentwig W., Bacher S., Kumschick S., Pyšek P., Vilà M. (2018): More than "100 worst" alien species in Europe. – Biological Invasions 20: 1611–1621. DOI: https://doi.org/10.1007/s10530-017-1651-6

Nuñez M.A., Dickie I.A. (2014): Invasive belowground mutualists of woody plants. – Biological Invasions 16: 645–661. DOI: https://doi.org/10.1007/s10530-013-0612-y

Ocasio-Morales R.G., Tsopelas P., Harrington T.C. (2007): Origin of *Ceratocystis platani* on native *Platanus orientalis* in Greece and its impact on natural forests. – Plant Disease 91: 901–904. DOI: https://doi.org/10.1094/PDIS-91-7-0901

Paap T., Wingfield M.J., Burgess T.I., Hulbert J.M., Santini A. (2020): Harmonising the fields of invasion science and forest pathology. – In: Wilson J.R., Bacher S., Daehler C.C., Groom Q.J., Kumschick S., Lockwood J.L., Robinson T.B., Zengeya T.A., Richardson D.M., eds, Frameworks used in invasion science. NeoBiota 62: 301–332. DOI: https://doi.org/10.3897/neobiota.62.52991

Paap T., Wingfield M.J., Burgess T.I., Wilson J.R.U., Richardson D.M., Santini A. (2022): Invasion frameworks: a forest pathogen perspective. – Current Forestry Reports 8: 74–89. DOI: https://doi.org/10.1007/s40725-021-00157-4

Palm M.E. (2001): Systematics and the impact of invasive fungi on agriculture in the United States. – BioScience 51: 141–147. DOI: https://doi.org/10.1641/0006-3568(2001)051[0141:SATIOI]2.0.CO;2

PETŘEKOVÁ V. (2018): Atlas vybraných druhů padlí (řád *Erysiphales*) v České republice [Atlas of selected powdery mildew species (order *Erysiphales*) in the Czech Republic]. – Academia, Praha. [in Czech]

PETRŽELOVÁ I., SOCHOR M. (2019): How useful is the current species recognition concept for the determination of true morels? Insights from the Czech Republic. – MycoKeys 52: 17–43. DOI: https://doi.org/10.3897/mycokeys.52.32335

PIETRAS M. (2024): Biogeography of potentially invasive non-pathogenic fungi in Europe. – In: Tomaszewski D., Jagodziński A.M., eds, Research and Practice in Forest Ecology, pp. 93–100. Kórnik.

PIMENTEL D. ET AL. (2001): Economic and environmental threats of alien plant, animal, and microbe invasions. – Agriculture, Ecosystems & Environment 84: 1–20. DOI: https://doi.org/10.1016/S0167-8809(00)00178-X

PYŠEK P. ET AL. (2020): Scientists' warning on invasive alien species. – Biological Reviews 95: 1511–1534. DOI: https://doi.org/10.1111/brv.12627

PYŠEK P. ET AL. (2022): Catalogue of alien plants of the Czech Republic (3rd edition): species richness, status, distributions, habitats, regional invasion levels, introduction pathways and impacts. – Preslia 94: 447–577. DOI: https://doi.org/10.23855/preslia.2022.447

PYŠEK P., RICHARDSON D.M. (2012): Invasive species. – In: Craig R.K., Nagle J.C., Pardy B., Schmitz O.J., Smith W.K., eds, Berkshire Encyclopedia of Sustainability 5/10: Ecosystem management and sustainability, pp. 211–219. Berkshire Publishing, Great Barrington. DOI: https://doi.org/10.2307/jj.9561413.51

PYŠEK P., SÁDLO, J., MANDÁK B. (2002): Catalogue of alien plants of the Czech Republic. – Preslia 74: 97–186.

R CORE TEAM (2021): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

RICCIARDI A., COHEN J. (2007): The invasiveness of an introduced species does not predict its impact. – Biological Invasions 9: 309–315. DOI: https://doi.org/10.1007/s10530-006-9034-4

RICHARDSON D.M., PYŠEK P., REJMÁNEK M., BARBOUR M.G., PANETTA F.D., WEST C.J. (2000): Naturalization and invasion of alien plants: concepts and definitions. – Diversity and Distributions 6: 93–107. DOI: https://doi.org/10.1046/j.1472-4642.2000.00083.x

RISTAINO J.B., GUMPERTZ M.L. (2000): New frontiers in the study of dispersal and spatial analysis of epidemics caused by species in the genus *Phytophthora*. – Annual Review of Phytopathology 38: 541–576. DOI: https://doi.org/10.1146/annurev.phyto.38.1.541

RIZZO D.M. (2005): Exotic species and fungi: interaction with fungal, plant and animal communities. – In: Dighton J., White J.F., Oudemans P., eds, The fungal community: Its organization and role in the ecosystem (3rd edn), pp. 857–877. Taylor & Francis, Boca Raton.

ROD J. (1988): Zástupci rodu *Botrytis* parazitující na cibuli kuchyňské [Species of the genus *Botrytis* parasitizing onion (*Allium cepa*)]. – Mykologické Listy 32: 10–14. [in Czech]

RODENBURG S.Y., DE RIDDER D., GOVERS F., SEIDL M.F. (2024): Oomycete metabolism is highly dynamic and reflects lifestyle adaptations. – Molecular Plant-Microbe Interactions 37(7): 571–582. DOI: https://doi.org/10.1094/MPMI-12-23-0200-R

ROY D. ET AL. (2020): DAISIE (Delivering Alien Invasive Species Inventory for Europe) – Inventory of alien invasive species in Europe. Version 1.7. – Research Institute for Nature and Forest (INBO), Brussels. DOI: https://doi.org/10.15468/ybwd3x

ROY H.E. ET AL. (2012): Non-native species in Great Britain: establishment, detection and reporting to inform effective decision making. – Report to Defra, NERC Centre for Ecology & Hydrology.

SAMEK M., NOVOTNÝ P., MODLINGER R., FULÍN M., BERAN F., ROY A., PEŠKOVÁ V. (2019): Impact of *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii* on the selection of suitable provenances of Douglas fir in Central Europe. – Forests 10: 204.

SANDVIK H. ET AL. (2019): Alien plants, animals, fungi and algae in Norway: an inventory of neobiota. – Biological Invasions 21: 2997–3012. DOI: https://doi.org/10.1007/s10530-019-02058-x

SANDVIK H. ET AL. (2020): Alien species in Norway: Results from quantitative ecological impact assessments. – Ecological Solutions and Evidence 1(1): e12006. DOI: https://doi.org/10.1002/2688-8319.12006

SANTINI A. ET AL. (2013): Biogeographical patterns and determinants of invasion by forest pathogens in Europe. – New Phytologist 197: 238–250. DOI: https://doi.org/10.1111/j.1469-8137.2012.04364.x

SCHERTLER A. ET AL. (2024): Biogeography and global flows of 100 major alien fungal and fungus-like oomycete pathogens. – Journal of Biogeography 51: 599–617. DOI: https://doi.org/10.1111/jbi.14755

SCHWARTZ M.W., HOEKSEMA J.D., GEHRING C.A., JOHNSON N.C., KLIRONOMOS J.N., ABBOTT L.K., PRINGLE A. (2006): The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. – Ecology Letters 9: 501–515. DOI: https://doi.org/10.1111/j.1461-0248.2006.00910.x

SEDLÁŘOVÁ M., MIESLEROVÁ B., DRÁBKOVÁ TROJANOVÁ Z., LEBEDA, A. (2021): Biotrofní houby a peronospory planě rostoucích rostlin [Biotrophic fungi and downy mildews of wild-growing plants]. – Česká fytopatologická společnost, Praha. [in Czech]

SEDLÁŘOVÁ M., ONDRYÁŠ S. (2023): Původci mykóz rostlin na území přírodní rezervace Plané loučky [Causal agents of plant mycoses in the Plané loučky Nature Reserve]. – Zprávy Vlastivědného muzea v Olomouci 325: 69–78. [in Czech]

SEEBENS H. ET AL. (2017): No saturation in the accumulation of alien species worldwide. – Nature Communications 8: 1–9. DOI: https://doi.org/10.1038/ncomms14435

SHORT D.P., GURUNG S., GLADIEUX P., INDERBITZIN P., ATALLAH Z.K., NIGRO F., LI G., BENLIOGLU S., SUBBARAO K.V. (2015): Globally invading populations of the fungal plant pathogen *Verticillium dahliae* are dominated by multiple divergent lineages. – Environmental Microbiology 17: 2824–2840. DOI: https://doi.org/10.1111/1462-2920.12789

SIKES B.A., BUFFORD J.L., HULME P.E., COOPER J.A., JOHNSTON P.R., DUNCAN R.P. (2018): Import volumes and biosecurity interventions shape the arrival rate of fungal pathogens. – PLOS Biology 16: e2006025. DOI: https://doi.org/10.1371/journal.pbio.2006025

SOTO I. ET AL. (2024): Taming the terminological tempest in invasion science. – Biological Reviews 99(4): 1357–1390. DOI: https://doi.org/10.1111/brv.13071

SUBBARAO K.V. (2020): *Verticillium dahliae* (verticillium wilt). – CABI Compendium. CAB International, Wallingford. https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.56275 [accessed 31 December 2023]

SZCZEPKOWSKI A., GIERCZYK B., KUJAWA A. (2014): Greenhouses of botanical gardens as a habitat of alien and native macrofungi: a case study in Poland. – Central European Journal of Biology 9: 777–795. DOI: https://doi.org/10.2478/s11535-014-0310-5

ŠEVČÍKOVÁ H., DIMA B. (2021): Variability and distribution of *Pluteus luteus*, a later synonym of *P. variabilicolor*. – Mycotaxon 136: 201–213. DOI: https://doi.org/10.5248/136.201

ŠTOCHLOVÁ P., NOVOTNÁ K., ČERNÝ K. (2016): Variation in *Alnus glutinosa* susceptibility to *Phytophthora ×alni* infection and its geographic pattern in the Czech Republic. – Forest Pathology 46: 3–10. DOI: https://doi.org/10.1111/efp.12205

TAYLOR J.W., TURNER E., TOWNSEND J.P., DETTMAN J.R., JACOBSON D. (2006): Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. – Philosophical Transactions of the Royal Society B 361: 1947–1963. DOI: http://doi.org/10.1098/rstb.2006.1923

THAKUR M.P., VAN DER PUTTEN W.H., COBBEN M.M.P., VAN KLEUNEN M., GEISEN S. (2019): Microbial invasions in terrestrial ecosystems. – Nature Reviews Microbiology 17: 621–631. DOI: https://doi.org/10.1038/s41579-019-0236-z

TRAGUST S., FELDHAAR H., ESPADALER X., PEDERSEN J.S. (2015): Rapid increase of the parasitic fungus *Laboulbenia formicarum* in supercolonies of the invasive garden ant *Lasius neglectus*. – Biological Invasions 17: 2795–2801. https://doi.org/10.1007/s10530-015-0917-0

TURNER R.S. (2005): After the famine: plant pathology, *Phytophthora infestans*, and the late blight of potatoes, 1845–1960. – Historical Studies in the Physical and Biological Sciences 35: 341–370. DOI: https://doi.org/10.1525/hsps.2005.35.2.341

URBAN Z., MARKOVÁ J. (2009): Catalogue of rust fungi of the Czech and Slovak Republics. – Karolinum, Praha.

VANNINI A., FRANCESCHINI S., VETTRAINO A.M. (2012): Manufactured wood trade to Europe: a potential uninspected carrier of alien fungi. – Biological Invasions 14: 1991–1997. DOI: https://doi.org/10.1007/s10530-012-0222-0

VEERABAHU A., BANIK M.T., LINDNER D.L., PRINGLE A., JUSINO M.A. (2025): Invasive golden oyster mushrooms are disrupting native fungal communities as they spread throughout North America. – Current Biology 35: 3994–4002. DOI: https://doi.org/10.1016/j.cub.2025.06.049

VETTRAINO A., ROQUES A., YART A., FAN J.T., SUN J.H., VANNINI A. (2015): Sentinel trees as a tool to forecast invasions of alien plant pathogens. – PLoS One 10: e0120571. DOI: https://doi.org/10.1371/journal.pone.0120571

VILJANEN-ROLLINSON S.L.H., CROMEY M.G. (2002): Pathways of entry and spread of rust pathogens: implications for New Zealand's biosecurity. – New Zealand Plant Protection 55: 42–48. DOI: https://doi.org/10.30843/nzpp.2002.55.3911

VLK L. ET AL. (2020): Alien ectomycorrhizal plants differ in their ability to interact with co-introduced and native ectomycorrhizal fungi in novel sites. – The ISME Journal 14: 2336–2346. DOI: https://doi.org/10.1038/s41396-020-0692-5

VOGLMAYR H., KRISAI-GREILHUBER I. (2002): Pilze. – In: Essl F., Rabitsch W., eds, Neobiota in Österreich, pp. 181–195. Umweltbundesamt, Wien. [in German]

VOGLMAYR H., RIETHMÜLLER A. (2006): Phylogenetic relationships of *Albugo* species (white blister rusts) based on LSU rDNA sequence and oospore data. – Mycological Research 110: 75–85. DOI: https://doi.org/10.1016/j.mycres.2005.09.013

VOGLMAYR H., SCHERTLER A., ESSL F., KRISAI-GREILHUBER I. (2023): Alien and cryptogenic fungi and oomycetes in Austria: an annotated checklist (2nd edition). – Biological Invasions 25: 27–38. DOI: https://doi.org/10.1007/s10530-022-02896-2

VOJAR J., SOLSKÝ M., BALÁŽ V., JEŘÁBKOVÁ L. (2021): Výskyt patogenní plísně *Batrachochytrium dendrobatidis* v rámci evropsky významných lokalit našich obojživelníků [The presence of pathogenic fungus *Batrachochytrium dendrobatidis* within Czech amphibian Sites of Community Importance]. – Příroda 42: 33–44. [in Czech]

WERRES S., MARWITZ R., MAN IN'T VELD W.A., DE COCK A.W.A.M., BONANTS P.J.M., DE WEERDT M., THEMANN K., ILIEVA E., BAAYEN R.P. (2001): *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. – Mycological Research 105: 1155–1165. DOI: https://doi.org/10.1016/S0953-7562(08)61986-3

WINGFIELD M.J., SLIPPERS B., ROUX J., WINGFIELD B.D. (2001): Worldwide movement of exotic forest fungi, especially in the tropics and the southern hemisphere. – BioScience 51: 134–140. DOI: https://doi.org/10.1641/0006-3568(2001)051[0134:WMOEFF]2.0.CO;2

WINGFIELD M.J., SLIPPERS B., WINGFIELD B.D., BARNES I. (2017): The unified framework for biological invasions: a forest fungal pathogen perspective. – Biological Invasions 19(11): 3201–3214. DOI: https://doi.org/10.1007/s10530-017-1450-0

WITTENBERG R., COCK M.J.W. (2001): Invasive alien species: a toolkit for best prevention and management practices. – CAB International, Wallingford.

WYLDER B., BIDDLE M., KING K., BADEN R., WEBBER J. (2018): Evidence from mortality dating of *Fraxinus excelsior* indicates ash dieback (*Hymenoscyphus fraxineus*) was active in England in 2004–2005. – Forestry 91: 434–443. DOI: https://doi.org/10.1093/forestry/cpx059

ZÝKA V., ČERNÝ K., STRNADOVÁ V., ZAHRADNÍK D., HRABĚTOVÁ M., HAVRDOVÁ L., ROMPORTL D. (2018): Predikce poškození porostů smrku pichlavého kloubnatkou smrkovou v Krušných horách [Prediction of damage to *Picea pungens* stands caused by *Gemmamyces piceae* in the Ore Mountains]. – Výzkumný ústav pro krajinu a okrasné zahradnictví, Průhonice. [in Czech]