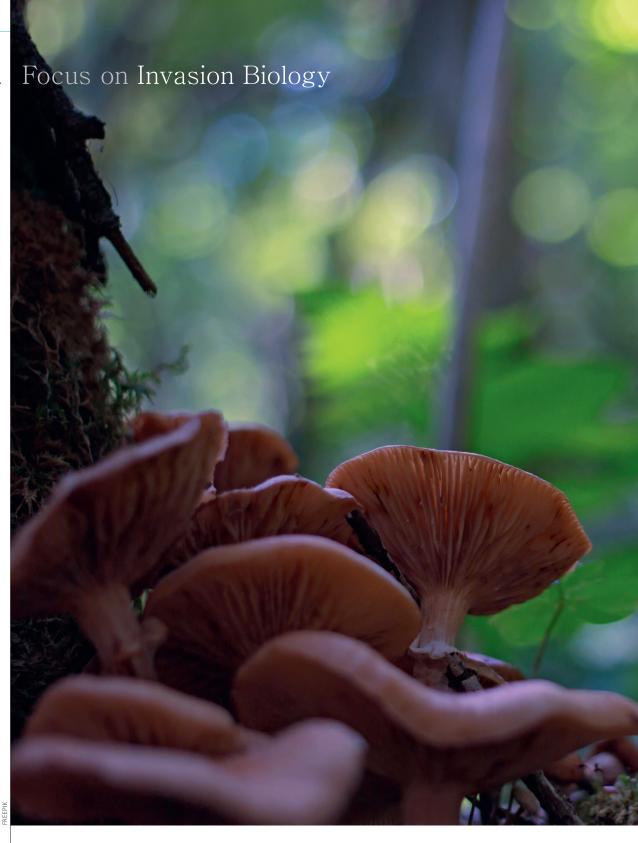
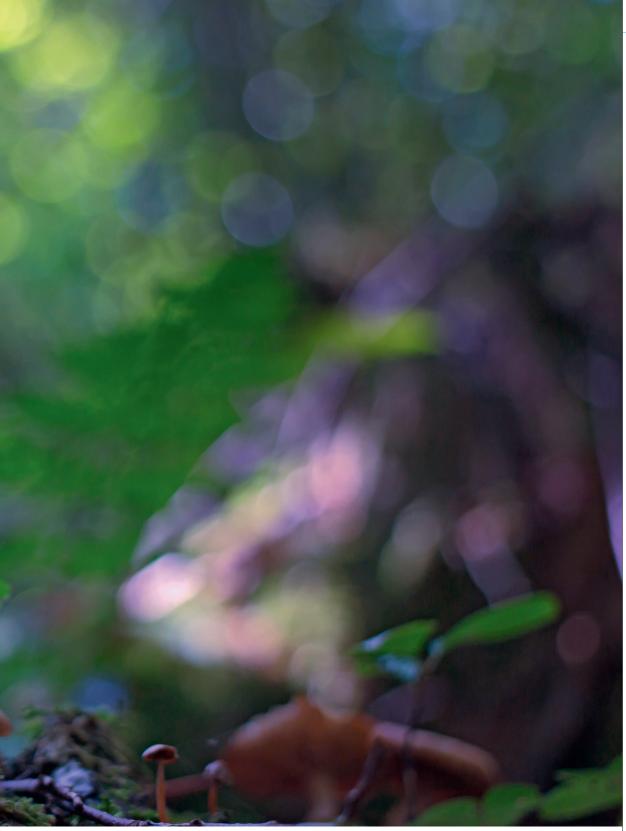
ACADEMIA



ALIENS AMONG US





Dr. Marcin Pietras (PhD)

is an Assistant Professor at the Laboratory of Symbiotic Associations of the PAS Institute of Dendrology. His research focuses on issues related to nature protection, in particular the occurrence and invasion of alien fungi and woody plants.

mpietras@man.poznan.pl

What happens in the world of fungi when a stranger appears in their midst?
What broader impact does such a "fungal invader" exert as it takes up living space and resources?

# Focus on Invasion Biology

An oak forest declining due to Phytophthora oomycetes, Piaski Forest District, 2010



#### **Marcin Pietras**

Institute of Dendrology, Polish Academy of Sciences, Kórnik

he forest is replete with thousands of different organisms, creating the most complex network of interconnections that can exist in nature. In forest ecosystems, fungi, which are some of the most ecologically and evolutionarily diverse organisms in the world, play a key role. It is estimated that the fungal kingdom has over 5 million species, making the fungi the second largest group of organisms on Earth behind insects. Fungi play a fundamental role in the functioning of entire ecosystems. They may live at the expense of others, as plant, animal or human pathogens. Many fungi, on the other hand, are saprotrophs, or organisms that break down organic matter, which are considered to be major soil decomposers.

Other fungi establish mycorrhizal symbiosis with plants, including trees, helping them develop and grow. Fungi are key organisms in the carbon cycle, at every level of biological system complexity, from the plant, through the ecosystem, even to the biome (a large region with similar climatic conditions and vegetation). At each of these levels, fungi interact with each other, competing for resources and space. In addition, they are part of a complicated dependency network with plants and animals, creating a specific status quo between organisms living together. This dependency network is not durable or stable because it must respond to changes in the environment. These changes are often natural and are a permanent part of shaping many ecosystems. Others are related to human activity, which directly or indirectly affects processes occurring in many ecosystems, including forests. In the Anthropocene, the age of man, nature must additionally face another serious threat, which is the presence of foreign or invasive organisms, such as plants, animals or fungi that have intentionally or accidentally been transported out of their natural environment. In their new location, these foreign organisms may change the structure and species composition of native biocoenoses, which is particularly evident in complex forest ecosystems.

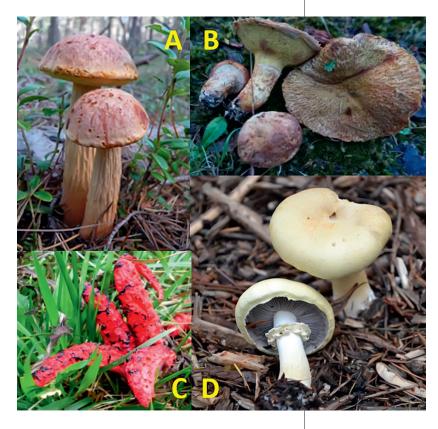
### A matter of life and death

It is a popular belief that some of the main problems of modern nature protection are foreign, often invasive organisms. With regards to fungi, most of the current research is focused on the process of introducing non-native species of pathogens into a given biocenosis, in the case of plants, animals, as well as humans. Pathogenic organisms usually occur in new areas by accident, and their presence can have important economic and even social consequences. The best example is the introduction of the oomycete Phytophthora infestans to Ireland in the mid-nineteenth century, which causes phytophthorosis, commonly known as potato blight disease. The appearance of this organism in Ireland caused the greatest famine in world history, during which one and a half million Irish people died and millions emigrated. Currently on the list of the "one hundred most invasive organisms" is another oomycete, Phytophthora cinnamomi, which kills many tree species. Phytophthora oomycetes occur naturally in the forests of the Northern Hemisphere, in North America and Europe. The introduction of P. cinnamomi, a species most likely originating in South Asia, into new areas very often leads to rapid changes in forest ecosystems, the most tragic of which is the massive forest decline. This process is observed throughout the world, both in temperate and tropical forests. In Europe, P. cinnamomi attacks most tree species, especially chestnut and various species of oak. Warm winters, as well as alternative periods of drought and excess soil water, contribute to the occurrence of this pathogen, which causes major losses worldwide, not only in economic terms with the loss of raw material in production forests, but mainly ecological, destroying the habitats for thousands of organisms in endangered forests.

The list of the "one hundred most invasive organisms" also includes a fungal pathogen that has become a real threat to many elm species over the last several decades. Ophiostoma novo ulmi (which causes Dutch elm disease) is a fungi with a mysterious history and complex biology. The earliest reports on the dieback of elms appeared at the beginning of the 20th century. At that time the pathogenic fungus causing this phenomenon was classified as Ophiostoma ulmi. It is estimated that 10-40% of all elm trees in Europe and North America died at that time. In the 1950s, a new species of fungi of unknown origin, O. novo ulmi, was discovered, which attacked elm trees in North America with even greater force. In the 1960s this fungi was introduced to Great Britain and over a course of several years nearly completely wiped out the mountain elm in southern England. Scolytus, small bark beetles, are the sole vectors transmitting the fungus to new areas, and thus contribute to the spread of Ophiostoma fungi. Currently, both O. novo ulmi and O. ulmi are mainly found in the Northern Hemisphere, but have also been found in New Zealand, and pose a great threat to many species of elm.

### Silent newcomers

Pathogenic fungi are not the only organisms that spread to new areas. Unlike pathogens, non-pathogenic fungi, under adverse conditions, can exist as mycelium in the soil, without appearing as a fruiting



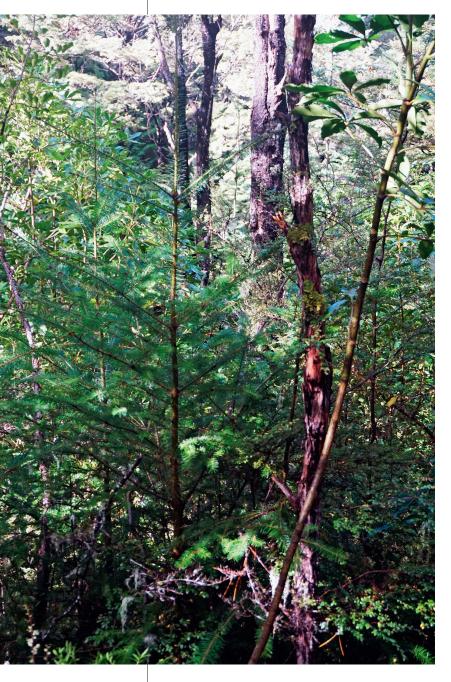
body. There have been cases of both intentional and accidental spreading of fungi that do not cause diseases. Stropharia rugosoannulata, also known as the wine cap stropharia, was introduced to Europe from North America in the mid-twentieth century for cultivating purposes. This fungus, although belonging to the Strophariaceae family, is a distant relative of our cultivated portobello mushrooms. Like them, it can be grown under controlled conditions, but it is not a high requirement species when it comes to the substrate. It usually has large, impressive sporocarps that grow in clusters even on sawdust or other organic substrates with a high content of cellulose and lignin. The wine cap stropharia never conquered Europe and never threatened the common mushroom as the preferred food of Europeans, but thanks to its great adaptability it escaped from the farm and is now found in home gardens all over Europe.

The fungus *Clathrus archeri*, also known as the devil's fingers, has had a completely different journey. Resembling a red flower or an octopus, it is native to Australia and New Zealand. It was introduced to Europe at the beginning of the 20th century on the boots of Australian soldiers fighting in World War I, or perhaps slightly earlier, with transports of Australian wool. This is an example of an accidental introduction of fungi to new areas. Over the last century *Clathrus archeri* has thrived in Europe, appearing numerous times mainly in man-made areas, parks and gardens, but also on forest edges, always on fertile, humus-rich

Foreign fungi found in Polish forests: the North American bolete Aureoboletus projectellus (A), the western painted Suillus (Suillus lakei) (B), the devil's fingers (Clathrus archeri) (C), the wine cap Stropharia (Stropharia rugosoannulata) – yellow variety (D)

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# Focus on Invasion Biology



A young Douglas Fir growing in virgin Nothofagus forest, Mount Richmond Park, South Island, New Zealand, 2017 soils. In Poland, it was first discovered in the 1970s and since then it has appeared in our country on 120 occasions, each year increasingly frequently in the northeast. For comparison, in Australia and New Zealand, where it occurs naturally, it is considered to be a rare species with only 80 records. We can certainly consider Clathrus archeri to be the most common species of alien non-pathogenic fungus in Europe. What's more, it has also been found in North America, and recently also in South America.

These examples show how easily newcomers from other continents are able to adapt and spread to new areas. How do they do it and what is their impact on the native mycobiota (world of fungi)? Undoubtedly,

alien species of saprotrophic fungi compete with native species for resources, thanks to which they can create a tangled network of mycelium in soil, as well as fruiting bodies, and spread millions of spores, which are then carried to new areas. Although there is no evidence yet of such competition, it seems obvious and its consequences are easily predictable. Studies conducted on other foreign, often invasive organisms, show that their success lies in winning the fight for resources and living space, modifying their living environment to adapt to changes unfavorable to other organisms, as well as significant reproductive success. Most likely we can expect the same to happen in the case of non-pathogenic alien fungi.

Thus, these silent newcomers from distant America or Australia should be treated as a threat to our native European mushrooms.

## Till death do us part

The spread of saprotrophic fungi in new areas does not require the presence of any other organism. Very often alien fungi need certain species of trees in order to acclimatize. This is the case with symbiotic fungi, which create mycorrhizal symbiosis with trees. To put it simply, this symbiotic fungi-tree association involves a two-way exchange of substances between partners. The fungus helps the plant get minerals and water, in return obtaining products created by photosynthesis in the treetops. The contact between the fungus and the plant occurs at the small roots of trees, which grow entwined with and colonized by mycelium hyphae to become mycorrhizae. The root system of a single tree has billions of mycorrhizae created by hundreds of different species of fungi. In addition, certain tree species are better suited to specific species or groups of fungi. That is why boletus mushrooms grow under pine trees, scaber stalks are found near birches, and the tastiest milk caps grow under firs. In the case of alien species of fungi, this relationship very often determines the range of spread and invasiveness of associated plants. This is known as co-introduction, or the simultaneous transfer of a tree along with its fungi symbionts. In the new area, the fungus and the plant are inseparable and spread together through the new environment.

There are many examples of such co-introduction. Suillus lakei, a mushroom that is known as the western painted Suillus and is closely related to the Douglas fir, was transported along with such firs outsideits natural habitat from western North America to New Zealand, Europe and South America. In Europe, Rhizopogon luteolus is occurs more frequently with the Eastern white pine. Fungi being transported along with their plant partners is the most common way symbiotic species spread. For plants, ectomycorrhizal symbioses with fungi is considered beneficial and desirable as it helps

them properly grow and develop. Symbiotic fungi, however, can cause significant negative effects on entire ecosystems. It has been proven that replacing natural plant communities with fast-growing tree plantations causes rapid changes in soil chemistry. The cultivation of Radiata pine in the grasslands of South America caused a sharp, nearly 30 percent decline in soil carbon content. The culprit turned out to be alien fungi, brought along with pine trees and introduced into the environment.

In turn, symbiotic fungi support the spread of the alien tree species to which they are linked. This means that certain tree species do not exhibit invasive behavior, but do become invasive only when their mycorrhizal partners are transported along with them. In New Zealand it was found that the Douglas fir originating in North America is linked to a European fungus, which is transported by an Australian marsupial, the common brushtail possum. This telling example, involving organisms from three different kingdoms (plant, animal, and fungi) and three different continents supporting each other's expansion, highlights the unpredictable consequences of transporting foreign organisms to new territories around the world.

### Let's be friends

Mycorrhizal fungi are transported much less often, regardless of the trees they are linked to. These fungi do not attach as well to their plant partners and often create new mycorrhizal relationships with trees with which it would not be able to do so under normal conditions due to geographical barriers. They also have a greater ability to spread within their new range. The European Amanita phalloides, also called the death cap, has permanently linked itself with many North American species of pine and oak, becoming a common fungus in the eastern United States. It has also spread to Australia and New Zealand, where it has poisoned many mushroom pickers, some even fatally. In recent years, a newcomer from America, Aureoboletus projectellus, has caused a sensation in Polish forests, where it has "madefriends" with our Scots pine. This edible bolete has turned up in Europe, being reported in Lithuania in 2011 and Poland in 2016. It can now be found not only on the shore of the Baltic Sea, where it appeared for the first time, but also inland. It has become a great attraction for mushroom pickers in coastal forests, with the outcome that in recent years thousands of fruiting bodies of this mushroom picked in coastal forests have been spread throughout Poland.

## Fungi in the light of changes

Fungi are some of the most evolutionarily diverse organisms in the world with hundreds of species found in various ecosystems. They exhibit enormous ada-

ptability to changing conditions, including climatic conditions. The fungal world never stops evolving. When certain species subside, others, better adapted to new conditions, immediately appear. Climate change, however, can be a threat to fungi, mainly by taking away their habitats and killing off their partner trees. As with plants, alien fungi species can end up benefitting from climate change. The destruction of forests caused by invasive pathogenic fungi has intensified in recent years, becoming a global problem. Foreign saprotrophic fungi, such as the thermophilic devil's fingers or the drought-withstanding wine cap Stropharia, significantly increase the acreage in which they occur outside their natural habitat. Symbiotic species support invasive tree species that colonize and change new areas. Climate models made for individual fungi species for the next century show that climate change will be their great ally.

Therefore, we can easily imagine a reality in which invasive pathogenic fungi will contribute to the mass decline of Poland's native forests. This has been occur-

Fungi are some of the most evolutionarily diverse organisms in the world, with hundreds of species found in various ecosystems.

ring since the 1990s and proves that a warming climate will be a factor in the dying out of forests, initiated by short-term drought or floods. This will weaken the forests and make them more susceptible to fungal pathogens, which will thrive in the same changing conditions. In many other places we will observe the expansion of invasive tree species, additionally supported by foreign symbiotic fungi. Saprotrophic fungi can also become more frequent, which, hidden deep in the soil, will gradually change our native ecosystems. As a consequence, native plant communities may be spontaneously and gradually replaced with artificial communities. In the longer term, this may contribute to the decline of native flora and fauna, along with particularly valuable endemic species. All this can have a disastrous effect on the conservation of biodiversity. Unfortunately, having observed the rapid changes and their catastrophic effects in recent years we can surmise that when it comes to environmental protection we can expect the worst-case scenarios to come true.

PHOTOGRAPHY BY MARCIN PIETRAS