

# Molecular Identification of Fungi

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1st Edition. 2010. Buch. xxii, 501 S. Hardcover

ISBN 978 3 642 05041 1

Format (B x L): 15,5 x 23,5 cm

Gewicht: 1037 g

[Weitere Fachgebiete > Chemie, Biowissenschaften, Agrarwissenschaften > Entwicklungsbiologie > Molekularbiologie](#)

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# Chapter 1

## Fungal Pathogens of Plants in the Holocene

George Newcombe and Frank M. Dugan

**Abstract** As the pace of biotic homogenization has accelerated over time, the threat of novel phytopathogens has become a question of growing importance for mycologists and plant pathologists. Meanwhile, this question is but one of a whole set of related questions that invasion biologists are attempting to answer. Pathogen release is of interest to both sets of scientists because it provides a measure of the extent to which previously isolated mycobiotas have undergone cryptic homogenization, and at the same time it is the basis for a promising hypothesis to explain plant invasions. We argue that only a fraction of all first encounters between novel pathogens and evolutionarily naive plants could result in susceptible outcomes. This is analogous to the fact that only a fraction of all plant introductions result in plant invasions.

### 1.1 Introduction

Geologists define the last 10,000 years, or our current epoch, as the Holocene (Bishop 2003). What has been described as the “Neolithic Revolution” also dates from 10,000 years ago (Wells 2007). Spurred by early developments in crop domestication in regions such as the Fertile Crescent (Wells 2007), Neolithic farmers began to move to and settle in new areas with their crops ten millennia ago (Vaughan et al. 2007). What was no doubt at first gradual and local ultimately became global. Human migrations and population expansions during the Holocene are mixing the previously isolated biotas of the world at an accelerating pace (Mooney and Cleland 2001). Organisms outside their native ranges bear many

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descriptors: non-native, nonindigenous, exotic, introduced, or alien. Non-native pathogens are additionally called “novel.” Some non-native organisms have proven invasive, and invasion biologists have begun to describe the latter part of our epoch as the Homogocene a term coined by Gordon Orians (Rosenzweig 2001a). This term invokes the global scope and increasing rate of anthropogenic, *biotic homogenization* that is defined as the “gradual replacement of native biotas by locally expanding non-natives” (Olden et al. 2004). The consequences of homogenization for biotic communities and ecosystem processes are the subject of a growing research effort; here we focus on fungal pathogens in the Homogocene.

Unsurprisingly, most of the literature of invasion biology focuses on plants and animals (Pyšek et al. 2006), leaving mycologically oriented ecologists to wonder about fungi. Crop pathogens are of course exceptional in this regard as they are often discussed in the phytopathological literature (Rossman 2009; Stukenbrock and McDonald 2008) and lists of such pathogens that are thought to be non-native are frequently compiled (Madden 2001). The most famous historical example is arguably the pseudo-fungus (oomycete) associated with the Irish potato famine, *Phytophthora infestans*. Both the host and pathogen probably originated from the Andes (Gómez-Alpizar et al. 2007), and their reunion in Ireland proved disastrous both for the crop and the people who depended on it. Other examples include black Sigatoka and yellow Sigatoka of banana (causal agents *Mycosphaerella musicola* and *M. fijiensis*, respectively). In these cases, the host is from Southeast Asia, and this may also be true for these fungi that were nevertheless first documented in Fiji; both diseases now constitute global epidemics on banana (Marín et al. 2003). Other instances from agriculture are concisely mentioned here and there in what follows.

However, this review emphasizes examples of plants from natural plant communities (i.e., nonagricultural settings). Chestnut blight and white pine blister rust (discussed below) are widely investigated, but we present many other instances much less familiar to the scientific public. We believe that a careful examination of the behavior of fungal phytopathogens in the Homogocene reveals ecologically significant patterns. These patterns should be of as much interest to invasion biologists and ecologists as they are to mycologists and plant pathologists, because fungi influence plants even while going unnoticed.

Voyaging peoples have likely always brought useful and favored plants and animals with them to be deliberately introduced to new lands that they encountered. Before Captain Cook landed in Hawaii in 1778, Polynesian seafarers had already discovered these remote, volcanic islands and introduced such plants as candlenut (*Aleurites moluccana*), ti (*Cordyline fruticosa*), taro (*Colocasia esculenta*), sweet potato (*Ipomoea batatas*), sugarcane (*Saccharum officinarum*), and perhaps two dozen other species (Carlquist 1980). Such early plant introductions were certainly not limited to Polynesia, or to plants brought with European colonists to the New World. Plant-hunting expeditions were probably initiated as early as 3,000 years before Columbus, as hieroglyphs appear to show that the Queen of Egypt sent out collectors of exotic plants for her gardens (Baskin 2003). Mycologists know that at least some endophytic and phytopathogenic fungi must have quietly accompanied these plant introductions (Palm 1999, 2001; Palm and Rossman 2003). But what can we say today about these co-introductions and their effects on Hawaiian

and other ecosystems around the world? Were those co-introduced endophytes so host-specific that we can be sure that they remained exclusive to their original hosts? If they jumped to other hosts, presumably related ones (Gilbert and Webb 2007), what ecological effects might they have had, and how can we distinguish them today from co-evolved interactions?

These questions go well beyond Hawaii, and include all fungi globally. Maritime explorations by western Europeans that began in the early fifteenth century (Love 2006) were initially restricted in scope, but they gradually became global and much more ambitious. Scientific travelers such as Alexander von Humboldt, Charles Darwin, and Alfred Russell Wallace began in the nineteenth century to discover how life's diversity was distributed around the world. At the same time, plant explorers of many nationalities were seeking to deliberately introduce desirable plants to their home countries (Reichard and White 2001). Crop plants had already been introduced almost everywhere that they would grow profitably; Columbus, for example, wasted no time in introducing one of the most important New World domesticates, maize, into Europe in 1493 (Rebourg et al. 2003); during the same year Columbus introduced orange trees of Asian origin to Hispaniola (Houghton 1978).

Ten thousand years ago, homogenization was undoubtedly not occurring at modern rates, although it had probably been initiated on local or regional scales. So, the Homogocene cannot be said to have begun with the Holocene. Instead, 1500 would appear to be a good year to choose for the beginning of the Homogocene. This date is also in agreement with the judgment of ecological, economic, and social historians, whose titles or subtitles accordingly include phraseology suggestive of worldwide movement of goods and peoples beginning at this time, e.g., "Accumulation on a World Scale," "Expansion of Europe," "Modern World-System," etc. (Amin 1974; Crosby 2004; Wallerstein 1974, 1980, 1989). Five hundred and nine years ago, the "Age of Discovery" was under way, and today, deliberate plant introductions are so common that the "majority of woody invasive plants in the United States were introduced for horticultural purposes – one study found that 82% of 235 woody plant species identified as colonizing outside of cultivation had been used in landscaping" (Reichard and White 2001). The "Homogocene" may not yet be a serious term in science but it does simply and directly evoke global commingling during the last half a millennium.

Plant-oriented invasion biologists in Europe already use 1500 to divide alien plants (Pyšek et al. 2004) into those that are called "archaeophytes" if introduced before 1500, and "neophytes" if introduced later. However, we hasten to make explicit what we have already hinted at: migration or purposeful import of plant materials well prior to 1500 probably made important contributions to homogenization on a regional, and sometimes even continental or oceanic, scale. In addition to the example of Polynesia above, expansion of Neolithic farming cultures such as the Arawak (from the upper Amazon and Orinoco basins to the West Indies), Bantu (from western to southern Africa), and Indo-European (from a still disputed location, perhaps Anatolia or the European steppes, but eventually throughout Europe and much of western and central Asia) moved plant materials considerable distances (Diamond and Bellwood 2003). Pronounced effects have been postulated for movement of plant pests and diseases in these distant times, e.g., the "honeymoon

hypothesis” of a comparatively pest- and disease-free agriculture in Neolithic Europe (Dark and Gent 2001), or the introduction of *Ascochyta* blight of chickpea, resulting in summer cropping systems in the Levant (Abbo et al. 2003). Literature on movement of plant pathogenic fungi from the Neolithic through classical antiquity has been summarized recently (Dugan 2008). Archaeobotanical or text-based analyses are particularly numerous for tracing the complex introduction of crops into medieval Europe (Behre 1992; Campbell 1988; Harvey 1984, 1992; Kroll 2005; Preston et al. 2004; Taavitsainen et al. 1998).

Introduced plants are not all equal ecologically. Introduced or alien plants can become naturalized if they survive and regularly reproduce outside of cultivation (Richardson et al. 2000b). Of course, only a small fraction of introduced plants become naturalized. For example, in Florida, of approximately 25,000 non-native or alien plant species, only 900 have become naturalized (Pimentel et al. 2005). A further winnowing occurs as only a small fraction of naturalized species become invasive, with invaders defined as species that have successfully spread away from sites of introduction (Richardson et al. 2000b). These successive winnowings characterize what is called the “tens rule” (Williamson and Fitter 1996), a rule of thumb that reflects the fact that relatively few aliens become invaders (Kolar and Lodge 2001). Plant and community ecologists are keenly interested in understanding this phenomenon.

In this chapter, we shall see how well concepts and definitions borrowed from invasion biology might apply to fungi, especially fungal pathogens of plants. Is there a “tens rule” for fungal pathogens, or are all alien fungal pathogens equally likely to attack evolutionarily naive plants or a host from which they had been separated? In describing the plants and pathogens that take part in “first encounters” as evolutionarily “naive” and “novel,” respectively, we are following the example of Parker and Gilbert (2004). If the “tens rule” does apply, do we have, or can we develop, hypotheses to predict which fungal pathogens will naturalize and which will become invaders? The threat of fungi as novel pathogens is a traditional topic for plant pathologists and mycologists (Rossman 2001). But, apart from the notorious example of chestnut blight, do novel pathogens generally act as “transformers” that “change the character, condition, form or nature of ecosystems over a substantial area” (Pyšek et al. 2004)? What are the roles of fungi as potential facilitators of plant invasions in the Holocene? Recognizing and predicting invasions are the central objectives of invasion biology (Kolar and Lodge 2001). But both objectives seem to be predicated on knowing the native, geographic ranges of the organisms in question, a problematic area for mycology.

## 1.2 Native Ranges of Fungi

In the eighteenth century, the French naturalist, Georges Buffon, had observed that different continents had different assemblages of macrobes (i.e., plants and animals) (Cox and Moore 2005). In the nineteenth century, Humboldt had

discovered the predictability of species–area relationships in that larger areas held more species (Rosenzweig 1995), but again this was known to apply only to macrobes. Spatial scaling and diversification of fungi were little studied until recently when species-area relationships of fungi were demonstrated to be similar to those of macrobes (Green et al. 2004). This was not a trivial finding because even today some microbiologists maintain the view that microbial eukaryotes have global ranges (Fenchel and Finlay 2004). The views of Beijerinck, that species of bacteria were cosmopolitan, or of Baas-Becking, that “everything is everywhere” (Fenchel and Finlay 2004), have also been challenged recently by application of the sequence-based phylogenetic species concept of fungi (Taylor et al. 2006).

Mycologists are now learning that most fungi do conform to Buffon’s Law and to spatial scaling rules for macrobes. However, it does not follow that it will be easy to determine the native ranges of those fungi that do conform, for reasons that will be discussed. And then there are undoubtedly fungi that do not conform. For example, some saprophytic hyphomycetes, such as common *Cladosporium* species, are associated with a very broad range of substrata. Such species do indeed seem to have cosmopolitan distributions as evidenced by their incorporation over long time periods into Arctic ice, alpine glaciers, and permafrost throughout the Northern Hemisphere (summarized in Dugan 2008).

Macrobiologists may be surprised to learn that the native ranges of fungi are largely unknown. Yet, how could it be otherwise? Today, 83% and 90% of vascular plants and vertebrates, respectively, are known to macrobiologists, whereas, at best, from 7% to perhaps 20% of the fungi are presently described (Cox and Moore 2005; Hawksworth 2001; Rossmann 2009). Now when a new species of fungus is described, its current, geographic pattern of occurrence might suggest an original native range. Unfortunately, that pattern could also be the product of homogenization since 1500. In contrast, the native ranges of macrobes are largely known, not only because the species are largely known, but because their ranges were documented early in the Homogocene before homogenization had had large effects. Disputes do exist, but they appear minor in scope to a mycologist. For instance, Gayther Plummer proposed that the most mysterious of native trees of North America, *Franklinia alata*, or the Franklin tree, was actually introduced from Asia a few decades before the Bartrams discovered a small grove in 1765 (Rowland 2006). Most botanists, however, disagree with Plummer (USDA n.d.). The native ranges of annual brome-grasses have more recently presented more serious challenges to botanists (Smith 1986), and other examples exist of course, but botanists have a set of criteria for dealing with problematic taxa: paleobotanical evidence of native status, records of their presence in their current range by early botanists, and current presence in natural habitats (Pyšek et al. 2004).

Mycologists face the unknown species problem, and the problem of the near total lack of knowledge of pre-Homogocene distributions. Mycologists were not on board the ships of the explorers and palaeomycology can hardly arbitrate disputes, as it is “in its infancy” (Stubblefield and Taylor 1988); others have even argued that the fungi lack “any significant fossil record” (Cain 1972). Even today fungi