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The population biology of fungal invasions

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Abstract

Fungal invasions are increasingly recognized as a significant component of global changes, threatening ecosystem health and damaging food production. Invasive fungi also provide excellent models to evaluate the generality of results based on other eukaryotes. We first consider here the reasons why fungal invasions have long been overlooked: they tend to be inconspicuous and inappropriate methods have been used for species recognition. We then review the information available on the patterns and mechanisms of fungal invasions. We examine the biological features underlying invasion success of certain fungal species. We review population structure analyses, revealing native source populations and strengths of bottlenecks. We highlight the documented ecological and evolutionary changes in invaded regions, including adaptation to temperature, increased virulence, hybridization, shifts to clonality and association with novel hosts. We discuss how the huge census size of most fungi allows adaptation even in bottlenecked, clonal invaders. We also present new analyses of the invasion of the anther smut pathogen on white campion in North America, as a case study illustrating how an accurate knowledge of species limits and phylogeography of fungal populations can be used to decipher the origin of invasions. This case study shows that successful invasions can occur even when life-history traits are particularly unfavorable to long-distance dispersal and even with a strong bottleneck. We conclude that fungal invasions are valuable models to contribute to our view of biological invasions, in particular by providing insights into the traits as well as ecological and evolutionary processes allowing successful introductions.

Key words: aggressiveness, admixture, multiple introductions, soft sweeps, mycorrhizal fungi, host shifts, plasticity, oomycetes, *Microbotryum*, *Silene latifolia*, *Cryphonectria*, *Batrachochytrium*, *Phytophthora*

Introduction

Biological invasions have become a major focus of ecologists and evolutionary biologists, due to their severe negative consequences and their potential usefulness as models for studying basic processes in population biology (Sakai *et al.* 2001). However, invasions by fungi have only recently come into the limelight (Desprez-Loustau *et al.* 2007), even though most biological invasions are probably caused by microorganisms, and fungal invasions may actually outnumber invasions caused by plants and animals. Furthermore, fungi, in the broad sense of the term (molds, yeasts, mushrooms, lichens, rusts, smuts, mildews, and including the phylogenetically distant oomycetes), display remarkably diverse life histories. This group includes everything from pathogens to mutualists and many free-living saprobes. They have a major impact on many different human activities and control essential ecosystem processes, like nutrient cycling and carbon storage (Stajich *et al.* 2009). Fungal invasions thus constitute a key component of global change that is often overlooked.

When we think about fungal invasions, the species that come to mind are generally those responsible for emerging fungal diseases that jeopardize food security or drive natural populations into decline or even extinction (Fisher *et al.* 2012; Palm 2001; Strange & Scott 2005). Jarrah dieback in Australia, caused by the oomycete *Phytophthora cinnamomi* (Hansen *et al.* 2012), and chestnut blight in North America, caused by the ascomycete *Cryphonectria parasitica* (Dutech *et al.* 2012), are textbook examples of ecological disasters caused by the establishment of pathogenic fungi outside their native range. However, it is important to recognize that non-pathogenic fungi are just as likely to have been moved across continents, even though their impact on ecosystem structure and function has rarely been quantified (Rizzo 2005). A particularly relevant example is that of mycorrhizal fungi (Schwartz *et al.* 2006), such as the infamous death-cap mushroom, *Amanita phalloides*, which was introduced into eastern North America, where it is now common (Pringle &

Vellinga 2006). Besides the effects of pathogenic fungi on their hosts, little is known about the ecological impact of invasive fungi, in particular on resident microbial communities at the same trophic level. Further community-level or competition studies are therefore required, similar to those typically carried out in the invasion ecology of plants and animals (Díez 2005; Rizzo 2005; Schwartz *et al.* 2006). Fungi play fundamental roles in terrestrial ecosystem function and composition, and there is no reason to assume that the effects of non-pathogenic invasive fungi would necessarily be negligible or positive (Desprez-Loustau *et al.* 2007).

One of the key challenges in fungal invasion ecology is understanding and predicting introduction and establishment pathways, but baseline data concerning the composition of endemic fungal communities are limited, even for well-studied environments in temperate regions, hampering efforts to monitor invasive species and to determine their origin (Pringle & Vellinga 2006). Many invasive species were actually introduced well before they were recognized as such or before their potential impact was understood (Palm 2001; Rizzo 2005). The amphibian-killing chytrid fungus, *Batrachochytrium dendrobatidis*, illustrates this point clearly. It was only after *B. dendrobatidis*, which belongs to an understudied basally branching lineage of fungi, was first described in 1998 (Berger *et al.* 1998) that efforts were made to characterize the diversity of animal-associated chytrids and their environmental reservoirs (Farrer *et al.* 2011; Fisher *et al.* 2009; Martel *et al.* 2013; McMahon *et al.* 2013; Morgan *et al.* 2007). Genetic analyses pointed to a single, recent origin of an asexual worldwide lineage of *B. dendrobatidis*, and revealed additional cryptic global lineages of the fungus (Farrer *et al.* 2013; Schloegel *et al.* 2012). However, early studies were unable to identify the origin of the disease. With the exception of a few well-known examples (Table S1), the sources of invasive fungi and the timing of their introduction remain a mystery. Even the invasive status of some fungi can be unclear, as problematic fungi may have been there

already and remained unidentified until their negative effects have begun to become apparent and of great concern. This uncertainty, in turn, impedes our capacity to manage possible invasion pathways in a proactive manner and to implement the regulatory mechanisms required to reduce the risks of further disasters (Sakalidis *et al.* 2013). Current efforts to catalog fungal diversity will allow increasingly precise and scientifically sound risk assessments, with the aim of preventing new introductions (Palm 2001).

Another important challenge in the field of invasion biology is determining whether adaptive evolution occurs in the invaded range or whether the successful invaders were already well suited for establishment and spread before their introduction (Facon *et al.* 2006), and which traits (*e.g.*, asexuality) or situations (*e.g.*, presence of naive hosts) facilitate invasions. Many invasive fungal populations are under sustained pressure to adapt to environments distinct from their endemic ranges. The response to these novel environments can lead to invasive fungi emerging on new hosts (Giraud *et al.* 2010), colonizing new varieties of their hosts (Brown 1994; Guérin *et al.* 2007), or re-emerging with greater pathogenicity (Hovmøller *et al.* 2008).

Here, we summarize and discuss recent studies on the ecology and population genetics of fungal invasions, with the dual aims of highlighting the features of these invasions and the ways in which they can help us to find out more about biological invasions in general. We begin by considering the reasons why fungal invasions have long been overlooked. We then examine the extrinsic factors and biological features underlying invasion success of certain fungal species. We present current knowledge about the origins and dispersal paths of invasive fungi, and documented ecological and evolutionary changes in regions where they have been introduced. We discuss how adaptation may occur so rapidly in bottlenecked, clonal fungal invaders. We also use a case study to illustrate the usefulness of baseline biodiversity data for the study of fungal invasions. For this, we present an original analysis of

the invasion of the fungus causing anther smut disease on white campion in the US; the interaction between *Microbotryum lychnidis-dioicae* and its host *Silene latifolia* is one of the best-studied non-agricultural plant-microbe pathosystems (Bernasconi *et al.* 2009). Overall, we aim at showing that fungi provide excellent and important models for studying the patterns and processes of biological invasions, for elucidating the factors favoring successful introductions, and for understanding their evolutionary and ecological mechanisms.

Fungal biogeography: ‘nothing is generally everywhere’

The first obvious step in any study of fungal invasions is the characterization of the geographic limits of endemic species of fungi. A failure to do this correctly can severely limit the ability to detect invasions and, thus, to infer their causal factors. Like other organisms of less than a few millimeters in length, fungi have long been thought to have global distributions, contrasting the highly restricted geographic ranges of larger organisms (Bisby 1943; Martiny *et al.* 2006; Taylor *et al.* 2006). This hypothesis was based on the observation that almost all fungi have small, powder-like propagules (typically spores <10 µm in diameter), and that many have structures favoring their dissemination (Pringle *et al.* 2005), suggesting that dispersal ability *per se* is unlikely to limit the geographic distribution of these organisms (Bisby 1943; Peay *et al.* 2010; Sato *et al.* 2012). The misconception that many fungi had global distributions also resulted from the use of morphological species recognition criteria that are largely inappropriate for fungi, providing an erroneous picture of fungal diversity, distributions and ecologies (Swann *et al.* 1999; Taylor *et al.* 2006). Obviously, if all fungi were ubiquitous, there would be no reason for writing this article, as no fungal species would be exotic anywhere. As startling as it may sound to researchers studying plants and animals, it is only recently that most fungi have been shown to have distributions similar to those of their distant microbial relatives (Green & Bohannan 2006; Thorsten Lumbsch *et al.*

2008). They are, for example, rarely present across entire continents (Tedersoo *et al.* 2012) and they satisfy the expectations of island biogeography theory (MacArthur & Wilson 2001; Peay *et al.* 2007).

The use of DNA markers have made it possible to identify new species that were previously cryptic, as these methods are more discriminating in fungi than traditional approaches based on morphological phenotypes or mating success (Giraud *et al.* 2008a). Modern evolutionary concepts of species are based on the lack of gene flow, with species being lineages that evolve independently (De Queiroz 2007; Giraud *et al.* 2008a), and DNA markers allow direct assessment of allelic exchange. In particular, genealogical concordance phylogenetic species recognition (GCPSR) is rapidly becoming the gold-standard approach for delimiting species (Henk *et al.* 2011; Hibbett & Taylor 2013). GCPSR uses breaks in the concordance of phylogenies for multiple genes to determine the limits of recombining entities (Avice & Wollenberg 1997; Taylor *et al.* 2000). It is one of the most objective, reproducible, achievable and widely applicable criteria for species identification (Giraud *et al.* 2008a). This approach appears to be the most powerful and accurate in fungi, leading to the identification of larger numbers of species than previously estimated (Giraud *et al.* 2008a; Stewart *et al.* 2014).

The cryptic species identified using DNA markers usually have narrower distributions in terms of geography range or host diversity than had been suggested in the prior literature (Taylor & Fisher 2003). The use of DNA markers has thus revealed that major geographic features (*e.g.*, continental breaks, mountains) can act as effective barriers to fungal dispersal, and that limited dispersal, combined with competitive advantage due to the colonization of resources ahead of competitors (Kennedy 2010), are a major driver of fungal endemism (Peay *et al.* 2010). In fungal symbionts, strong specialization on different hosts and host characteristics (*e.g.*, life history traits and distribution) appear to be key elements underlying biogeographic patterns (Hood *et al.* 2010; Schulze-Lefert & Panstruga 2011; Vellinga *et al.* 2009).

Which biological features underlie the success of invasive fungal species?

Most fungi thus did not have cosmopolitan distributions, but an increasing number of fungi are spreading around the world, some with dramatic effects on plant or animal populations (Fisher *et al.* 2012). It is therefore of paramount importance to examine the extrinsic factors and biological features underlying invasion success of certain fungal species. The success of invasive species is dependent on their ability to overcome a series of barriers, from introduction to establishment and invasion in a novel environment (Kolar & Lodge 2001), which involve stochastic and selection events in addition to initial transport by humans (Figure 1). Many fungal species are highly prolific, producing large numbers of spores (Peay *et al.* 2012; Prussin *et al.* 2014), thereby increasing propagule pressure, and potentially facilitating dispersal and persistence in the new environment, even if the initial degree of adaptation is low (Giraud *et al.* 2010).

Unlike many invasive plant and animal species that were initially deliberately introduced into new areas for economic or other purposes (*e.g.*, recreational), fungal introductions are mostly an unintended consequence of human-mediated movement and trade (Desprez-Loustau *et al.* 2007). Such “hitchhiking” dispersal is favored by some typical fungal features, including their inconspicuousness and the production of numerous, small propagules. The trade of animal and plant goods is a major pathway of fungal introductions, due to the close association of many fungi with plant or animal hosts (in mutualistic, pathogenic or saprotrophic interactions; Desprez-Loustau *et al.* 2010; Liebhold *et al.* 2012). Even though some fungi provide striking examples of long-distance aerial dispersal (Brown & Hovmøller 2002) and of global distributions (Henk *et al.* 2011; Pringle *et al.* 2005), it is generally very difficult to discount a role for human-mediated long-range movement in current distributions or migration pathways. Dispersal rates of several kilometers or even up to tens of kilometers per day over a season have nevertheless been reported for some

species (Aylor 2003; Mundt *et al.* 2013). Dispersal capacity, including fecundity and spore traits in particular, is critical in determining colonization success following the introduction of a species into a new environment and has been shown to affect variation in invasion success between species in a large dataset of fungal tree pathogens (Philibert *et al.* 2011). Mode of dispersal may also account for the overrepresentation of aerial pathogens among invasive plant pathogenic fungi (Desprez-Loustau *et al.* 2010).

As with other organisms, the successful establishment of fungal species outside their native range can often be accounted for by some level of pre-adaptation: the presence of attributes allowing these species to survive elsewhere, in novel environments (Janzen 1985; Mayr 1965), possibly due to traits displaying relatively high phenotypic plasticity or conferring a broad ecological niche, *e.g.*, in terms of temperature or possible host range (Agosta & Klemens 2008; Hulme & Barrett 2013; Parker & Gilbert 2004). Pre-adaptation has been proposed to explain the ability of fungal species to colonize extreme environments (Gostinčar *et al.* 2010; Robert & Casadevall 2009). An example of phenotypic plasticity that has been experimentally evaluated for the potential to facilitate invasion is the breadth of potential host range in pathogens. Pathogenicity tests have indeed shown that fungal pathogens of plants are often able to infect hosts closely related to their original host, although initially with low aggressiveness (Table 1; de Vienne *et al.* 2009; Gilbert & Webb 2007).

Alternatively, successful invaders may adapt to the new environment after their introduction, and rapid and drastic evolutionary changes may be facilitated by the huge census population size and mixed mating systems of fungi. Many fungal species can undergo both sexual and asexual reproduction, which could facilitate establishment from few founding propagules and accelerate adaptation in new environments. Theoretical studies have shown that species with mixed mating systems (both asexual reproduction and rare sex events) have the highest potential for invasion success in terms of probability and time to establishment

(Bazin *et al.* 2014). Mitotic spores and vegetative reproduction promote rapid increases in population size and the spread of the fittest genotypes, and several cycles of asexual reproduction may be completed in a single season (*e.g.*, polycyclic plant pathogens). Meiotic spores promote the creation of novel genotypes through recombination, and they are mostly used as dispersal and survival structures (Taylor *et al.* 1999).

Several traits have been shown to be predictive of invasion success for forest pathogenic fungi, including traits relating to long-distance dispersal, sexual reproduction combined with asexual reproduction, spore shape and size, number of cells in spores, optimal temperature for growth and broad host range for pathogens (host range and infected organs; Hayes & Barry 2008; Philibert *et al.* 2011; Pyšek *et al.* 2010). The traits cited above are intuitively appealing as facilitators of introduction and establishment, but other, more complex factors, such as spore resistance, competitive ability, host range for symbionts and evolutionary or plasticity potential, are also probably important. Indeed, fungal invaders successfully establish themselves in new environments, to which they probably must adapt despite their low genetic diversity. This expectation to evolve despite the genetic resources is often described as the “genetic paradox of invasions”. Below, we call into question the reality of this paradox in fungal invasions and we review some of the solutions adopted by fungi.

The fungal solution to the genetic paradox of invasions

Is reduced genetic diversity commonplace in invasive fungi?

Colonization bottlenecks are generally thought to decrease adaptive potential. Nevertheless, founder events have been shown to contribute to invasion success in some cases, by increasing the genetic variance through the conversion of epistatic to additive variance (Naciri-Graven & Goudet 2003) or by reducing the genetic load (Facon *et al.* 2006).

Admixture between populations from multiple introduction sources can also promote adaptation by rapidly creating novel allelic combinations (Prentis *et al.* 2008).

In order to assess whether bottlenecks or admixture occurred, one first needs to determine the origin of the invasive species and the genetic make-up of the source populations. For fungal symbionts of domesticated agricultural and forest plants, it is tempting to speculate that the origin of an invasive population is the geographic origin of the host. This has been shown to be the case for many crop pathogens (Table S1), through the demonstration that the center of diversity of the fungus coincides with the center of origin of its host plant (Gladieux *et al.* 2008; Munkacsı *et al.* 2008). However, some fungal pathogens have been found to have a higher level of diversity outside the center of origin of their current host, and this has been taken as indirect evidence for diversification following host-shift/range expansion (Ali *et al.* 2014; Zaffarano *et al.* 2009). Advances in clustering methods and approximate Bayesian computation have made it possible to carry out rigorous comparisons of complex scenarios modeling genealogical relationships between populations and their geographic and demographic dynamics (*e.g.*, Barrès *et al.* 2012; Dilmaghani *et al.* 2012; Dutech *et al.* 2012; Goss *et al.* 2014). Despite these methodological advances, it remains difficult to identify the origin of invasive symbiotic fungi because they are inconspicuous, hindering delimitation of the possible regions, substrates and hosts of origin. This uncertainty raises possibilities for endless disputes between experts (Goss *et al.* 2014) and hampers our understanding of the initial steps leading to invasion, such as the prevalence of major niche shifts.

In most cases in which genetic diversity has been compared between introduced and native fungal populations, a bottleneck signal has been detected, but such footprints have rarely been quantified in terms of effective population size ratios (Figure 2; Table S1). Highly contrasting situations have been reported, from the introduction of a single genetic lineage (*e.g.*, Hovmøller *et al.* 2008; Raboin *et al.* 2007) to greater genetic diversity in the invaded

area than in the native range due to multiple introductions from diverse sources (Dilmaghani *et al.* 2012; Figure 2; Table S1). Admixture between heterogeneous genetic pools has been detected in several studies on invasive fungi (*e.g.*, Ahmed *et al.* 2012; Dilmaghani *et al.* 2012; Dutech *et al.* 2012; Jezic *et al.* 2012), but the source populations have rarely been identified (Figure 2; Table S1). The detection of older admixture events requires the use of coalescent theory-based methods if several rounds of reproduction have erased allele frequency differences between the founding populations.

Interspecific hybridization: increased genetic diversity promoting rapid evolutionary changes

Interspecific hybridization can also promote rapid adaptation (Prentis *et al.* 2008) and has been reported between native and invasive species in fungi (*e.g.*, Bovers *et al.* 2008; Brasier 2001; Gonthier *et al.* 2007; Lin *et al.* 2007; Montarry *et al.* 2010; Stukenbrock *et al.* 2012; Figure 2; Table S1). In some cases, hybridization has been shown to be a powerful mechanism of fungal adaptation to new hosts and environments, allowing the acquisition of a missing mating type, for example in *Ophiostoma novo-ulmi* (Paoletti *et al.* 2006).

Interspecific hybridization, as a process allowing the adaptation of organism to new environments, may be facilitated in fungi by the large number of sibling species with incomplete reproductive isolation (Le Gac & Giraud 2008) and by the possibility of non-Mendelian forms of exchange, such as hyphal anastomosis that allows, for instance, the transfer of supplementary chromosomes (Gladieux *et al.* 2014; Roper *et al.* 2011).

Changes in life history traits during fungal invasions: mode of reproduction, virulence, host range and adaptation to abiotic factors

Investigators are generally interested in the questions discussed above, regarding levels of genetic diversity in invasive populations, because they implicitly assume a direct relationship between genetic variation and adaptive potential and a need for evolutionary change in introduced ranges. Many changes in life history traits during fungal invasions have actually been documented, with most studies focusing on ecological interactions of symbiotic fungi and particularly on plant pathogens. These changes have involved the infection of a new host population or species, adaptation to abiotic factors (*e.g.*, temperature), and changes in reproductive mode (Figure 2; Table S1). New ecological associations may result from fungi exhibiting wide ecological niches breadth, plasticity (*i.e.*, phenotypic changes without evolution) or, alternatively, may have involved adaptation or trade-offs, but these possibilities are rarely tested experimentally. For instance, the infection of a new host by a fungal population may involve a pre-existing broad host range, a host shift, a host-range expansion or plasticity, but the relative importance of these processes is difficult to establish unequivocally, as the pathogenicity of fungal populations infecting ancestral and new hosts has rarely been compared directly. For simplicity, we will use the term “host shift” below, but it should be borne in mind that it has not been clearly demonstrated whether these phenomena correspond to host shifts in the narrow sense (*i.e.*, with evolution, allowing infection of a new host and a decrease in the ability to infect the original host), host range expansion (*i.e.*, with evolution increasing host range), plasticity (*i.e.*, expansion of observed host range without genetic change), or an initially broad host range (*i.e.*, with no expansion of observed host range).

Several well-documented cases of emerging plant diseases have been attributed to such infection of a new host by introduced fungal pathogens (Desprez-Loustau *et al.* 2007; Giraud *et al.* 2010; Stukenbrock & McDonald 2008). Examples include wild tree or shrub pathogens, with the devastating shifts of *Cryphonectria parasitica* from the Asian to

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European and North American chestnuts, *Cronartium ribicola* from Asian to American and European pines, and *Discula destructiva* from Asian to American *Cornus* spp. (Palm & Rossman 2003, and references therein). Other examples, for crop pathogens, include the rice blast fungus *Magnaporthe oryzae*, which originated on *Setaria* millet (Couch *et al.* 2005), or the wheat pathogen *Zymoseptoria tritici*, which is derived from wild species infecting other grasses (Stukenbrock *et al.* 2007). The Irish potato famine pathogen was also recently shown to have emerged from populations infecting wild relatives of potato in Mexico (Goss *et al.* 2014). These host shifts may be due to recent contact with naïve host or may have involved evolutionary changes to permit infection of the new host. Such shifts to a new host would be facilitated by certain life history traits of fungal pathogens favoring the colonization of new hosts, such as mating within hosts and strong selective pressure on a limited number of genes (Giraud *et al.* 2010; Gladieux *et al.* 2011). Host shifts have actually been shown to be the main mode of diversification in fungal pathogens (de Vienne *et al.* 2013b; Giraud *et al.* 2010; Giraud *et al.* 2008a).

Associations with new hosts after introductions into new geographic regions have been less frequently documented for mutualists. There are nonetheless several examples in ectomycorrhizal fungi, such as *Laccaria* spp. in Costa Rica (Mueller & Strack 1992) and the emblematic *Amanita muscaria*, where introductions of these fungi appear to have occurred with their host tree species, followed by the formation of new associations with native hosts (Bagley & Orlovich 2004; Díez 2005; Jarius *et al.* 2011 ; Rizzo 2005; Vellinga *et al.* 2009).

Aside from host shifts or host range expansion occurring in introduced ranges due to contact with new hosts, several invasive crop pathogens have also emerged through host-tracking (Table 1), a process by which host and pathogen co-diverge during crop domestication and the development of agro-ecosystems (Stukenbrock & McDonald 2008). Movement of the pathogen from the wild progenitor of the crop to incipient domesticated populations can be followed by invasion at a worldwide scale associated with agricultural trade and product distributions. Examples include corn smut, caused by *Ustilago maydis*

(Munkacsı *et al.* 2008) and ascochyta blight of chickpea, caused by *Didymella rabiei* (Frenkel *et al.* 2010). An interesting case is *Venturia inaequalis*, causing apple scab, which tracked its host tree during domestication in Asia and along the Silk Route to Europe, where host range expansion to the European wild apple occurred, with a certain degree of pathogen specialization on apple varieties (Gladieux *et al.* 2008; Gladieux *et al.* 2010; Le Van *et al.* 2012). In this case, cross-inoculation experiments indicated the occurrence of evolutionary change, in particular the increased aggressiveness and the acquisition of new virulence traits (Le Van *et al.* 2012).

Only a few studies have investigated whether changes in life history traits have occurred in introduced fungal populations, and whether such changes were due to adaptation in particular. However, some evidence has been obtained for adaptation in the form of ecological traits that function to enhance fitness in the new environments. Such changes include an increase in aggressiveness and/or larger numbers of virulence traits in introduced regions (Table 1; Figure 2; Table S1; Enjalbert *et al.* 2005; Gilbert & Parker 2010; Le Van *et al.* 2012; Markell & Milus 2008; Milus *et al.* 2009; Rouxel *et al.* 2013). The development of greater aggressiveness or a broader virulence spectrum may be a general feature of crop pathogens, connected to the agricultural practice of very dense, homogeneous populations of host plants growing on a vast scale (McDonald 2010; Stukenbrock & McDonald 2008). Indeed, the presence in the environment of numerous individual hosts with the same genotype strengthens the selection on the pathogen for the ability to infect this genotype. Furthermore, the availability of numerous, regularly replanted host individuals should select for higher aggressiveness, because the pathogen would not benefit from a prudent host exploitation strategy when there are constantly new host individuals to infect in its environment (Frank 1996).

Another frequent change in life history traits of introduced fungi is the loss of sexual reproduction. Many studies have documented clonal population structures throughout the entire introduced range (Table S1; Figure 2; Ali *et al.* 2010; Couch *et al.* 2005; Dobrowolski

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et al. 2003; Duan *et al.* 2010; Enjalbert *et al.* 2005; Farrer *et al.* 2011; Fisher *et al.* 2009; Goodwin *et al.* 1994; Goss *et al.* 2009; Ivors *et al.* 2006; Mboup *et al.* 2007; Mboup *et al.* 2009; Saleh *et al.* 2012a; Saleh *et al.* 2012b; Singh *et al.* 2011; Smart & Fry 2001; Stajich *et al.* 2009), or over parts of that range (Dilmaghani *et al.* 2012; Dutech *et al.* 2009; Gladioux *et al.* 2008). Evidence has also been provided for an evolution towards a lower capacity for sexual reproduction in introduced regions (Ali *et al.* 2010; Couch *et al.* 2005; Duan *et al.* 2010; Enjalbert *et al.* 2005; Mboup *et al.* 2007; Mboup *et al.* 2009; Saleh *et al.* 2012a; Saleh *et al.* 2012b). F_{ST} versus Q_{ST} comparisons have suggested that this pattern is indeed an adaptation, rather than merely the consequence of genetic drift (Ali *et al.* 2010).

There may initially be several proximal causes for a loss of sexual reproduction: 1) a lack of appropriate mates where asexual propagation is possible, as in the case of *Phytophthora infestans*, *P. cinnamomi*, *P. ramorum*, and *O. novo-ulmi*, for which a single mating type was present for long periods in introduced ranges (Brasier 2001; Dobrowolski *et al.* 2003; Goodwin *et al.* 1994; Hardham 2005); 2) a hybridization event, *e.g.*, in the human pathogen *Cryptococcus neoformans* (Lin *et al.* 2007); and 3) a lack of the alternate host on which sex occurs in the case of complex life cycles, *e.g.*, in the rusts *Puccinia striiformis f. sp. tritici* and *Melampsora larici-populina* (Barrès *et al.* 2008; Mboup *et al.* 2007; Mboup *et al.* 2009).

There may also be diverse evolutionary causes for the selection against sexual reproduction (Bazin *et al.* 2014): 1) reducing advantages of sex due to the release of an enemy, such as viral pathogens of fungi, or the lower host resistance variation in the case of pathogens introduced into large, genetically homogeneous crops; 2) in heterokaryotic fungi and diploid oomycetes, preservation of the initial heterozygosity, which might otherwise rapidly convert to homozygosity in small founder populations, leading to inbreeding depression; 3) a release of constraints not related to recombination, maintaining sex in the short term in native ranges, such as the need for sexual spores for winter survival or long-distance dispersal (de Vienne *et al.* 2013a), which is particularly likely for introduced

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pathogens on crops, due to the availability of large, regular, homogeneous host populations; and 4) clonality may allow the locally adapted genotypes to be propagated without breaking up adaptive allelic combinations; again, this is advantageous on genetically homogeneous crops planted over vast areas.

Finally, abiotic factors can indeed limit the success of introductions or require adaptation, as a tolerance to high temperatures has been shown to have evolved in the introduced ranges of some fungi. In models of distribution range, temperature has been shown to be a critical factor for successful establishment of invasive fungi (Wolfe *et al.* 2010). Some populations of wheat yellow rust in the Mediterranean basin and south–eastern regions of the USA have evolved temperature-specific adaptations (Mboup *et al.* 2012), as did the *D. rabiei* population infecting domesticated chickpea (Frenkel *et al.* 2010). Furthermore, the successful establishment of exotic fungi has been shown to be sensitive to moisture conditions in attempts to deliberately introduce edible fungi such as truffles (Vellinga *et al.* 2009).

Invasive fungi, particularly pathogens of agricultural and forest plants, thus provide many examples of environmental change or colonization of a new niche acting as the primary drivers of post-colonization adaptive evolution. It is clearly important to understand the biological parameters driving selection on pathogens and disease outbreaks, given their impact on ecosystem functioning, human health and agricultural production.

Fungal pathogens evolve rapidly in agricultural and forest ecosystems

The potential for a fast pace of evolution in invasive fungal pathogens is a major impediment to maintaining ecosystem health and sustainable agricultural production. Measurements of genetic diversity and population structure are commonly used to draw inferences regarding the evolutionary potential of these pathogens, based on the assumption that adaptation can proceed quickly only from standing variation (McDonald 2014; McDonald & Linde 2002).

Life history strategies (*e.g.*, transmission and dispersal, virulence, mode of reproduction) are considered to be important determinants of diversity and, thus, for the potential of pathogens to colonize and spread on new host genotypes (Barrett *et al.* 2008). While standing genetic variation in a population is clearly a key influence on its ability to adapt in response to an environmental challenge, the general validity of predictive frameworks based on measured diversity patterns is questionable, given that evolution occurs rapidly in many invasive plant pathogens despite relatively modest levels of genetic diversity. For instance, some of the textbook examples of rapidly adapting fungal pathogens, such as lettuce downy mildew and wheat yellow rust, are also notoriously clonal and harbor little genetic diversity (Ali *et al.* 2014; Valade 2012).

The classical model of positive selection assumes that adaptation proceeds principally from *de novo* mutations, in a mutation-limited regime (Maynard-Smith *et al.* 1974). Under this regime, the lag time to adaptation depends on the product of the rate of mutation to the adaptive variant at the relevant locus and effective population size (N_e ; Charlesworth 2009; Garud *et al.* 2013). Many plant pathogens have a small N_e as estimated from levels of standing neutral variation (*e.g.*, Ali *et al.* 2014; Dilmaghani *et al.* 2012; Zaffarano *et al.* 2009). This apparent barrier to adaptation is because the “diversity N_e ” values are primarily determined by long-term population dynamics, which are dominated by extreme episodes of population crashes (bottlenecks or founder events; Lewontin 1974), hallmarks coincidentally of both disease cycles and invasions dynamics. If we consider the mutation rate per site to be between 10^{-8} and 10^{-10} (Kasuga *et al.* 2002), the adaptation of invasive fungi should, therefore, be strongly mutation-limited, *i.e.*, relatively slow and involving a single adaptive variant (a “hard selective sweep”).

At least two factors may nevertheless allow the rapid adaptation of invasive fungi, despite their relatively small “diversity N_e ”. First, recent studies have shown that predicting

the pattern of adaptation (speed of adaptation and number of adaptive alleles) is more accurate if N_e is estimated over timescales relevant to adaptation (Karasov *et al.* 2010). For an invasive fungal pathogen, this may be the timescale over which a new fungicide is applied or a new resistant variety is released. Despite the regular crashes of fungal populations (*e.g.*, during winters), their short-term N_e can be expected to be much higher than their long-term N_e , particularly as they generally have periods of huge census size. In such very large populations, the distinction between standing variation and *de novo* mutations becomes blurred, because almost all the possible mutations of the target gene are presented in the population (Barton 2010; Karasov *et al.* 2010).

Second, adaptation may be faster if the mutational targets are larger than a single nucleotide (Pritchard *et al.* 2010). The mutational target size is the number of base pairs within an allele for which mutations would alter a particular phenotype and increase fitness in the new environment. For fungal secreted virulence determinants (effectors, Table 1), for instance, the mutational target size may be of the order of hundreds of base pairs within the gene, rather than one: changing any one among hundreds of nucleotide, or even a large deletion in fungal effectors, may allow escaping host recognition (Rafiqi *et al.* 2012). Adaptive alleles would thus be expected to evolve repeatedly, and relatively quickly.

Recent case studies in invasive fungal pathogens have revealed several examples of adaptive mutations of multiple, independent *de novo* origins sweeping through populations (so-called “soft selective sweeps”), providing evidence that adaptation is not necessarily mutation-limited in these organisms. For instance, the molecular characterization of virulence alleles of effector genes in *Leptosphaeria maculans* (stem canker of oilseed rape) and *Rhynchosporium secalis* (barley leaf scald) revealed a diversity of mutational events consistent with a model of adaptation via soft sweeps (Daverdin *et al.* 2012; Fudal *et al.* 2009; Gout *et al.* 2007; Schürch *et al.* 2004). Another example is provided by fungicide

resistance in *Plasmopara viticola* (grapevine downy mildew), which has arisen from several independent mutations (Chen *et al.* 2007).

Case study of anther smut fungus on white campion

The insights into fungal invasions using comprehensive analyses of species boundaries, population structure, and life history traits can be illustrated using the anther-smut disease of Caryophyllaceae, caused by the basidiomycete *Microbotryum violaceum sensu lato*. The anther-smut fungi produce spores in anthers of diseased plants and are mostly transmitted by pollinators. A sex event is required before infection of a new plant, and the mating system is highly selfing (Giraud *et al.* 2008b). *Microbotryum* pathogens on the Caryophyllaceae are relatively uniform morphologically and were long thought to be a single, widely distributed species. However, GCPSR has shown that the old epithet actually consists of a large number of different, host-specialized species (Le Gac *et al.* 2007; Lutz *et al.* 2005) that diversified following host-shifts (Refregier *et al.* 2008). One of the defined species, *Microbotryum lychnidis-dioicae*, and its particular host plant, *Silene latifolia*, are native to Europe. Based on a collection of samples of unprecedented density and geographic scale for a pathogen, cluster analyses revealed the existence of strong subdivisions within the geographic range of this fungal species, reflecting recolonization from southern glacial refugia (Gladieux *et al.* 2013; Vercken *et al.* 2010). The genetic structure of the pathogen populations was found to be generally congruent with the genetic structure of the host, *S. latifolia* (Taylor & Keller 2007), both exhibiting three genetic clusters distributed, respectively, across western Europe, Eastern Europe and Italy. This congruence of population structures suggests that the migration pathway of the fungus had been dependent on its host over a time scale of hundreds or thousands of years. However, *M. lychnidis-dioicae* exhibited a much stronger structure than observed for its host, each of the three main fungal clusters being subdivided into further

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genetic clusters, with more restricted geographic distributions (Vercken *et al.* 2010). This suggested that *M. lychnidis-dioicae* has recolonized central and northern Europe from more numerous, smaller refugia than sheltered its plant host and that it has experienced fewer large-scale dispersal events.

Both the pathogen and its host were introduced relatively recently in North America, and the invasion history of *S. latifolia* has been extensively studied (Keller *et al.* 2012; Keller *et al.* 2009). The diversity of the host plant, *S. latifolia*, was found to be high in the introduced range, with the introduction of multiple lineages from several European genetic clusters that are now spread across North America (Keller *et al.* 2012; Keller *et al.* 2009). The anther smut disease appeared much more recently on *S. latifolia* in North America, and with a more eastern restricted distribution, than observed for the host plant (Antonovics *et al.* 2003; Fontaine *et al.* 2013). The delimitation of anther smut species confirms that the disease on the introduced *S. latifolia* was the result of a later introduction by its specialist pathogen, *M. lychnidis-dioicae*, instead of the host shift of a *Microbotryum* species endemic to North America on other *Silene* species or from another European host species (Fontaine *et al.* 2013). The very strong genetic structure of *M. lychnidis-dioicae* in Europe made it possible to identify the United Kingdom as the most probable source of the limited set of genotypes introduced into the central East Coast of North America. Given the assignment results and the limited number of genotypes in North America, a single introduction event appeared the most likely scenario (Fontaine *et al.* 2013). However, only a few samples from the United Kingdom were available for study at that time, and we have since identified an additional diseased population in the state of Massachusetts.

We therefore sampled further populations in the United Kingdom and from the newly identified diseased regions in North America, in an effort to ascertain the origin of the invasion more precisely and to check whether independent introductions may be responsible

for the invasions of central East Coast and more northern populations. The samples analyzed here represent an exhaustive sampling of the extant North American populations of *M. lychnidis-dioicae*, and a representative subset of the European populations previously analyzed (Fontaine *et al.* 2013; Vercken *et al.* 2010). Fungal isolates were genotyped and analyzed as previously described (Fontaine *et al.* 2013), with the inclusion here of more microsatellite markers (fourteen, see data on dryad). Fourteen multilocus genotypes were found in North America, representing a strong bottleneck compared to the diversity of *M. lychnidis-dioicae* across Europe, where 174 genotypes were detected in the present sample. The values of allelic richness, a standardized measure of diversity corrected for sample size differences, also pointed to a strong bottleneck: allelic richness was 3.78 in North America versus 7.46 in Europe and 5.55 in the UK alone. Genotypes were highly homozygous in all geographic regions, and no admixture was detected, indicating that the fungus has retained its highly selfing mating system in the introduced range (Giraud *et al.* 2008b). Sexual reproduction has also remained obligate for plant infection in the introduced range (MEH, pers. obs.)

We used STRUCTURE assignment analyses to investigate the origin of invasive fungal populations. This provided evidence for an additional, independent introduction of *M. lychnidis-dioicae* in North America (Figure 3A; Figure S1, Supporting information). The previously sampled populations in Virginia and one of the populations from Massachusetts still appeared, as in our previous study (Fontaine *et al.* 2013), to have originated in the Lothian (Edinburgh) region in southern Scotland (red cluster in Figure 3A). However, the second Massachusetts population was assigned to another genetic cluster (yellow cluster in Figure 3A), which included populations spread across the UK and could not be separated by further increasing the *K* parameter in STRUCTURE analyses (number of clusters). The examination of individual genotypes however allowed narrowing down the possible sources

of this second introduction. Genotypes that were identical to the ones found in the North American yellow cluster (Figure 3A) were also found in the North of Scotland, in the Moray council area and in the Highland close to cities of Inverness and Thurso (Figure 3B). The finding of two distinct genetic clusters in North American populations of *M. lychnidis-dioicae*, found in different locations and assigned to clusters originating from different regions in Scotland, altogether strongly suggest two or more independent introductions of the anther smut fungus.

The fungal invasion history still represents a much smaller number of introductions than for its host plant species (Keller *et al.* 2012; Keller *et al.* 2009), probably reflecting a restriction by the pathogen's life history traits. Indeed, this obligate, specialized pathogen is neither transmitted by the seeds of its host nor persistent in the environment. It can be transmitted only from a living plant to another living plant. This life-history trait limits the probability of introduction with its host plants, as weed introduction often occurs through seeds. The question of which traits prevent or facilitate invasions, during the several steps of dispersal and establishment, is of particular importance for fungal invasions in general. The *Microbotryum* case nevertheless shows that even the specialized, obligate fungus unable to disperse by wind (being mostly insect-borne) or seeds, or to persist in contaminated soil, can successfully invade a new continent, and multiple times independently. This case study further illustrates the importance of delimiting cryptic species in the native range and the usefulness of comprehensive sampling for performing relevant population structure analyses and identifying the locations of invasion source populations. It also highlights the possibility of successful invasion without change in mode of reproduction and despite a strong bottleneck.

Conclusion and future prospects

In conclusion, fungal invasions are valuable yet often overlooked models to contribute to our view of biological invasions. In particular, studies on large datasets including many fungal tree pathogens have been successful at identifying the traits favoring fungal invasions, *e.g.*, fecundity and spore traits favoring dispersal, as well as mixed-mating systems, with both clonal and sexual reproduction. Furthermore the ecological and evolutionary processes favoring successful introductions could be revealed in several case studies, such as adaptation to higher temperatures, increased aggressiveness, acquisition of novel virulences, phenotypic plasticity, novel host associations, and admixture under multiple introductions or hybridization. Sophisticated methods of population genetic inference have elucidated the dispersal pathways and native sources of several fungal invasions, pinpointing in particular host-tracking for pathogens and the possibility of invasions even with low genetic variability, *i.e.*, following strong bottlenecks or loss of sex. The rapid adaptation of invasive fungi, in particular of crop pathogens, often despite limited standing variation, is likely facilitated by their huge population sizes and the large genomic targets of selection, where any change within an effector gene for instance may allow escaping host recognition. Altogether, these insights broaden our understanding of biological invasions in eukaryotes.

Fungal invasion biology is a dynamic, recently emergent area of research. Many fungal invasions, possibly even the majority that exist, remain to be discovered, and there is much yet to be learned. The use of high-throughput sequencing technologies and the availability of universal primers for the sequencing of a single fungal barcode, the ITS (White *et al.* 1990), are greatly advancing our understanding of fungal diversity (Peay *et al.* 2008; Talbot *et al.* 2014) and increasing the power to detect invasive fungi, which are often concealed within the soil or in plant tissues. The use of sequencing technologies and substantial sampling efforts should shed light on the processes underlying invasions by nonpathogenic fungi, about which

we know very little, despite their tremendous importance in ecosystem functioning, as decomposers for example. More generally, technological advances in the characterization of fungal populations and progress in inference methods (Neher 2013; Stukenbrock & McDonald 2008) are creating new, unprecedented opportunities to study fungal ecology and evolution, and fungi are proving to be excellent organisms for challenging the universality of expectations derived from plants and animals (Gladieux *et al.* 2014).

Progress has recently been made towards determining the origins and pathways of fungal invasions, but a more comprehensive understanding of the processes underlying fungal invasions will require integrating population and comparative genomics within an experimental frameworks as has been applied to plant models. Phenotypic differences between introduced and native populations occur under non-equilibrium demographic conditions and may be affected by chance events, evolutionary history, and adaptive responses to divergent selection (Taylor & Keller 2007). Experimental comparisons of species from their native and introduced ranges, testing hypotheses of adaptation against null models of neutral phenotypic evolution, should make it possible to determine whether the causal mechanisms of phenotypic change are adaptive. It is now increasingly feasible to push such studies further with population genetics to identify potentially adaptive genomic features and then to make use of bioinformatics and reverse genetics tools to connect selected genomic features to important phenotypes. Full-genome sequencing of multiple strains is now routinely carried out in fungi. Improvements in the functional annotation of fungal genomes, and their amenability to experimental manipulation, are making it possible to implement a genuine “reverse ecology” approach involving the identification of genes with unusual patterns of evolution and environmental parameters consistent with the function of the genes, and then testing hypotheses experimentally (Ellison *et al.* 2011; Ellison *et al.* 2014).

Adaptive evolution in invasive fungi may pose a major threat to plant and animal health, but it also provides us with interesting opportunities to improve our understanding of the evolution of biotic interactions (McDonald 2010). We must not waste this opportunity to learn from the natural experiments represented by fungal invasions if we are to develop sustainable regulatory mechanisms based on evolutionary models, using predictive frameworks to control the pace of pathogen evolution in natural and agro-ecosystems (Parker & Gilbert 2004; Thrall *et al.* 2007; Thrall *et al.* 2011).

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Author Information Box. All the authors are interested in uncovering the mechanisms behind invasions by exotic fungi, plants and animals. They use population genetics, comparative genomics, laboratory and *in situ* experiments, or literature and herbarium surveys to understand the biogeography, ecology and evolution of invasive species.

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Data Accessibility. Information on sampling locations as well as the microsatellite genotypic data has been deposited at Dryad: doi:10.5061/dryad.k5786

References

- Agosta SJ, Klemens JA (2008) Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecology letters* **11**, 1123-1134.
- Ahmed S, de Labrouhe DT, Delmotte F (2012) Emerging virulence arising from hybridisation facilitated by multiple introductions of the sunflower downy mildew pathogen *Plasmopara halstedii*. *Fungal Genetics and Biology* **49**, 847-855.
- Ali S, Gladioux P, Leconte M, *et al.* (2014) Origin, migration routes and worldwide population genetic structure of the wheat yellow rust *Puccinia striiformis f. sp. tritici*. *PLoS Pathogens* **10**, e1003903.
- Ali S, Leconte M, Walker A-S, Enjalbert J, de Vallavieille-Pope C (2010) Reduction in the sex ability of worldwide clonal populations of *Puccinia striiformis f.sp. tritici*. *Fungal Genetics and Biology* **47**, 828-838.
- Antonovics J, Hood ME, Thrall PH, Abrams JY, Duthie GM (2003) Herbarium studies on the distribution of anther-smut fungus (*Microbotryum violaceum*) and *Silene* species (Caryophyllaceae) in the eastern United States. *American Journal of Botany* **90**, 1522-1531.
- Avise JC, Wollenberg K (1997) Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences* **94**, 7748-7755.
- Aylor DE (2003) Spread of plant disease on a continental scale: role of aerial dispersal of pathogens. *Ecology* **84**, 1989-1997.
- Bagley SJ, Orlovich DA (2004) Genet size and distribution of *Amanita muscaria* in a suburban park, Dunedin, New Zealand. *New Zealand Journal of Botany* **42**, 939-947.

- Barrès B, Carlier J, Seguin M, *et al.* (2012) Understanding the recent colonization history of a plant pathogenic fungus using population genetic tools and Approximate Bayesian Computation. *Heredity* **109**, 269-279.
- Barrès B, Halkett F, Dutech C, *et al.* (2008) Genetic structure of the poplar rust fungus *Melampsora larici-populina*: Evidence for isolation by distance in Europe and recent founder effects overseas. *Infection, Genetics and Evolution* **8**, 577-587.
- Barrett LG, Thrall PH, Burdon JJ, Linde CC (2008) Life history determines genetic structure and evolutionary potential of host-parasite interactions. *Trends in Ecology & Evolution* **23**, 678-685.
- Barton N (2010) Understanding adaptation in large populations. *PLoS genetics* **6**, e1000987.
- Bazin E, Mathe-Hubert H, Facon B, Carlier J, Ravigne V (2014) The effect of mating system on invasiveness: some genetic load may be advantageous when invading new environments. *Biological Invasions* **16**, 875-886.
- Berger L, Speare R, Daszak P, *et al.* (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences* **95**, 9031-9036.
- Bernasconi G, Antonovics J, Biere A, *et al.* (2009) *Silene* as a model system in ecology and evolution. *Heredity* **103**, 5-14.
- Bisby GR (1943) Geographical distribution of fungi. *The Botanical Review* **9**, 466-482.
- Bovers M, Hagen F, Kuramae EE, Boekhout T (2008) Six monophyletic lineages identified within *Cryptococcus neoformans* and *Cryptococcus gattii* by multi-locus sequence typing. *Fungal Genetics and Biology* **45**, 400-421.
- Brasier CM (2001) Rapid evolution of introduced plant pathogens via interspecific hybridization. *BioScience* **51**, 123-133.
- Brown JKM (1994) Chance and selection in the evolution of barley mildew. *Trends in Microbiology* **2**, 470-475.
- Brown JKM, Hovmøller MS (2002) Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* **297**, 537-541.
- Charlesworth B (2009) Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics* **10**, 195-205.
- Chen W-J, Delmotte F, Cervera SR, *et al.* (2007) At least two origins of fungicide resistance in grapevine downy mildew populations. *Applied and Environmental Microbiology* **73**, 5162-5172.
- Couch BC, Fudal I, Lebrun MH, *et al.* (2005) Origins of host-specific populations of the blast pathogen *Magnaporthe oryzae* in crop domestication with subsequent expansion of pandemic clones on rice and weeds of rice. *Genetics* **170**, 613-630.

- Daverdin G, Rouxel T, Gout L, *et al.* (2012) Genome structure and reproductive behaviour influence the evolutionary potential of a fungal phytopathogen. *PLoS Pathogens* **8**.
- De Queiroz K (2007) Toward an integrated system of clade names. *Systematic Biology* **56**, 956-974.
- de Vienne DM, Giraud T, Gouyon P-H (2013a) Lineage selection and the maintenance of sex. *PLoS One* **8**.
- de Vienne DM, Hood ME, Giraud T (2009) Phylogenetic determinants of potential host shifts in fungal pathogens. *Journal of Evolutionary Biology* **22**, 2532-2541.
- de Vienne DM, Refregier G, Lopez-Villavicencio M, *et al.* (2013b) Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. *New Phytologist* **198**, 347-385.
- Desprez-Loustau M-L, Courtecuisse R, Robin C, *et al.* (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.
- Desprez-Loustau M-L, Robin C, Buee M, *et al.* (2007) The fungal dimension of biological invasions. *Trends in Ecology & Evolution* **22**, 472-480.
- Díez J (2005) Invasion biology of Australian ectomycorrhizal fungi introduced with eucalypt plantations into the Iberian Peninsula. *Biological Invasions* **7**, 3-15.
- Dilmaghani A, Gladieux P, Gout L, *et al.* (2012) Migration patterns and changes in population biology associated with the worldwide spread of the oilseed rape pathogen *Leptosphaeria maculans*. *Molecular Ecology* **21**, 2519-2533.
- Dobrowolski MP, Tommerup IC, Shearer BL, O'Brien PA (2003) Three clonal lineages of *Phytophthora cinnamomi* in Australia revealed by microsatellites. *Phytopathology* **93**, 695-704.
- Dodds PN, Rathjen JP (2010) Plant immunity: towards an integrated view of plant-pathogen interactions. *Nature Reviews Genetics* **11**, 539-548.
- Duan X, Tellier A, Wan A, *et al.* (2010) *Puccinia striiformis f.sp. tritici* presents high diversity and recombination in the over-summering zone of Gansu, China. *Mycologia* **102**, 44-53.
- Dutech C, Barres B, Bridier J, *et al.* (2012) The chestnut blight fungus world tour: successive introduction events from diverse origins in an invasive plant fungal pathogen. *Molecular Ecology* **21**, 3931-3946.
- Dutech C, Fabreguettes O, Capdevielle X, Robin C (2009) Multiple introductions of divergent genetic lineages in an invasive fungal pathogen, *Cryphonectria parasitica*, in France. *Heredity*.
- Ellison CE, Hall C, Kowbel D, *et al.* (2011) Population genomics and local adaptation in wild isolates of a model microbial eukaryote. *Proceedings of the National Academy of Sciences* **108**, 2831-2836.

- Accepted Article
- Ellison CE, Kowbel D, Glass NL, Taylor JW, Brem RB (2014) Discovering functions of unannotated genes from a transcriptome survey of wild fungal isolates. *mBio* **5**, e01046-01013.
- Enjalbert J, Duan X, Leconte M, Hovmøller MS, De Vallavieille-Pope C (2005) Genetic evidence of local adaptation of wheat yellow rust (*Puccinia striiformis* f. sp. *tritici*) within France. *Molecular Ecology* **14**, 2065-2073.
- Facon B, Genton BJ, Shykoff J, *et al.* (2006) A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology & Evolution* **21**, 130-135.
- Farrer RA, Henk DA, Garner TWJ, *et al.* (2013) Chromosomal copy number variation, selection and uneven rates of recombination reveal cryptic genome diversity linked to pathogenicity. *PLoS genetics* **9**, e1003703.
- Farrer RA, Weinert LA, Bielby J, *et al.* (2011) Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. *Proceedings of the National Academy of Sciences* **108**, 18732-18736.
- Fisher MC, Garner TWJ, Walker SF (2009) Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. *Annual Review of Microbiology* **63**, 291-310.
- Fisher MC, Henk DA, Briggs CJ, *et al.* (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186-194.
- Fontaine MC, Gladieux P, Hood ME, Giraud T (2013) History of the invasion of the anther smut pathogen on *Silene latifolia* in North America. *New Phytologist* **198**, 946-956.
- Frank SA (1996) Models of parasite virulence. *Quarterly Review of Biology* **71**, 37-78.
- Frenkel O, Peever TL, Chilvers MI, *et al.* (2010) Ecological genetic divergence of the fungal pathogen *Didymella rabiei* on sympatric wild and domesticated *Cicer* spp. (Chickpea). *Applied and Environmental Microbiology* **76**, 30-39.
- Fudal I, Ross S, Brun H, *et al.* (2009) Repeat-Induced Point Mutation (RIP) as an alternative mechanism of evolution toward virulence in *Leptosphaeria maculans*. *Molecular Plant-Microbe Interactions* **22**, 932-941.
- Garud NR, Messer PW, Buzbas EO, Petrov DA (2013) Soft selective sweeps are the primary mode of recent adaptation in *Drosophila melanogaster*. *arXiv preprint arXiv:1303.0906*.
- Gilbert GS, Parker IM (2010) Rapid evolution in a plant-pathogen interaction and the consequences for introduced host species. *Evolutionary Applications* **3**, 144-156.
- Gilbert GS, Webb CO (2007) Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 4979-4983.
- Giraud T, Gladieux P, Gavrillets S (2010) Linking the emergence of fungal plant diseases with ecological speciation. *Trends in Ecology & Evolution* **25**, 387-395.

- Giraud T, Refregier G, Le Gac M, de Vienne DM, Hood ME (2008a) Speciation in fungi. *Fungal Genetics and Biology* **45**, 791-802.
- Giraud T, Yockteng R, Lopez-Villavicencio M, Refregier G, Hood ME (2008b) Mating system of the anther smut fungus *Microbotryum violaceum*: Selfing under heterothallism. *Eukaryotic Cell* **7**, 765-775.
- Gladieux P, Devier B, Aguilera G, Cruaud C, Giraud T (2013) Purifying selection after episodes of recurrent adaptive diversification in fungal pathogens. *Infection Genetics and Evolution* **17**, 123-131.
- Gladieux P, Guerin F, Giraud T, *et al.* (2011) Emergence of novel fungal pathogens by ecological speciation: importance of the reduced viability of immigrants. *Molecular Ecology* **20**, 4521-4532.
- Gladieux P, Ropars J, Badouin H, *et al.* (2014) Fungal evolutionary genomics provides insight into the mechanisms of adaptive divergence in eukaryotes. *Molecular Ecology* **23**, 753-773.
- Gladieux P, Zhang XG, Afoufa-Bastien D, *et al.* (2008) On the origin and spread of the scab disease of apple: Out of Central Asia. *PLoS One* **3**.
- Gladieux P, Zhang XG, Roldan-Ruiz I, *et al.* (2010) Evolution of the population structure of *Venturia inaequalis*, the apple scab fungus, associated with the domestication of its host. *Molecular Ecology* **19**, 658-674.
- Gonthier P, Nicolotti G, Linzer R, Guglielmo F, Garbelotto M (2007) Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. *Molecular Ecology* **16**, 1389-1400.
- Goodwin SB, Cohen BA, Fry WE (1994) Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 11591-11595.
- Goss EM, Carbone I, Grunwald NJ (2009) Ancient isolation and independent evolution of the three clonal lineages of the exotic sudden oak death pathogen *Phytophthora ramorum*. *Molecular Ecology* **18**, 1161-1174.
- Goss EM, Tabima JF, Cooke DEL, *et al.* (2014) The Irish potato famine pathogen *Phytophthora infestans* originated in central Mexico rather than the Andes. *Proceedings of the National Academy of Sciences*, 201401884.
- Gostinčar C, Grube M, De Hoog S, Zalar P, Gunde-Cimerman N (2010) Extremotolerance in fungi: evolution on the edge. *FEMS Microbiology Ecology* **71**, 2-11.
- Gout L, Kuhn ML, Vincenot L, *et al.* (2007) Genome structure impacts molecular evolution at the AvrLm1 avirulence locus of the plant pathogen *Leptosphaeria maculans*. *Environmental Microbiology* **9**, 2978-2992.
- Green J, Bohannan BJM (2006) Spatial scaling of microbial biodiversity. *Trends in Ecology & Evolution* **21**, 501-507.

- Guérin F, Gladieux P, Le Cam B (2007) Origin and colonization history of newly virulent strains of the phytopathogenic fungus *Venturia inaequalis*. *Fungal Genetics and Biology* **44**, 284-292.
- Hansen EM, Reeser PW, Sutton W (2012) Phytophthora beyond agriculture. *Annual Review of Phytopathology* **50**, 359-378.
- Hardham AR (2005) *Phytophthora cinnamomi*. *Molecular Plant Pathology* **6**, 589-604.
- Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? *Biological Invasions* **10**, 483-506.
- Henk DA, Eagle CE, Brown K, *et al.* (2011) Speciation despite globally overlapping distributions in *Penicillium chrysogenum*: the population genetics of Alexander Fleming's lucky fungus. *Molecular Ecology* **20**, 4288-4301.
- Hibbett DS, Taylor JW (2013) Fungal systematics: is a new age of enlightenment at hand? *Nature Reviews Microbiology* **11**, 129-133.
- Hood ME, Mena-Ali JI, Gibson AK, *et al.* (2010) Distribution of the anther-smut pathogen *Microbotryum* on species of the Caryophyllaceae. *New Phytologist* **187**, 217-229.
- Hovmøller MS, Yahyaoui AH, Milus EA, Justesen AF (2008) Rapid global spread of two aggressive strains of a wheat rust fungus. *Molecular Ecology* **17**, 3818-3826.
- Hulme PE, Barrett SCH (2013) Integrating trait-and niche-based approaches to assess contemporary evolution in alien plant species. *Journal of Ecology* **101**, 68-77.
- Ilanzen DH (1985) On ecological fitting. *Oikos* **45**, 308-303.
- Ivors K, Garbelotto M, Vries IDE, *et al.* (2006) Microsatellite markers identify three lineages of *Phytophthora ramorum* in US nurseries, yet single lineages in US forest and European nursery populations. *Molecular Ecology* **15**, 1493-1505.
- Jairus T, Mpumba R, Chinoya S, Tedersoo L (2011) Invasion potential and host shifts of Australian and African ectomycorrhizal fungi in mixed eucalypt plantations. *New Phytologist* **192**, 179-187.
- Jezic M, Krstin L, Rigling D, Curkovic-Perica M (2012) High diversity in populations of the introduced plant pathogen, *Cryphonectria parasitica*, due to encounters between genetically divergent genotypes. *Molecular Ecology* **21**, 87-99.
- Karasov T, Messer PW, Petrov DA (2010) Evidence that adaptation in *Drosophila* is not limited by mutation at single sites. *PLoS genetics* **6**, e1000924.
- Kasuga T, White TJ, Taylor JW (2002) Estimation of nucleotide substitution rates in eurotiomycete fungi. *Molecular Biology and Evolution* **19**, 2318-2324.
- Keller SR, Gilbert KJ, Fields PD, Taylor DR (2012) Bayesian inference of a complex invasion history revealed by nuclear and chloroplast genetic diversity in the colonizing plant, *Silene latifolia*. *Molecular Ecology* **21**, 4721-4734.

- Keller SR, Sowell DR, Neiman M, Wolfe LM, Taylor DR (2009) Adaptation and colonization history affect the evolution of clines in two introduced species. *New Phytologist* **183**, 678-690.
- Kennedy P (2010) Ectomycorrhizal fungi and interspecific competition: species interactions, community structure, coexistence mechanisms, and future research directions. *New Phytologist* **187**, 895-910.
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**, 199-204.
- Le Gac M, Giraud T (2008) Existence of a pattern of reproductive character displacement in *Homobasidiomycota* but not in *Ascomycota*. *Journal of Evolutionary Biology* **21**, 761-772.
- Le Gac M, Hood ME, Fournier E, Giraud T (2007) Phylogenetic evidence of host-specific cryptic species in the anther smut fungus. *Evolution* **61**, 15-26.
- Le Van A, Gladieux P, Lemaire C, *et al.* (2012) Evolution of pathogenicity traits in the apple scab fungal pathogen in response to the domestication of its host. *Evolutionary Applications* **5**, 694-704.
- Lewontin RC (1974) *The genetic basis of evolutionary change* Columbia University Press New York.
- Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. *Frontiers in Ecology and the Environment* **10**, 135-143.
- Lin X, Litvintseva AP, Nielsen K, *et al.* (2007) α AD α hybrids of *Cryptococcus neoformans*: evidence of same-sex mating in nature and hybrid fitness. *PLoS genetics* **3**, e186.
- Lutz M, Göker M, Piatek M, *et al.* (2005) Anther smuts of Caryophyllaceae: molecular characters indicate host-dependent species delimitation. *Mycological Progress* **4**, 225-238.
- MacArthur RH, Wilson EO (2001) The theory of island biogeography. *Princeton landmarks in biology*.
- Markell SG, Milus EA (2008) Emergence of a novel population of *Puccinia striiformis f. sp. tritici* in eastern United States. *Phytopathology* **98**, 632-639.
- Martel A, Spitzen-van der Sluijs A, Blooi M, *et al.* (2013) *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. *Proceedings of the National Academy of Sciences* **110**, 15325-15329.
- Martiny JBH, Bohannan BJM, Brown JH, *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* **4**, 102-112.
- Maynard-Smith J, Smith NH, O'Rourke M, Spratt BG (1974) The hitch-hiking effect of a favourable gene. *Genetical Research* **23**, 23-35.

- Mayr E (1965) The nature of colonization of birds. *The Genetics of Colonizing Species*. Academic Press, New York, London, 29-44.
- Mboup M, Bahri B, Leconte M, *et al.* (2012) Genetic structure and local adaptation of European wheat yellow rust populations: the role of temperature-specific adaptation. *Evolutionary Applications* **5**, 341-352.
- Mboup M, Leconte M, De Vallavieille Pope C, Enjalbert J (2007) Evidence of genetic recombination in Chinese wheat yellow rust populations. *Phytopathology* **97**, S72-S73.
- Mboup M, Leconte M, Gautier A, *et al.* (2009) Evidence of genetic recombination in wheat yellow rust populations of a Chinese overwintering area. *Fungal Genetics and Biology* **46**, 299-307.
- McDonald B (2010) How can we achieve durable disease resistance in agricultural ecosystems? *New Phytologist* **185**, 3-5.
- McDonald BA (2014) Using dynamic diversity to achieve durable disease resistance in agricultural ecosystems. *Tropical Plant Pathology* **39**, 191-196.
- McDonald BA, Linde C (2002) Pathogen population genetics, evolutionary potential, and durable resistance. *Annual Review of Phytopathology* **40**, 349-379.
- McMahon TA, Brannelly LA, Chatfield MWH, *et al.* (2013) Chytrid fungus *Batrachochytrium dendrobatidis* has nonamphibian hosts and releases chemicals that cause pathology in the absence of infection. *Proceedings of the National Academy of Sciences* **110**, 210-215.
- Milus EA, Kristensen K, Hovmøller MS (2009) Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis f. sp. tritici* causing stripe rust of wheat. *Phytopathology* **99**, 89-94.
- Montarry J, Andrivon D, Glais I, *et al.* (2010) Microsatellite markers reveal two admixed genetic groups and an ongoing displacement within the French population of the invasive plant pathogen *Phytophthora infestans*. *Molecular Ecology* **19**, 1965-1977.
- Morgan JAT, Vredenburg VT, Rachowicz LJ, *et al.* (2007) Population genetics of the frog-killing fungus *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 13845-13850.
- Mueller GM, Strack BA (1992) Evidence for a mycorrhizal host shift during migration of *Laccaria trichodermophora* and other agarics into neotropical oak forests. *Mycotaxon*. **45**, 249-256.
- Mundt CC, Wallace LD, Allen TW, *et al.* (2013) Initial epidemic area is strongly associated with the yearly extent of soybean rust spread in North America. *Biological Invasions* **15**, 1431-1438.
- Munkacsı AB, Stoxen S, May G (2008) *Ustilago maydis* populations tracked maize through domestication and cultivation in the Americas. *Proceedings of the Royal Society B-Biological Sciences* **275**, 1037-1046.

- Naciri-Graven Y, Goudet J (2003) The additive genetic variance after bottlenecks is affected by the number of loci involved in epistatic interactions. *Evolution* **57**, 706-716.
- Neher RA (2013) Genetic draft, selective interference, and population genetics of rapid adaptation. *arXiv preprint arXiv:1302.1148*.
- Palm ME (2001) Systematics and the impact of invasive fungi on agriculture in the United States. *BioScience* **51**, 141-147.
- Palm ME, Rossman AY (2003) Invasion pathways of terrestrial plant-inhabiting fungi. *Bioinvasions: pathways, vectors, and management strategies*. Island Press, New York, New York, USA, 31-43.
- Paoletti M, Buck KW, Brasier CM (2006) Selective acquisition of novel mating type and vegetative incompatibility genes via interspecies gene transfer in the globally invading eukaryote *Ophiostoma novo-ulmi*. *Molecular Ecology* **15**, 249-262.
- Parker IM, Gilbert GS (2004) The evolutionary ecology of novel plant-pathogen interactions. *Annual Review of Ecology, Evolution and Systematics* **35**, 675-700.
- Peay KG, Bidartondo MI, Arnold AE (2010) Not every fungus is everywhere: scaling to the biogeography of fungal-plant interactions across roots, shoots and ecosystems. *New Phytol* **185**, 878-882.
- Peay KG, Bruns TD, Kennedy PG, Bergemann SE, Garbelotto M (2007) A strong species–area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecology letters* **10**, 470-480.
- Peay KG, Kennedy PG, Bruns TD (2008) Fungal community ecology: a hybrid beast with a molecular master. *BioScience* **58**, 799-810.
- Peay KG, Schubert MG, Nguyen NH, Bruns TD (2012) Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. *Molecular Ecology* **21**, 4122-4136.
- Philibert A, Desprez-Loustau M-L, Fabre B, *et al.* (2011) Predicting invasion success of forest pathogenic fungi from species traits. *Journal of Applied Ecology* **48**, 1381-1390.
- Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ (2008) Adaptive evolution in invasive species. *Trends in Plant Science* **13**, 288-294.
- Pringle A, Baker D, Platt J, *et al.* (2005) Cryptic speciation in the cosmopolitan and clonal human pathogenic fungus *Aspergillus fumigatus*. *Evolution* **59**, 1886-1899.
- Pringle A, Vellinga EC (2006) Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides* (Vaill. ex Fr.: Fr.) Link. *Biological Invasions* **8**, 1131-1144.
- Pritchard JK, Pickrell JK, Coop G (2010) The genetics of human adaptation: hard sweeps, soft sweeps, and polygenic adaptation. *Current Biology* **20**, R208-R215.

- Prussin AJ, Szanyi NA, Welling PI, Ross SD, Schmale Iii DG (2014) Estimating the production and release of ascospores from a field-scale source of *Fusarium graminearum* inoculum. *Plant Disease* **98**, 497-503.
- Pyšek P, Jarošík V, Hulme PE, *et al.* (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences* **107**, 12157-12162.
- Raboin L-M, Selvi A, Oliveira KM, *et al.* (2007) Evidence for the dispersal of a unique lineage from Asia to America and Africa in the sugarcane fungal pathogen *Ustilago scitaminea*. *Fungal Genetics and Biology* **44**, 64-76.
- Rafiqi M, Ellis JG, Ludowici VA, Hardham AR, Dodds PN (2012) Challenges and progress towards understanding the role of effectors in plant–fungal interactions. *Current Opinion in Plant Biology* **15**, 477-482.
- Refregier G, Le Gac M, Jabbour F, *et al.* (2008) Cophylogeny of the anther smut fungi and their Caryophyllaceae hosts: Prevalence of host shifts and importance of delimiting parasite species for inferring cospeciation. *BMC Evolutionary Biology* **8**, 100.
- Rizzo DM (2005) Exotic species and fungi: Interactions with fungal, plant and animal communities. In: *The Fungal Community: Its Organization and Role in the Ecosystem*, pp. 857-880. CRC Press, Boca Raton.
- Robert VA, Casadevall A (2009) Vertebrate endothermy restricts most fungi as potential pathogens. *Journal of Infectious Diseases* **200**, 1623-1626.
- Roper M, Ellison C, Taylor JW, Glass NL (2011) Nuclear and genome dynamics in multinucleate ascomycete fungi. *Current Biology* **21**, R786-R793.
- Rouxel M, Mestre P, Comont G, *et al.* (2013) Phylogenetic and experimental evidence for host-specialized cryptic species in a biotrophic oomycete. *New Phytologist* **197**, 251-263.
- Sakai AK, Allendorf FW, Holt JS, *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology & Systematics* **32**, 305-332.
- Sakalidis ML, Slippers B, Wingfield BD, Hardy GESJ, Burgess TI (2013) The challenge of understanding the origin, pathways and extent of fungal invasions: global populations of the *Neofusicoccum parvum*–*N. ribis* species complex. *Diversity and Distributions* **19**, 873-883.
- Saleh D, Milazzo J, Adreit H, Tharreau D, Fournier E (2012a) Asexual reproduction induces a rapid and permanent loss of sexual reproduction capacity in the rice fungal pathogen *Magnaporthe oryzae*: results of *in vitro* experimental evolution assays. *BMC Evolutionary Biology* **12**, 42.
- Saleh D, Xu P, Shen Y, *et al.* (2012b) Sex at the origin: an Asian population of the rice blast fungus *Magnaporthe oryzae* reproduces sexually. *Molecular Ecology* **21**, 1330-1344.

- Sato H, Tsujino R, Kurita K, Yokoyama K, Agata K (2012) Modelling the global distribution of fungal species: new insights into microbial cosmopolitanism. *Molecular Ecology* **21**, 5599-5612.
- Schloegel LM, Toledo LF, Longcore JE, *et al.* (2012) Novel, panzootic and hybrid genotypes of amphibian chytridiomycosis associated with the bullfrog trade. *Molecular Ecology* **21**, 5162-5177.
- Schulze-Lefert P, Panstruga R (2011) A molecular evolutionary concept connecting nonhost resistance, pathogen host range, and pathogen speciation. *Trends in Plant Science* **16**, 117-125.
- Schürch S, Linde CC, Knogge W, Jackson LF, McDonald BA (2004) Molecular population genetic analysis differentiates two virulence mechanisms of the fungal avirulence gene NIP1. *Molecular Plant-Microbe Interactions* **17**, 1114-1125.
- Schwartz MW, Hoeksema JD, Gehring CA, *et al.* (2006) The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology letters* **9**, 501-515.
- Singh RP, Hodson DP, Huerta-Espino J, *et al.* (2011) The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production. In: *Annual Review of Phytopathology*, pp. 465-481.
- Smart CD, Fry WE (2001) Invasions by the late blight pathogen: renewed sex and enhanced fitness. *Biological Invasions* **3**, 235-243.
- Stajich JE, Berbee ML, Blackwell M, *et al.* (2009) The Fungi. *Current Biology* **19**, R840-R845.
- Stewart JE, Timmer LW, Lawrence CB, Pryor BM, Peever TL (2014) Discord between morphological and phylogenetic species boundaries: incomplete lineage sorting and recombination results in fuzzy species boundaries in an asexual fungal pathogen. *BMC Evolutionary Biology* **14**, 38.
- Strange RN, Scott PR (2005) Plant Disease: A Threat to Global Food Security. *Annual Review of Phytopathology* **43**, 83-116.
- Stukenbrock EH, Banke S, Javan-Nikkhah M, McDonald BA (2007) Origin and domestication of the fungal wheat pathogen I via sympatric speciation. *Molecular Biology and Evolution* **24**, 398-411.
- Stukenbrock EH, Christiansen FB, Hansen TT, Dutheil JY, Schierup MH (2012) Fusion of two divergent fungal individuals led to the recent emergence of a unique widespread pathogen species. *Proceedings of the National Academy of Sciences* **109**, 10954-10959.
- Stukenbrock EH, McDonald BA (2008) The origins of plant pathogens in agro-ecosystems. In: *Annual Review of Phytopathology*, pp. 75-100.
- Swann EC, Frieders EM, McLaughlin DJ (1999) *Microbotryum*, *Kriegeria* and the changing paradigm in basidiomycete classification. *Mycologia*, 51-66.

- Talbot JM, Bruns TD, Taylor JW, *et al.* (2014) Endemism and functional convergence across the North American soil mycobiome. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 6341-6346.
- Taylor DR, Keller SR (2007) Historical range expansion determines the phylogenetic diversity introduced during contemporary species invasion. *Evolution* **61**, 334-345.
- Taylor JW, Fisher MC (2003) Fungal multilocus sequence typing—it's not just for bacteria. *Current Opinion in Microbiology* **6**, 351-356.
- Taylor JW, Jacobson D, Fisher M (1999) The evolution of asexual fungi: reproduction, speciation and classification. *Annual Review of Phytopathology* **37**, 197-246.
- Taylor JW, Jacobson DJ, Kroken S, *et al.* (2000) Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology* **31**, 21-32.
- Taylor JW, Turner E, Townsend JP, Dettman JR, 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-Biological Sciences* **361**, 1947-1963.
- Tedersoo L, Bahram M, Toots M, *et al.* (2012) Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology* **21**, 4160-4170.
- Thorsten Lumbsch H, Buchanan PK, May TW, Mueller GM (2008) Phylogeography and biogeography of fungi. *Mycological Research* **112**, 423-424.
- Thrall PH, Hochberg ME, Burdon JJ, Bever JD (2007) Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution* **22**, 120-126.
- Thrall PH, Oakeshott JG, Fitt G, *et al.* (2011) Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evolutionary Applications* **4**, 200-215.
- Valade R (2012) Potentiel évolutif et adaptation des populations de l'agent du mildiou de la laitue, *Bremia lactucae*, face aux pressions de sélection de la plante hôte, *Lactuca sativa*.
- Vellinga EC, Wolfe BE, Pringle A (2009) Global patterns of ectomycorrhizal introductions. *New Phytologist* **181**, 960-973.
- Vercken E, Fontaine MC, Gladioux P, *et al.* (2010) Glacial refugia in pathogens: European genetic structure of anther smut pathogens on *Silene latifolia* and *Silene dioica*. *PLoS Pathogens* **6**, e1001229.
- White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR protocols: a guide to methods and applications* **18**, 315-322.
- Wolfe BE, Richard F, Cross HB, Pringle A (2010) Distribution and abundance of the introduced ectomycorrhizal fungus *Amanita phalloides* in North America. *New Phytologist* **185**, 803-816.

Zaffarano PL, McDonald BA, Linde CC (2009) Phylogeographical analyses reveal global migration patterns of the barley scald pathogen *Rhynchosporium secalis*. *Molecular Ecology* **18**, 279-293.

Figure legends:

Figure 1: An invasion scenario typical for fungi and essential questions to illuminate the process. A) The figure shows the phylogenetic diversity and geographic distribution of a fungal group from which a species has invaded other regions and lists the questions fundamental to invasion dynamics: recognition of local species diversity in the native range, with the delimitation of sibling species, identification of the traits facilitating invasion, source populations, introduction pathways, occurrence of bottlenecks or of multiple introductions, possible evolutionary or ecological changes, such as host shift, changes in mode of reproduction or in other traits. The red circles represent introduced populations while the non-red circles represent native fungal species. B) Successive filters that species must pass for invasions to be successful (dispersal, abiotic and biotic interactions) and possible mechanisms facilitating invasions (Human-mediated dispersal, available abiotic and biotic niche, enemy release, spore resistance, dispersal ability, plasticity, mixed-mating systems, host range for symbionts, or competitive ability).

Figure 2: Pie charts representing the frequency of documented cases of associations with novel hosts, bottlenecks, multiple introductions, hybridization/admixture, and changes in mode of reproduction (shift to clonality), in a sample of $N=47$ invasive fungi or oomycetes. These are the 47 cases, found in an exhaustive literature search, for which data were available on the population genetics of invasion or on the occurrence of genetic changes in introduced regions. Details and references are presented in Table S1, Supporting Information. For each of the 47 cases, the following information was recorded when

available: species name, taxonomic affiliation (*e.g.*, Basidiomycota, Oomycota), lifestyle (*e.g.*, tree mutualist, animal pathogen, crop pathogen, tree pathogen), native region, introduced area, host in native range, host in introduced range, change in mode of reproduction (shift to clonality), change in other life history traits (*e.g.*, increase in aggressiveness, new virulence traits, adaptation to higher temperatures), putative introduction pathway (*e.g.*, trade of host plants), evidence for the occurrence of a bottleneck and its strength, evidence for the occurrence of multiple introductions in at least one introduced area, evidence for the occurrence of hybridization between species or admixture between gene pools, and the corresponding references. Admixture refers to cases where the mixing of two distinct lineages has been shown in clustering analyses or when it has been explicitly tested using simulations (*i.e.*, the occurrence of multiple introduction *per se* is not considered as sufficient to infer 'admixture'). When the native region has not been identified, an emergence without invasion (*e.g.*, by evolution of higher virulence or host shift) can often not be excluded.

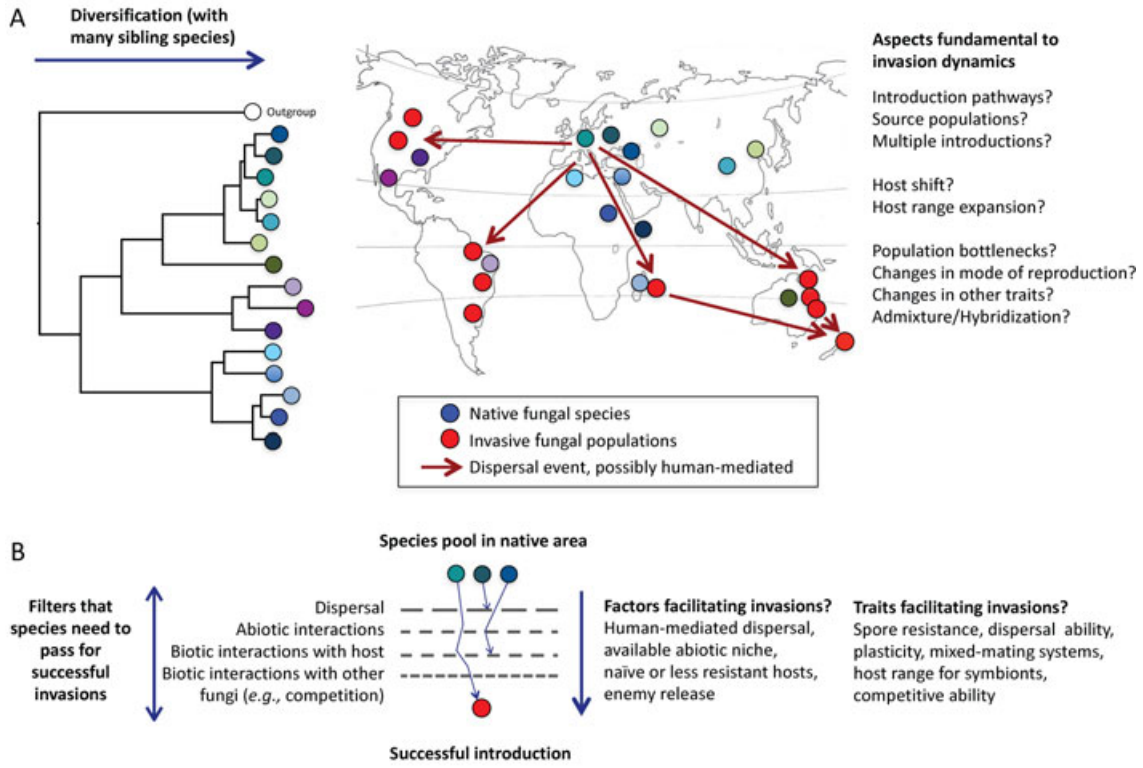
Figure 3: Assignment of North American fungal *Microbotryum lychnidis-dioicae* samples, collected on *Silene latifolia*, to European populations. **A)** Map of the samples collected in the United States and Europe ($N=328$ individuals), with colors representing the mean membership proportions inferred by STRUCTURE for $K=6$; higher K did not allow assigning more precisely American isolates to European populations, see Figure S1, Supporting Information. **B)** Map of the samples assigned to the yellow cluster in A and with identical genotypes in the US and in Scotland; a specific color (yellow or brown) has been given for each of the two multilocus genotypes of the yellow cluster in the USA.

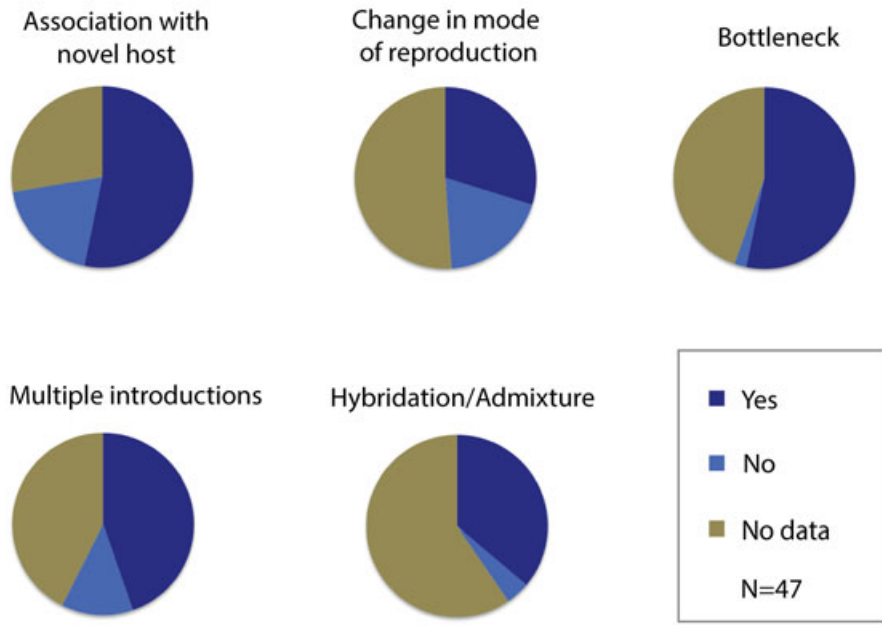
Supplementary Figure S1: Population structure of fungus *Microbotryum lychnidis-dioicae* collected on *Silene latifolia* ($N=328$ individuals), inferred with STRUCTURE, for $K=2$ to $K=8$.

Each vertical line represents an individual. Individuals are grouped on the horizontal axis by country. Colors represent the inferred ancestry from K ancestral populations. The percentages indicated are the proportions of runs that found the main solution shown here.

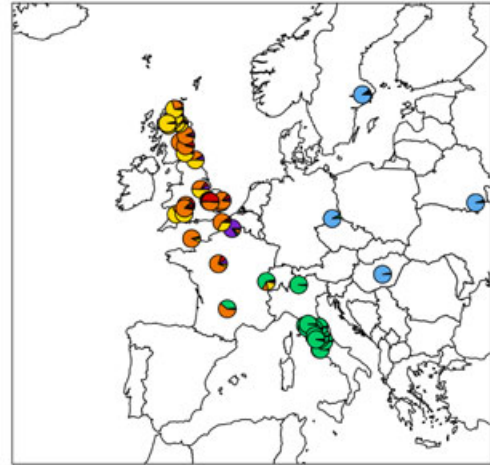
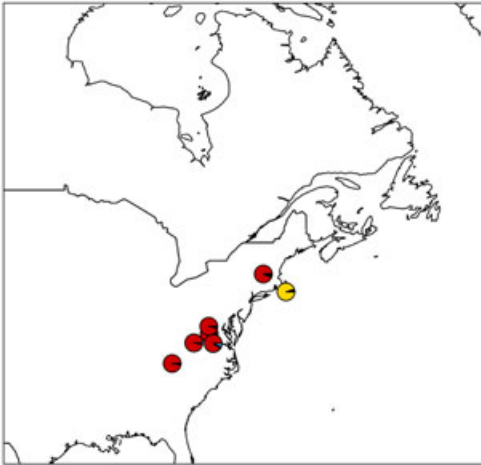
Table 1: Glossary

Term	Definition
Host range expansion	colonization of a new host species, while retaining the ability to infect the ancestral host
Host shift	colonization of a new host species associated with a loss of the ability to infect the ancestral host
Host-tracking	codivergence of the host and the pathogen during crop domestication, with a lineage of fungal pathogens differentiating from that infecting wild crop progenitors, specialization on the domesticated species, and the subsequent invasion of crops worldwide
Effectors	secreted proteins that manipulate host innate immunity, enabling infection to occur (Dodds & Rathjen 2010)
Virulence	ability of a pathogen to cause disease on a host (qualitative measure of pathogenicity)
Aggressiveness	degree of damage caused by a pathogen on a host (quantitative measure of pathogenicity)





(A)



(B)

