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The fungal dimension of biological invasions

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Fungi represent an essential component of biodiversity, not only because of the large number of species, but also for their ecological, evolutionary and socio-economic significance. Yet, until recently, fungi received scant consideration in ecology, especially invasion ecology. Their under-representation is largely the result of a lack of scientific knowledge of fungal biodiversity and ecology. With the exception of pathogenic fungi, which cause emergent infectious diseases, the impact of fungal invasions is often difficult to quantify owing to limited baseline data on fungal communities. Here, we aim to raise awareness among mycologists and ecologists of the fungal dimension of invasions and of the need to intensify research in fungal ecology to address issues of future introductions.

Introduction

Fungi, in the broad sense, are among the most ecologically and evolutionarily diverse organisms on Earth and are classified within three eukaryotic kingdoms (Fungi, Stramenopila and Protista). They are of considerable economic and social importance through beneficial uses (e.g. as sources of food, antibiotics, and industrial enzymes) and as causes of plant and animal (including human) diseases [1–2]. The ecological significance of fungi as symbionts and decomposers has been well recognized and new studies continue to increase our knowledge of their role in the functioning of ecosystems [1,3–5]. Even so, relative to their ecological and evolutionary diversity, fungi have only recently begun to receive consideration from the wider ecology research community [6].

The introduction and spread of exotic and invasive species (see Glossary) is one of the most important problems in conservation biology [7]. A large body of theoretical and empirical work has been built up, primarily directed at invasive plant and animal species [8–10]. Although some recent papers have focused on fungi as invaders (e.g. Refs [11–13]), most books or review articles on invasive species aimed at a broad audience either do not mention fungi or considered them only briefly (e.g. Ref. [14]). In most of these contributions, fungi are considered primarily from a plant or animal-centric point of view [15–17] (Box 1). With the exception of a few well known examples of invasive plant or animal pathogens, fungi are often poorly represented in invasive or alien species databases (Table 1).

We suggest that the fungal dimension of biological invasions deserves additional consideration, not only because of the importance of this group of organisms, but also because advances in fungal ecology can provide insights that are relevant to general issues of biological invasions. When considering invasive fungi, thoughts turn first toward destructive plant diseases, such as chestnut blight (caused by *Cryphonectria parasitica*) [18] or Dutch elm disease (caused by *Ophiostoma ulmi* and *O. novo-ulmi*) [19]. But many non-parasitic fungi are as likely to have been moved from one geographical location to another, even if the impact of their introduction is often

Glossary

Alien (non-native, exotic, non-indigenous, foreign): a species, sub-species or lower taxon occurring outside of its natural range and dispersal potential (from IUCN, see http://www.issg.org).
Invasive species (invader): an alien species that becomes established in natural or semi-natural ecosystems or habitat, is an agent of change and threatens native biological diversity (from IUCN; see http://www.issg.org).
Invasiveness: the ability of an organism to arrive, spread beyond its introduction site and become established in new locations where it might provide a deleterious or harmful effect on the resident organisms and ecosystem.
Invasibility: the vulnerability or susceptibility of a community or ecosystem to invasions, resulting from its intrinsic properties [9].
Parasexuality: a type of reproduction described in some fungi in which genetic recombination is not based on sexual reproduction (meiosis) but on the mitotic cycle; it involves intra-hyphal nuclear fusion in a heterokaryotic haploid mycelium, followed by mitotic crossing-over, and haploidization of the diploid nuclei [89]
Symbiosis: the relationship between two intimately interacting organisms or populations, commonly used to describe all relationships (including mutualism, commensalism and parasitism) between members of two different species, and also to include intraspecific associations. The members are called symbionts. The term 'symbiosis' is sometimes restricted to associations that are mutually beneficial, and this practice has resulted in some confusion.

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Box 1. Fungus-mediated invasions

Fungal species that form mutualistic symbiotic associations with plants (e.g. mycorrhizal fungi or leaf endophytes) can help plants to become invasive by improving their fitness. The invasion of some alien weeds has been facilitated by arbuscular mycorrhizal fungi [70]. Similarly, the leaf endophyte *Neotyphodium coenophialum* might have increased the invasive success of the grass *Festuca arundinacea*, introduced to North America from Europe, by inducing higher vigour, toxicity to herbivores and drought resistance than in uninfected native grasses [71–72]. However, for both types of symbiosis, it has not always been clearly established whether the fungal symbionts had been introduced together with the invasive weeds or were native to the new habitat. This issue is better documented for ectomycorrhizal trees. Some pines and eucalypt species became invasive in Africa, Australia and New Zealand by escaping from plantation forests with assistance from their specific fungal symbionts [12,70]. In this case, the causal role of the accompanying fungi has been demonstrated by the fact that the seedlings always wilted and died until adequate symbionts were introduced as soil or mycorrhizal planting stock from tree native areas.

An opposite situation occurs when the absence of specific fungi favours invasion. The enemy release (ERH) and the evolution of increased competitive ability (EICA) hypotheses argue that the success of invasive species results from reduced attacks by natural enemies, for example, plant pathogenic fungi, from their native habitat and re-allocation of resources from defence to size or fecundity [15,16,73]. CBC is used to fight alien invasive weeds by re-uniting them with their native pathogens. An example is the European leaf rust *Phragmidium violaceum* introduced into Australia to fight the invasive European blackberry *Rubus fruticosus* [74] (Figure I). The invasion success of CBC agents is selected for and focused on a highly susceptible target host, and possible non-target effects, that is, effects on non-target hosts, are carefully examined before release [45]. This applies especially to fungi, which, compared with insects, have been used relatively recently as agents of CBC. Only 26 fungal pathogens, most of which are rust fungi chosen for their high level of host specificity, have been released to date and unexpected non-target effects have not yet been observed [45].

Figure I. Blackberry plants infected with European rust fungus *Phragmidium violaceum*, a biological control agent for blackberry in Australia. The newly released strains of *P. violaceum* are highly host specific for weedy blackberries. Reproduced with permission from CSIRO.

difficult to assess. Here, we explore how fungi and fungal communities fit into the broader picture of invasion biology and we strongly support future research in fungal biodiversity and ecology to address issues of future introductions.

The impacts of fungal invasions

The commonly used definition of biological invasions, in management and policy but also scientific communities, implies a negative ecological impact. With the exception of emerging infectious diseases in natural ecosystems, the ecological impacts of non-native fungi have not yet been well quantified. This is probably a major reason for the under-representation of fungi in the literature and many databases. In this regard, we agree with the use of the term ‘invasive’ to include any non-indigenous species that has spread and become abundant in a new geographical location regardless of the actual or perceived ecological impact [20,21]. Using this definition, fungi with unknown impact (most saprotrophs and mycorrhizal fungi) and fungi with economic, but unknown ecological impact (pathogens of crop plants), should be included as invaders.

The most obvious impacts of fungal invasions are epidemics caused by exotic pathogenic fungi (Box 2). It has been estimated that 65–85% of plant pathogens worldwide are alien in the location where they were recorded [2]. Such invasions can have significant ecological, economic and social consequences. The European epidemics of *Phytophthora infestans*, the causal agent of potato late blight that led to the Great Irish Famine during 1845–1849, are a prominent example [22]. Invasive plant pathogens have also had dramatic impacts in natural ecosystems [18–19,23]. The introduction of *Phytophthora cinnamomi* into south-western Australia has substantially altered the native plant communities by killing not only the dominant jarrah *Eucalyptus marginata*, but also many understorey

Table 1. Representation of fungi in available databases of alien (invasive) species[a]

Region	List	Fungi	Vascular plants	Vertebrates	Insects	Others	Total	Source
Austria	Neobiota (invasive)	83 (6)	1110 (17)	>500 Animalia (6)		11	1704 (29)	[84]
England	Non-native species	198	1854	109	339	222	2722	[85]
India	Invasive species (in progress)	5	40	59			104	http://www.ncbi.org.in/invasive/search/index.html
Latvia	Alien species	7	629	44	99 (invertebrates)	2	781	http://lv.invasive.info/
Lithuania	Invasive species	98	520	26	8	17	669	http://www.ku.lt/lisd/
Nordic–Baltic Europe	Alien species	98	3321	442	1245	397	5503	http://sns.dk/nobanis/
Poland	Alien species	81	282	78	38	132	611	http://www.iop.krakow.pl/ias/
Switzerland	Alien species (invasive)	?[b] (6)	362 (48)	40 (20)	311 (16)	87 (17)	800 (107)	[86]
USA	Invasive species	38	427	11	160	44	680	http://www.invasive.org
World	Global invasive species (worst)	9 (5)	142 (35)	73 (30)	42 (14)	53 (16)	319 (100)	http://www.issg.org/database/welcome/

[a] When fungi are included; several other databases without fungi.

[b] Only alien species threatening biodiversity were listed for fungi. It was considered impossible to list all neomycetes.

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Box 2. Fungal invasions and emerging infectious diseases

Emerging infectious diseases can be defined as diseases caused by pathogens showing a new or increased geographical range, a new host range or caused by new or recently evolved pathogens. Fungi is the second taxonomic group, after viruses, responsible for plant emerging infectious diseases (30% are caused by fungi) and 40% of new fungal diseases are associated with the introduction of an exotic pathogen species [75]. Introduced pathogens have also been recognized as an important cause of emerging diseases in animals, although fungi are less represented among animal pathogens [76,77]. The crayfish plague is a well documented example (Table 2, main text). The recent worldwide outbreaks of amphibian chytridiomycosis, implicated in population declines, might also be caused by anthropogenic introduction of the pathogen, *Batrachochytrium dendrobatidis,* outside its endemic range [33].

Emerging infectious diseases caused by invasive fungi are the result of novel host–pathogen interactions [13], which often involve a new host species (host jump) or different populations of the same host. Many emerging infectious diseases have arisen after host jumps, often occurring between species from the same genus (e.g. from Asian to American and European chestnut for *Cryphonectria parasitica*, from Asian to American and European pines for *Cronartium ribicola,* from Asian to American *Cornus* spp. for *Discula destructive* [46]), although host jumps between unrelated taxa are possible [58]. In the case of many cultivated plants, novel interactions occur at the infra-specific (cultivar) level, when exotic fungi recolonize their natural hosts that had remained free of their pathogens since their introduction (Box 3).

Emerging infectious diseases might also be caused by 'new pathogens' arising from hybridization favoured by novel co-occurrence of allopatric fungal species of related taxa. Hybrids of *Melampsora* spp., the cause of poplar rust, have overcome resistance of previously resistant cultivars [78]. *Phytophthora alni* ssp. *alni*, the most widespread subspecies of a new taxon (*P. alni*) spreading in European riparian forests and killing alders, appears to be the result of several hybridizations between *P. alni uniformis* and *P. alni multiformis*, themselves hybrids or the result of autopolyploidization [79] (Figure I). Introgression of genes can also occur from resident species to an invasive species, resulting in increased fitness of the invader, as documented for *Ophiostoma ulmi* and *O. novo-ulmi* [19].

Figure I. Typical crown symptoms of alder decline caused by *Phytophthora alni* compared with healthy trees **(a)**. **(b)** Ornamented oogonium and bicellular amphigynous antheridium of the interspecific hybrid *Phytophthora alni* subsp. *alni*. Reproduced with permission from C. Husson, INRA Nancy (a) and R. Ioos, LNPV Nancy (b).

species (85% of the Proteaceae are susceptible to this pathogen in Western Australia) [24]. There are, however, distinct ecological and evolutionary differences between the introduction of fungi into agricultural and natural ecosystems (Box 3). In addition, the impact of the potential exchange of fungal pathogens between agriculture and native plant communities has not been extensively studied [25,26].

Beyond well known plant and animal pathogens causing emerging diseases, the impacts of exotic fungi on ecosystem structure and function have not been extensively characterized. This is especially true when we consider potential effects of exotic plants, animals and microbes on native fungal communities. Quantifying the impacts of exotic species is often impossible or difficult because of a lack of baseline ecological data on invaded ecosystems [27]. Compared with plant and animal communities, a lack of baseline data is especially glaring for fungal communities in many ecosystems.

The impacts of invasive organisms can be measured on many different spatial and temporal scales and lead to cumulative and indirect effects that result in a cascade of changes throughout an ecosystem [28]. Much research on exotic plants and animals has been directed at competitive interactions at the same trophic level. Invasions by related species can disrupt the composition and functioning of entire communities [28]. With fungi, most research has been conducted on the effects of the exotic fungus on other trophic levels; that is, plant and animal pathogens in agricultural and natural ecosystems (Boxes 2,3). How have exotic fungi and other microbes interacted with native fungal communities? This is probably the least studied area concerning exotic fungi. The introduction and spread of saprotrophic and mycorrhizal fungi have been documented, but their potential impacts are unclear. *Clathrus archeri*, the octopus stinkhorn, is a typical example. After its accidental arrival in Europe in 1920, probably through wool trade from Australia, it spread throughout Europe, reaching high population levels (hundreds of fruiting bodies) in some locations [29]. However, the possible negative interactions with native fungal decomposers have not yet been studied. The potential impact of introduced mycorrhizal fungi has long been assumed to be negligible or positive (but see Box 1); however, this field deserves more attention [12,30].

Basic knowledge of fungal diversity and biogeography is crucial

The number of fungal species has been estimated to be at least 1.5 million, but <10% have been described [6,31]. Determining what is an exotic species can be difficult to do for fungi. Baseline data on the diversity of resident fungal species is limited even for well studied environments in temperate regions. Biodiversity studies continue to reveal numerous undescribed species or potentially much larger geographical ranges for well known species. In understudied environments, such as the tropics and the soil, researchers are only now coming to grips with the true amount of fungal diversity. When undescribed species are found, how likely is it that they are native to that geographic location [32]? In contrast to most terrestrial plant and animal species, fungi are often listed as cosmopolitan and many are described as having circumglobal geographical ranges. Unlike many plants and animals, fungi are

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Box 3. Fungal invasion of agricultural versus natural ecosystems

Major agricultural food crops, most horticultural plants and many forest plantations can be considered exotic plants in most areas where they are grown. During fungal invasions of agroecosystems, plants are often re-united with pathogens with which they coevolved. Agriculture, therefore, offers an interesting twist to the enemy escape hypothesis. The planting of large monocultures without devastating epidemics can be accomplished by growing plants without their coevolved pathogens. An illustrative example is *Hevea brasiliensis*, for which exotic plantations established in South-Eastern Asia provide most of the current supply of rubber, whereas plantations in South America, where *H. brasiliensis* is endemic, are severely affected by the native fungus *Microcyclus ulei,* the causal agent of Southern American Leaf Blight [80] (Figure I).

If the host–pathogen system is brought back together in a different geographical setting under different environmental conditions (e.g. monocultures, reduced genetic variability in the host and increased moisture regimes) the result is often devastating epidemics. Two classic examples include late blight of potato (caused by *Phytophthora infestans*) in Europe [22] and coffee rust (caused by *Hemileia vastatrix*) on coffee in Asia [81]. Both of these crops were grown for many years in the exotic locations before the introduction of their respective pathogens. Other important examples include soybean rust in the Americas [82], grapevine powdery and downy mildew in Europe, and wheat stripe rust in Australasia [50]. The historical and potential impacts of these invasive pathogens in agriculture have long justified regulatory efforts at regional, national and international levels [83].

By contrast, pathogens introduced into natural ecosystems do not share a coevolutionary history (under any environmental condition) with potential hosts. There are many examples of exotic fungal plant pathogens in natural ecosystems, particularly forests, where naïve hosts have shown very high susceptibility to infection and death [11] (Figure II). In most of these cases, the pathogens were completely unknown before their introduction and only in a few cases has the geographical area of origin of the pathogen been determined [11,33]. Because of the potential for host switching and different ecological behavior under changing environmental conditions, it has been difficult to predict which pathogens would be damaging to natural ecosystems in exotic locations. Therefore, more broadly defined regulations are necessary to prevent invasions than have been utilized with agriculture (i.e. focus on individual pathogens).

Figure I. Invasion of a rubber plantation by South American leaf blight **(a)**. The trees in the foreground have been killed by the disease whereas those in the background have not yet been infected. **(b)** Lesions caused by *Microcyclus ulei* on a rubber leaf. **(c)** *Bicellular conidia* (asexual spores) of *M. ulei*. Reproduced with permission from Carlos Mattos, Michelin Corp. (a); Jean Guyot, CIRAD (b) and Fabrice Pinard (c).

Figure II. Extensive mortality of tanoak *Lithocarpus densiflorus* in native forests of coastal California caused by the exotic plant pathogen *Phytophthora ramorum*. Reproduced with permission from Dave Rizzo.

often difficult to detect without a concerted effort using special cultural methods or molecular tools. Even for fungal plant pathogens that are apparently novel and causing major ecological impact, their native range often remains unknown [11,33].

The notion of an ‘exotic’ or ‘invasive’ species requires a precise, accurate taxon identification. For example, Pringle and Vellinga [34] point out many contradictions in the extensive literature about *Amanita phalloides* (the death cap) as a putative invader from Europe to North America that were linked to vague or incorrect species definitions. Over the past ten years, species concepts in the fungi have undergone a shift from an emphasis on morphology-based species concepts to concepts based on evolutionary biology [35–36]. The use of molecular tools and phylogenetic analysis has enabled finer distinctions in delimitation of fungal lineages and species recognition. Many morphospecies have been shown to be a complex of several cryptic species differing in their ecology (e.g. geographical or host range) and evolutionary history (e.g. Ref. [37]). As often argued for plants and animals [21], the infraspecific level might be the most relevant in fungal invasions. Many fungi once thought to have broad geographical distributions have been shown to have strongly structured populations at scales ranging from landscapes to continents. Considering this infraspecific level is especially important for parasitic fungi that exhibit differing host preferences based on pathogen genotype or for heterothallic species where the presence of the two mating types is needed for sexual reproduction (e.g. Ref. [22]).

The continued use of modern population genetic tools and analyses will further refine hypotheses of the geographical origin and movements of fungal species and genotypes [38]. Founder effects can lead to populations with relatively little genetic variation [39]. *Cryphonectria parasitica* and *Fusarium circinatum*, causal agents of chestnut blight and pitch canker of pine, respectively, are examples of plant pathogens that have limited genetic variation, based on genotypic and phenotypic markers, in their area of introduction as compared to their native geographical range [40–41]. For other plant pathogenic fungi, such as *Phytophthora lateralis* and *P. ramorum*, limited genetic variation in the putative exotic location supports the idea of a recent introduction even though

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their native geographical range is not known [11]. Using mtDNA haplotypes and herbarium specimens, May and Ristaino [42] suggested the origin of the strains of *P. infestans* responsible for the historic epidemics in Ireland. By contrast, multi-gene phylogenies have shown that the fungus associated with beech bark disease, *Neonectria faginata*, long considered to be an exotic species in North America introduced along with a scale insect, is probably native to North America [43].

Can we predict the future of fungal invasions?

The invasive potential of fungi

Successful invaders can be defined as species able to pass through a series of filters corresponding to the successive steps of an invasion: transport, establishment and spread [10,20,39]. In contrast to plant and animal invasions, deliberate introductions have probably had a minor role in fungal introductions. Desirable fungi introduced in new habitats mostly include pathogenic fungi used for classical biological control (CBC) and species used for mycorrhization. Few, if any, examples of fungal invasions resulting from the escape of purposefully introduced pathogenic or mycorrhizal fungi have been reported (Box 1) [12,44]. The low invasive success of these deliberate introductions could lie in the low genetic diversity of the introduced material and in the absence of close relatives of the target hosts to which fungi could extend their ranges [45]. Still, increased knowledge is needed to minimize the likelihood of deleterious invasive species problems associated with the intentional movement of fungi [12].

Conversely, unintentional introduction is a common pathway for invasive fungi [46]. The introduction of exotic tree species has been a vector of introduction of specific mycorrhizal species, such as Australian fungal species introduced with eucalypts in Spain [30]. Many fungal pathogens have also been introduced with their host plants; for example, *P. infestans* in infected tubers from America to Europe, *C. parasitica* on infected Japanese chestnut trees from Asia to North America, or *Sphaeropsis sapinea* in pine seeds imported in South Africa [47]. The inconspicuousness of fungi, either in a mycelium form in asymptomatic plants, or as microscopic propagules, clearly favours multiple introductions with high propagule pressures, which is a factor of invasive success [48]. Several studies have demonstrated the variety of fungal species and the large number of viable spores brought in by incoming passengers in airports [49–50]. Spread by insects is a further way of dissemination for some fungi, such as *Seiridium cardinale*, the causal agent of cypress canker, or *O. ulmi* and *O. novo-ulmi,* causes of Dutch elm disease [51–52]. Many fungi also produce propagules that are resistant to environmental stresses and represent an important survival advantage during transport or in the initial stages of an invasion. Sexual reproduction by selfing for homothallic species, asexual reproduction, or parasexuality enable some fungal species to persist and establish in novel environments in spite of a limited genetic diversity of the migrants. For example, *P. cinnamomi* has been able to establish worldwide in a large range of subtropical to temperate areas, although only one mating type is found outside its native region in Indonesia [24].

Competitive ability, especially in relation to invasiveness, has been little documented for fungi. The replacement of *O. ulmi* (responsible for the first pandemic of Dutch Elm disease in Europe) by the closely related *O. novo-ulmi* (cause of the second pandemic) is perhaps the best example [19] (Box 2). Epidemic development of cypress canker was also shown to be associated with a shift in the fungal load of the cypress bug, *Orsillus maculatus*, from the endemic *Pestalotia funerea* to the invasive *S. cardinale* [53]. The replacement of the local and saprophytic species *Cryphonectria radicalis* in Europe by the alien pathogenic *C. parasitica* has also been hypothesized [54].

Phenotypic plasticity and evolutionary potential are other key features in invasive success, which have been observed for many fungi. Phenotypic plasticity in fungi applies to their response both to abiotic and biotic environments. Some fungi have invaded semi-arid areas where they were hardly expected to survive [55]. *Suillus luteus* and *A. phalloides* have been shown to display different host ranges in their native and introduced areas [12,34]. The evolutionary potential of many pathogenic fungi has been demonstrated by their ability to overcome host plant resistance [4,56]. Host jumps, changes of virulence and hybridizations have been shown to have a major role in fungal pathogen invasions and the emerging infectious diseases that they cause [13,5–58] (Box 2).

Predicting which species within a taxonomic group are more likely to become invasive is an important issue [10], although the success of quantitative approaches to forecasting has been questioned [59]. These types of analyses, however, remain to be done among fungi [12–13].

The invasibility of communities by fungi

The concept of niche opportunity, that is, ‘the potential provided by a given environment for alien organisms to have a positive rate of increase from low density’, has recently been proposed to define the conditions that promote invasions [60]. This concept encompasses several hypotheses or theories proposed to explain invasion success: resource opportunities, including fluctuation of resources and disturbance, biotic resistance and natural enemy release, and species richness [9,15–17,59–61].

In contrast to invasive plants, most of these hypotheses have not yet been investigated in fungi. The virus that infects *C. parasitica* (*Cryphonectria* Hypovirus) is a well-known example of a hyperparasite infecting an invasive fungus [18]. The virus decreases the virulence, fecundity and growth of the fungus and its absence in the American continent could account for the rapid invasion by the fungus, in accordance to the enemy release hypothesis. However, the presence of the virus in Europe, where it was introduced along with the fungus, enabled chestnut recovery but did not impede the spread of *C. parasitica*.

Invasion success in plants and animals has focused mainly on factors affecting the relative competitive abilities of invaders and residents, that is, interactions at the same trophic level. Conversely, for pathogenic and mycorrhizal fungi, the niche opportunity seems to be mostly shaped by the strong functional interactions between the invader and the components of other trophic levels, especially plants, which act as the resource. Species richness has

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been related to vulnerability to fungal diseases. Natural ecosystems, with high biodiversity, generally have a lower vulnerability to disease than do agroecosystems characterized by the cultivation on a large scale of a few species of plants with the same or similar genetic background (Box 3) [4,62]. It has also been shown experimentally that a reduction in grassland plant richness increases the invasibility of the community by fungal pathogens [63]. Regional coevolutionary trajectories [64] with plants are a key determinant in the outcome of interactions with symbiotic fungi. Fungi and their host plants have potentially coevolved for long periods of time in their centres of origin

Table 2. Observed or potential ecological interactions among invasive fungi, plants, animals and other microbes

Invader	Interaction	Result	Examples	Refs
Fungal plant parasites	Agricultural pathogen reunited with coevolved host	Emerging disease	Potato late blight *Phytophthora infestans* (worldwide); soybean rust (North America); rubber leaf blight (South America); coffee rust (Asia and South America)	[2,22,80–82]
	Specialist pathogen (relatively) in natural ecosystem; host–pathogen not coevolved (host jump)	Emerging disease	Chestnut blight *Cryphonectria parasitica* (North America and Europe); Dutch elm disease *Ophiostoma ulmi* and *O. novo-ulmi* (North America and Europe); cypress canker (Europe); white pine blister rust *Cronartium ribicola* (North America)	[18–19, 51,81]
	Generalist pathogen in natural ecosystem; host–pathogen not coevolved (host jump)	Emerging disease	*Phytophthora cinnamomi* (Australia, Jarrah decline; Europe, oak decline; North America); sudden oak death *Phytophthora ramorum* (North America)	[23–24]
	Hybridization or introgression with resident (native or other invasive) species	Emerging disease	*Phytophthora alni* (Europe); hybrids between *O. ulmi* and *O. novo-ulmi*; *Melampsora* spp. hybrids on poplar	[19,78–79]
Fungal animal parasites	Specialist pathogen (relatively) in natural ecosystem; host–pathogen not coevolved (host jump)	Emerging disease	Crayfish plague *Aphanomyces astaci* (Europe), carried by introduced North American crayfish, with chronic infections, and transmitted to native European crayfish	[77]
	Generalist pathogen in natural ecosystem; host–pathogen not coevolved (host jump)	Emerging disease	Frog chytrid *Batrachochytrium dendrobatidis* (Australia, North America, South America and Europe); coral fungus *Aspergillus sydowii* (Caribbean)	[33,77]
Fungal mutualists	Mycorrhizae or endophytes interact with exotic plants	Facilitate exotic plant invasions	Invasion of exotic pines in southern hemisphere from plantation forests; invasive success of several weeds and grasses	[12,70–72]
	Arbuscular mycorrhizae act as parasites on native plants	Reduce competitive ability of native plants	Experimental, no clear examples in the field	[12]
	Exotic mycorrhizae or endophytes interact with indigenous species	Impact fungal community	Many ectomycorrhizal fungi (e.g. *Amanita phalloides*, *A. muscaria*) have been introduced into numerous locations; impact unknown	[12,30]
	Ectomycorrhizae interact with native decomposers	Impact decomposition systems	*Suillus luteus* associated with carbon depletion in *Pinus* plantations and surrounding grassland	[12]
Fungal saprobes	Interact with native decomposers	Outcompete native mycoflora? Impact decomposition systems?	*Clathrus archeri* (Europe; North America); *Perenniporia ochroleuca*, *Flaviporus brownei* (Europe); impacts unknown	[29]
Plants	Interact with native fungal mutualists (mycorrhizae or endophytes)	Facilitation of exotic plants; loss of native fungal diversity	*Neotyphodium coenophialum* (endophyte) enhance invasiveness of tall fescue *Festuca arundinacea*; *Rhododendron maxum* forms dense thickets that reduced number and changed composition of mycorrhizal fungi on the roots of hemlock *Tsuga canadensis* seedlings	[11,70–72]
	Interact with native saprobes	Impact decomposer systems through changes in quantity, quality and diversity of litter; change fungal diversity	Exotic *Eucalyptus* spp. in riparian areas correlated with reduced aquatic hyphomycete diversity	[11]
	Interact with invasive parasites	Vectors and/or source material	*Berberis vulgaris* facilitates *Puccinia graminis* spread (North America); *Phytophthora ramorum* and ornamental plants (North America and Europe)	[11,23,81]
	Lack of interactions with native parasites	Enemy release hypothesis; evolution of increased competitive ability	*Prunus serotina* (Europe) has limited interactions with root disease pathogens (e.g. *Pythium*)	[15,73,87]
	Interact with released coevolved parasites	Classical biological control	26 fungal pathogens, mainly rust fungi chosen for high level of host specificity, released to date with variable success in controlling invasive plants; unexpected non-target effects not yet observed	[45,74]
Animals	Interact with native mycorrhizae	Disrupt mycorrhizal communities	Exotic earthworms (*Lumbricus rubellus*, *L. terrestris* and *Octolasion tyrteum*) correlated with reductions in colonization by arbuscular mycorrhizal on sugar maple	[11]
	Interact with native saprobes and soil fungi	Positive or negative influences on native decomposer communities	Exotic earthworm (*Dendrobaena octaedra*) reduces densities and community composition of microfungi	[11]
	Interact with native and invasive fungal parasites	Vectors of exotic and native parasites; increase populations of native parasites	*Saprolegnia ferax*, a pathogen of amphibians, is greater in toad populations exposed to hatchery-reared trout; Exotic reptiles can serve as vectors of *Basidiobolus ranarum* (causes basidiobolomycosis in humans, horses and other vertebrates); European elm bark beetle *Scolytus multistriatus* is vector for *O. ulmi* and *O. novo-ulmi* (North America)	[11,52]
Other microbes (e.g. viruses, bacteria)	Interact with native and invasive fungal parasites	Increase levels of fungal parasites through host stresses	HIV infection predisposes humans to fungal pathogens; e.g. *Pneumocystis carinii*, *Cryptococcus neoformans*, *Histoplasma capsulatum*, *Candida albicans* and *Penicillium marneffei*	[88]

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[4]. By contrast, invasions by pathogenic fungi are usually characterized by an absence of coevolution between the fungus and its new hosts, referred to as 'new encounter' or 'novel interaction' [13,65], or re-encounter for many crop pathosystems (Box 3). The success of invasive pathogens in these new encounters might be explained by an increased aggressiveness against naïve host species that have not had an opportunity to evolve resistance. A similar evolutionary process has been referred to in the 'novel weapons' hypothesis to explain interactions between invasive and resident plants [16,61].

There have been many ecological studies in recent years concerning the dynamics of fungal communities [5]. These have not been directed at invasions *per se*, but their results indicate the potential impacts that plant, animal, fungal and other microbial invaders can have on native fungal communities. For example, changes in saprobic and mycorrhizal fungal communities during plant community succession have been well documented and it is probable that exotic species-mediated successional changes would result in changes in fungal communities. Plant defoliation has been shown to influence mycorrhizal community structure [66]. These studies with native defoliating insects suggest the possibility of impacts on mycorrhizal communities through introductions of exotic defoliating insects such as the gypsy moth. An increased knowledge of the assemblage of fungal species in the resident community, and its disruption by invaders, should lead to a better understanding of invasibility, even for plant symbiotic fungi. For instance, recent experimental studies have suggested that colonization of plant tissues by fungal endophytes decreased their subsequent colonization by pathogenic fungi at the plant level [67].

Conclusion

We believe that the under-representation of fungi in invasion ecology is largely the result of a lack of scientific knowledge of the fungal biodiversity and ecology. Until recently, many mycologists, especially plant pathologists, have remained isolated from the mainstream of ecology and, reciprocally, scant attention has been paid to fungi by ecologists. There are obvious links between epidemiology and invasion biology, both of which are concerned with processes of population increase and spread, including evolutionary dynamics [11,13,68,69]. Continued research on emerging fungal diseases of plants and animals is imperative. But there are other key areas that we believe have been under-represented in the fungal invasive literature [11,12]. In particular, these include the invasiveness of non-parasitic fungi, and the impact of invasive plants, animals and other microbes on the diversity and functioning of native fungal communities (Table 2).

With a few exceptions, most research has been carried out at the level of interactions between individual species rather than at the fungal community level. Studies of exotics must also be carried out along with other fungal ecology research, not considered separately. We must also recognize that the biology of organisms in their native environment can be different than in their place of introduction. This has been especially true for plant pathogens that might be more destructive in different environments. The more we begin to understand fungal ecology in general, the better we will be able to predict the ecological trajectories of future introductions. We advocate better connections between scientific fields, especially ecology, mycology and plant pathology, to exchange knowledge, cross fertilize concepts and eventually make progress in the understanding and control of biological invasions.

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