Biol Invasions (2010) 12:157–172
DOI 10.1007/s10530-009-9439-y

ORIGINAL PAPER

Species diversity and drivers of spread of alien fungi (*sensu lato*) in Europe with a particular focus on France

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Received: 11 July 2008 / Accepted: 20 January 2009 / Published online: 5 February 2009

Abstract A first comprehensive inventory of alien fungi and fungal-like organisms (in Stramenopila) recorded in France since 1800 was established, comprising 227 species, with 64.7% plant pathogens, 29.5% saprotrophic species, 3.5% ectomycorrhizal fungi, 1.3% animal parasites and 0.9% mycopathogenic fungi. Using this and a previously built European dataset, correlates of invasion success in fungi (*sensu lato*) were investigated, especially for pathogenic species occurring in wild environments (mostly forest tree pathogens). Several common features were demonstrated at the two spatial scales. Some taxonomic/phylogenetic orders were shown to be over-represented in alien fungi and Stramenopila pseudo-fungi, e.g. Peronosporales and to have faster spread, e.g. Erysiphales. Residence time and economic variables, especially imports, were important explaining variables of the levels of invasion. The influence of climatic factors was also suggested.

Keywords Biological invasions · Fungi · Oomycota · Plant pathogen · Forest tree pathogen · Invasion success · Invasiveness

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Electronic supplementary material The online version of this article (doi:10.1007/s10530-009-9439-y) contains supplementary material, which is available to authorized users.

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Introduction

Fungi, in the broad classical sense, are an assemblage of polyphyletic origin including eukaryotic species sharing morphological and ecological similarities but belonging to different lineages, mainly in Eumycota, (in Opistokonta) and Stramenopila (=Heterokonta, Chromista *auct*.). This assemblage is a major component of biodiversity on Earth, as the second largest group of Eukaryotes, after insects. Recent estimates of the number of fungal species range from 712,000 (conservative estimation by Schmit and Mueller 2007) to 1.5 million (Hawksworth and Mueller 2005) for Eumycota at least, of which less than 10% have been described (Hawksworth 2001). As inconspicuous organisms, fungi have been far less studied than mammals or vascular plants. Invasion ecology has paid very limited attention to fungi (Pyšek et al. 2008), which are usually poorly, if at all, represented in alien species databases: fungi hardly represent 5% of the species listed in the Global Invasive Species Database (http://www.issg.org/database/welcome/). The five fungal species listed in the "One Hundred of the World's Worst Invasive Alien Species" subset of the Global Invasive Species Database are two animal pathogens (*Aphanomyces astaci*, the crayfish plague; *Batrachochytrium dendrobatidis*, the frog chytrid fungus) and three forest tree pathogens (*Cryphonectria parasitica*, the agent of chestnut blight; *Ophiostoma ulmi sensu lato*, the agent of Dutch elm disease; *Phytophthora cinnamomi*, an agent of decline in many woody species). The focus on pathogenic fungi can easily be explained by their devastating, visible effect on native animals or trees and the resulting loss in biodiversity. Despite their less apparent impact, non pathogenic fungi could affect important functions in the ecosystems, e.g. regulation of the mineral and energy cycling, through their interactions with the invaded local communities, especially with native fungi (see examples and references in Desprez-Loustau et al. 2007). From a more human point of view, fungal introductions may entail various relevant problems, e.g. introduction of toxic species such as *Amanita phalloïdes* in North America (Pringle and Vellinga 2005), or repellent fungi such as the stinking *Clathrus archeri* in Europe (Parent et al. 2000).

The low representation of fungi in the invasive species databases is most likely due to a poor knowledge of the fungal communities rather than to a low invasion success in fungi (Desprez-Loustau et al. 2007). The alien status itself which takes into account three dimensions, systematics, geographical range and time of introduction (Pascal et al. 2006) is often difficult to assess for fungi. When an undescribed species is found, how likely is it that it is actually native to the geographic location of the first record? For example, the previously undescribed *Phytophthora ramorum* was recently discovered both in Europe and Northern America. It has been assumed to be alien in both regions, since multilocus analysis demonstrates an extremely narrow genetic structure (Ivors et al. 2006) but its region of origin is still unknown. The biogeography of fungi in general remains largely unknown. Many fungal species, as other microbial eukaryotes, are viewed as cosmopolitan organisms (Finlay 2002), which precludes the assignment of an alien status in a particular region. However, the lack of endemism in fungi probably reflects in many cases a lack of recognition of different allopatric species, phylogenetically distinct but hidden within a single morphological species with a global distribution (Taylor et al. 2006). Many fungal species previously defined on the grounds of morphology (or of symptomatology for plant pathogens) have been shown to be a complex of several cryptic species differing in their ecology, and, especially in their geographic range. Among several recent examples is *Mycosphaerella pini*, a foliar pathogen of pines, which was shown to be a complex of two phylogenetic species, one being found worldwide while the other is restricted to the North-Central USA (Barnes et al. 2004). The study of fungal invasions is thus inseparable of a geographically large taxonomical expertise.

Understanding and, subsequently, predicting fungal invasions requires the analysis of comprehensive lists of alien fungi, supplemented with characteristics relevant to invasion biology and history (phylogeny, ecology, reproduction biology, region of origin, pathways of introduction, invasion patterns…). A few national inventories of alien fungi have been recently published, especially in North and Central Europe: Germany (Kreisel and Scholler 1994; Kreisel 2000, 103 species), Austria (Essl and Rabitsch 2002, 82 species), Lithuania (Kutorga 2004, 95 species), England (Hill et al. 2005, 197 species), Northern Europe (NOBANIS 2007, 31 species), Poland (Solarz

2007, 89 species), Norway (Gederaas et al. 2007, 263 species). However, patterns and drivers of fungal invasions remain poorly known. In a recent study, Jones and Baker (2007) compiled a list of 234 alien plant pathogens, among which 157 fungi, recorded in Great Britain between 1970 and 2004 and analyzed their introduction patterns. Within the European DAISIE project (http://www.europe-aliens.org), we compiled a dataset of 84 alien invasive fungi in Europe, with data on first record and geographical distribution in European countries, which allowed us to analyse temporal and spatial patterns of fungal invasions across Europe since 1800 (Desprez-Loustau 2008). In the present study, we aimed at getting a better knowledge of the diversity of alien fungi (in the broad sense) and of the drivers of fungal invasions across Europe. To complement existing data for Europe, we built a first comprehensive database of alien fungi recorded in France, where the diversity of bioclimatic zones (continental, alpine, oceanic and Mediterranean) might allow the establishment of a wide range of species. Using this and the already available European dataset, we addressed the two following specific questions:

(1) Are some phylogenetic and functional groups of fungi (and fungal-like organisms) more successful invaders? Prediction of the invasive potential of organisms based on their biological and ecological traits, has been a major research topic for plants and animals (Mack et al. 2000), but remains to be investigated for fungi *sensu lato* (Parker and Gilbert 2004). Our European and French datasets were used to establish preliminary correlations between fungal phylogeny and/or life traits and invasion level.

(2) What are the main factors determining the level of fungal invasions in Europe? The geographic distribution of fungi often matches the distribution of their hosts for pathogens and mycorrhizae but is also strongly influenced by environment (climate) and human activities (such as agriculture and forestry; Dighton et al. 2005). Since unintentional introduction is a common pathway for invasive fungi (Palm and Rossman 2003), the regional distribution of invasive fungi might be shaped by regional patterns of trade and transport of plant material (Schwartz et al. 2006; Brasier 2008) and passengers (Viljanen-Rollinson and Cromey 2002). We tested geographical, climatic and economic factors as explanatory variables of the distribution of alien fungi across European countries and French regions.

Materials and methods

Inventory of alien fungi (*sensu lato*) in France

A fungal species was considered as alien according to the definition used in the Convention on Biological Diversity (http://www.cbd.int/), i.e. a species occurring outside of its natural range and dispersal potential. As aerial spore dispersal in fungi can occur on very long distances (Brown and Hovmøller 2002), only species with a known extra-European origin were considered as alien for France. The native range of fungi is usually poorly known, partly due to the lack of relevant paleontological data and comprehensive biogeographical knowledge. A number of species for which the native range was unknown but that were presumably of extra-European origin based on new occurrence, and sometimes other pieces of evidence such as genetic data, were included as “cryptogenic”. Our inventory was based on the French Mycological Society database (Courtecuisse 1992) and on an intensive literature survey, with the main sources being CABI searchable database (http://www.cabi.org/) as well as the textbooks by Viennot-Bourgin (1949) and Smith et al. (1988). Synonymies were resolved with the help of the Index Fungorum (www.indexfungorum.org). We included species with records providing the date and reference of their first observation in France, while restricting our investigations to the 1800–June 2007 timeframe. Most included species occur in natural and cultivated environments, but some species only found in artificial environments (greenhouses) were also listed. Human fungal pathogens were excluded (see Warnock et al. 1998 for information).

Dataset of alien pathogenic fungi occurring in wild environments in Europe

The dataset, more thoroughly described in Desprez-Loustau (2008), encompassed 84 fungal species (Appendix 1—Electronic Supplementary Material):

(1) known or presumed to be alien to Europe, i.e. not indigenous to any part of Europe; and
(2) pathogenic on indigenous (European) species and/or on species occurring in wild environments (e.g. forest trees).

For each species, the date of the first record in Europe and the presence/absence in each European country was documented.

Statistical analyses

The number of European countries where each species has been recorded (*N*) was used as a proxy of invasiveness, assuming that this number is a good estimate of spread (records are often made at the country level and more detailed distribution data are not available for most species and countries). Potential relationships between species attributes (phylogeny, parasitic lifestyle) and invasiveness were investigated via analyses of covariance with *N* as the dependent variable, and several explaining variables. The analyses were performed with the GLM procedure (type III sums of squares, i.e. adjusted sums of squares for all variables) of the SAS/Stat Software (SAS Institute, Cary, North-Carolina, USA). Species residence time was included as the covariable. Phylogeny and parasitic lifestyle (which are related variables) were then tested separately as explaining factors in the two following models:

$$N = \mathrm{RT},\ \mathrm{ORDER},\ \mathrm{RT} \times \mathrm{ORDER} \qquad (1)$$

where RT (years) = residence time = 2007—year of first record in Europe

ORDER = taxonomic/phylogenetic order the species belongs to.

Only orders represented by at least three species were retained (i.e. Botryosphaeriales, Capnodiales, Diaporthales, Dothideales, Erysiphales, Helotiales, Hypocreales, Peronosporales, Pucciniales, Xylariales).

The systematics of fungi has recently undergone dramatic changes, as phylogenetic information from molecular data has become more available (Hibbett et al. 2007). In this study, we used the up-to-date classification, mostly based on phylogeny, used in the Index Fungorum and in the last edition of the dictionary of fungi (Kirk et al. 2008), which gives the number of species in each order.

$$N = \mathrm{RT},\ \mathrm{PAR},\ \mathrm{RT} \times \mathrm{PAR} \qquad (2)$$

where PAR = parasitic life-style

Six categories of parasitic life-styles were defined: animal pathogen, systemic, foliar necrotroph, obligate, root and stem plant pathogens.

A second group of analyses was performed to analyse the number of alien fungi per European country/French region in relation to various geographical, climatic and economic data. For Europe, 84 species and 28 countries (EU27 excluding Luxemburg, with no alien fungi in our dataset, Switzerland and Norway) were included, according to the availability of data. For France, data on the distribution of alien fungi across the 21 French metropolitan “régions” were only available for 24 species (forest tree pathogens). These were compiled from the national Forest Health Department database (see Vacher et al. 2008 for database description). For both analyses at European and French levels, the dependent variable was the number of species per country or region and the explanatory variables were the following: latitude, longitude and their squares, surface area, average annual rainfall, average annual temperature, human population, average annual merchandise imports. For the analysis at the European level, imports were characterized by two variables in average monetary values for 1999–2006: total imports (i.e. including all goods) and agricultural imports. For the analysis at the French level, imports were also characterized by two variables but on different grounds: total imports (i.e. by terrestrial ways-road, railway-, and navigable waterways) and imports by road only (in tons, 2006 value). Interaction terms between variables were not considered because of the insufficient numbers of observations compared to variables, and the difficulty to interpret these interactions. Geographical, climatic and economic data used as explanatory variables were obtained from Wikipedia (www.en.wikipedia.org), Worldclim (www.worldclim.org/), Meteo France (www.meteofrance.com), the French Ministry of transport (www.statistiques.developpement-durable.gouv.fr, SitraM database), OECD (www.oecd.org) and Eurostat (www.ec.europa.eu/eurostat/). A stepwise multivariate regression was performed with the REG procedure of the SAS/Stat Software with a 10% threshold for entry/removal of variables, after log transformation of the number of species, the area and the population. Since the species-area relationship is a fundamental "law" in ecology (Connor and McCoy 1979), area was forced as the first explanatory variable into the model. To interpret the model that was selected by stepwise analysis, we performed a selection of the 100 best models based on Akaike Information Criterion (AIC), whatever the number of explanatory variables. The analyses at the French level were made after removal of the "Nord-Pas de Calais" région, which was a clear outlier in the data cloud (with extremely high levels of imports—3.5 times the highest value in other regions-, and low number of alien fungi; this region is by far the less forested region in France). The appropriateness of the models was checked by the study of residuals (normality, plots of residual versus predicted values).

Results

Inventory of alien fungi in France

The 227 alien species (and a few lower taxa) of fungi (191) and pseudo-fungi (36) recorded since 1800 in France are presented in Appendix 2—Electronic Supplementary Material, including cryptogenic species, i.e. with no indication of a region of origin. Among these species, 178 can be considered as established, i.e. having self-sustaining populations in natural environments, based on repeated observations of the species across years. This might be questioned for the 21 species (mostly mushrooms) which have a single record in natural conditions, especially for older records. Among the 26 remaining species, 21, mostly tropical humicolous basidiomycetes, have only been observed in greenhouses (and most often with few records), one species, with a single record in 2005, is expected to be eradicated (*Gibberella circinata*, agent of the pitch canker of pines) and the four last species are considered extinct. These four species are plant pathogens, with three of them only recorded once long time ago in a wheat field (*Tilletia controversa*, 1966), on greenhouse palmtrees (*Phytophthora palmivora*, 1931) or in imported commodities (*Nematospora coryli*, 1931). The last one, a serious pathogen of potato (*Synchytrium endobioticum*), was successfully eradicated and is still submitted to very strict regulation measures.

All alien species were introduced undeliberately, except *Lentinula edodes*, the edible shii-take mushroom (with first trials for cultivation starting in the 1970s, Callac personal communication), and *Psilocybe mexicana*, the Mexican psychedelic mushroom, first cultivated in 1956 at the Museum National d'Histoire Naturelle in Paris (Heim et al. 1958). Both fungi have only one record in France in natural environment, dating back from 1990 and not confirmed ever since. Other species arrived as contaminants of various commodities. Although specific pathways are rarely documented, a significant number of plant pathogens are obligate biotrophic parasites (rusts, powdery mildews) and most of them are therefore assumed to have been introduced with their living host plant. Other contaminated commodities include seeds, timber, wood packaging, potting media. A relatively high number of tropical species were first introduced in greenhouses, some of them later escaping in the wild, e.g. *Collybia luxurians*, *Leucocoprinus cepistipes* and *L. straminellus*.

A majority of species have a most probable origin in North America (40% of documented origins), followed by "tropical regions" (without further indication of continent, 19%) and Asia (18%). It is, however, noteworthy that in many cases the origin is uncertain and that a large proportion of species (24%) remain "cryptogenic".

Only three animal pathogens are included among the 227 species, i.e. *Aphanomyces astaci* on crayfish, *Batrachochytrium dendrobatidis* on frogs, and the entomopathogen: *Cordyceps tuberculata*. This is consistent with the much tighter associations occurring between fungi and plants than between fungi and animals (Berbee 2001). Plant pathogens are the most numerous ecological category, with 65% of all species, of which 46, 31 and 22% primarily on crop plants, ornamental plants and forest trees, respectively. Very few species were first described on wild plants (but see Viennot-Bourgin 1964 for some exceptions). Ectomycorrhizal fungi represent 4% and saprobes 30% (with approximately two thirds humicolous and one third lignicolous species).

Phylogeny, life-style of fungi and invasiveness

The distribution of alien fungi among taxonomic orders was mostly similar for the French and European lists, except for Agaricales (in Basidiomycota), not represented in the latter (Fig. 1). This can

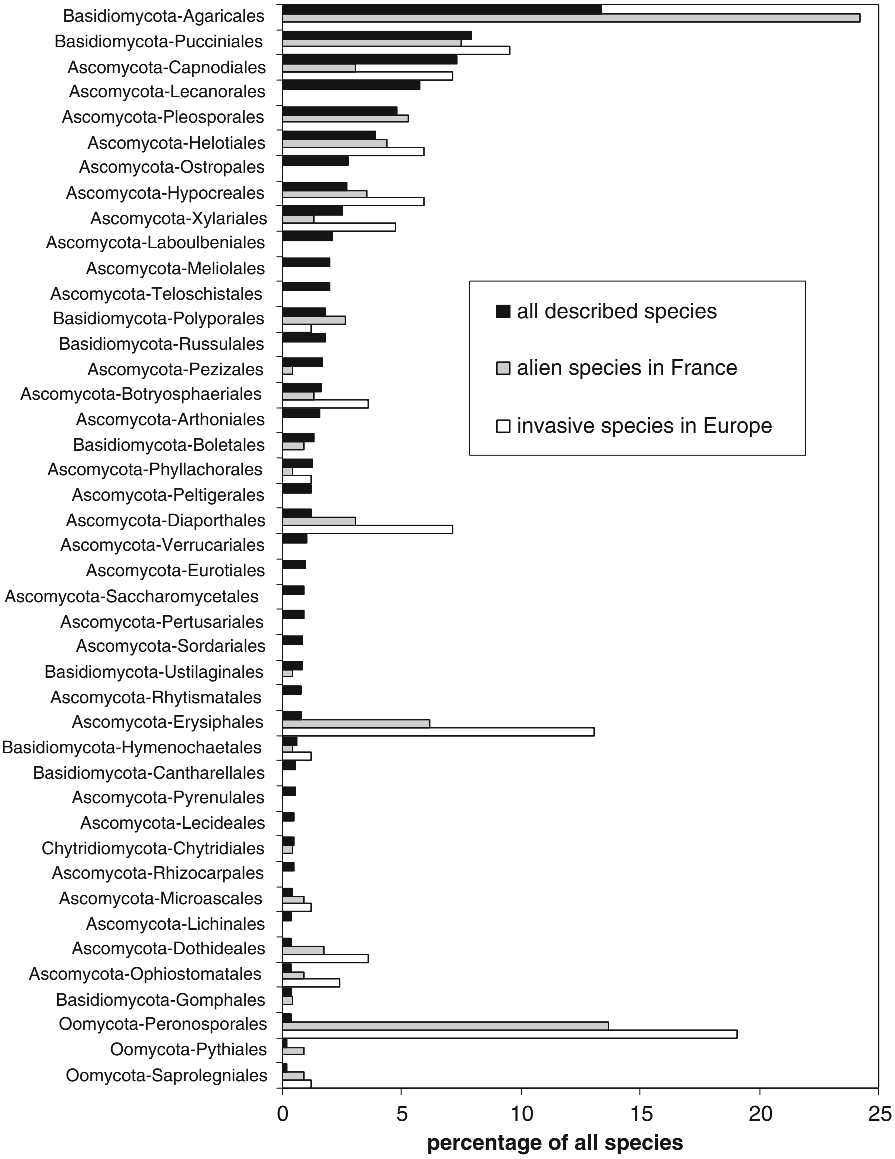

Fig. 1 Distribution of species in major orders of Fungi (40 top orders for the number of species in phyla: Ascomycota, Basidiomycota and Chytridiomycota) and of pseudo-fungi (in Stramenopila) belonging to Oomycota. Data for all described species (total = 97,861 fungi + 1,036 pseudo-fungi) come from Kirk et al. (2008)

easily be explained by the fact that many species in this group are saprobes or ectomycorrhizal fungi, which had not been considered in the European dataset. This order is conversely well represented in the French dataset.

However, important and consistent discrepancies between the two alien species datasets and all described fungal species (data from Kirk et al. 2008) were observed. First, some major orders within the Ascomycota phylum were not represented in the alien species datasets. This is especially the case of Lecanorales which mainly contains lichen-forming species and is one of the largest orders in the Ascomycota. Other non-represented orders included Laboulbeniales (mainly parasites of insects) and Meliolales (mostly tropical) (Kirk et al. 2008). In contrast, some orders were over-represented in alien fungi and fungal-like organisms, both in Europe and in France. This especially applies to Peronosporales, belonging to Oomycota (in Stramenopila), and to Erysiphales, i.e. agents of powdery mildews, and to a lesser extent Diaportales in the Ascomycota.

Covariance analyses of the potential relationship between species attributes and invasiveness across Europe revealed a highly significant effect of the residence time but also significant (or marginally significant) interactions with parasitic life-style and taxonomic/phylogenetic order (Tables 1, 2). Steep slopes and high R^2 were obtained for Erysiphales (0.26 country/year, $R^2 = 0.83$, $n = 11$) and Pucciniales (0.15 country/year, $R^2 = 0.56$, $n = 8$), and therefore obligate parasites, which belong to these two phylogenetic groups (0.18 country/year, $R^2 = 0.64$, $n = 19$). Conversely, Peronosporales (including root and foliar parasites) and root parasites showed a slower increase (0.06 and 0.05 country/year) but R^2 values were low (0.20, $n = 16$ and 0.21 $n = 14$, respectively; Fig. 2a). No significant effect of either order or pathogen type could be demonstrated on residence time (not shown).

These analyses could not be performed on the French dataset due to the insufficient number of species with distributional data. However, within the subset of 24 forest pathogenic fungi (for which these data were available), a positive relationship between the number of regions with records and the residence time of the species was also observed ($r = 0.39$; probability = 0.058; Fig. 2b).

A significant correlation was observed between the number of countries within Europe and the number of regions in France where alien species (forest tree pathogens) have been recorded (Fig. 3).

Table 1 Analysis of covariance with invasiveness (estimated by the number of countries with records of the species) as the dependent variable and residence time and parasitic life-style as explaining variables

Source	*df*	Sums of squares	*F* value	*P* value
Residence time (RT)	1	638.39	12.13	0.0009
Parasitic life-style (PAR)	5	464.22	1.76	0.1314
RT × PAR	5	703.30	2.67	0.0286
Error	71	3,736.86		
Corrected total	82	7,052.17		

Table 2 Analysis of covariance with invasiveness (estimated by the number of countries with records of the species) as the dependent variable and residence time and phylogenetic/taxonomic order as explaining variables

Source	*df*	Sums of squares	*F* value	*P* value
Residence time (RT)	1	396.20	7.56	0.0084
Order	9	209.44	0.44	0.9036
RT × order	9	911.51	1.93	0.0699
Error	47	2,461.89		
Corrected total	66	5,829.04		

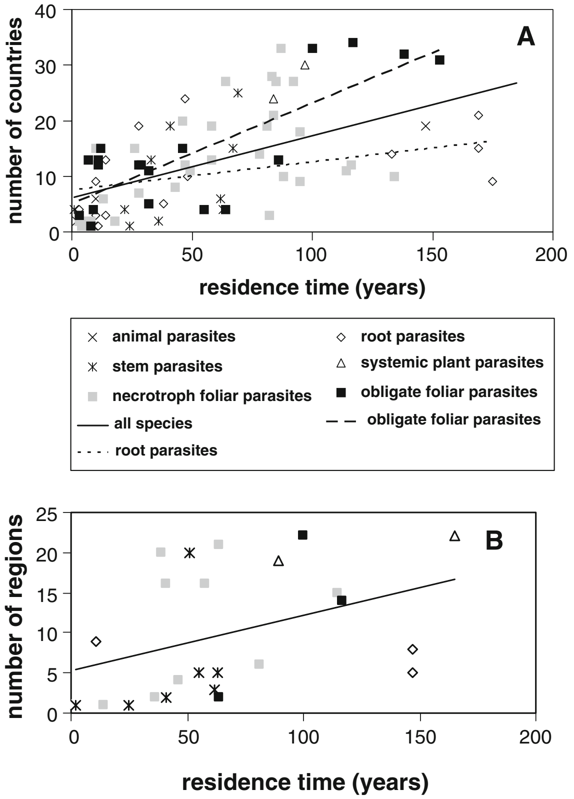

Fig. 2 Relationship between residence time of alien fungal species in Europe and the number of countries with recorded occurrence (**a**), or in France and number of regions (**b**)

Geographical, climatic and economic factors and levels of invasion across France and Europe

In the stepwise analysis performed on European countries, a three-variable model was selected to explain the number of alien fungi per country. The explanatory variables, in addition to area, were first

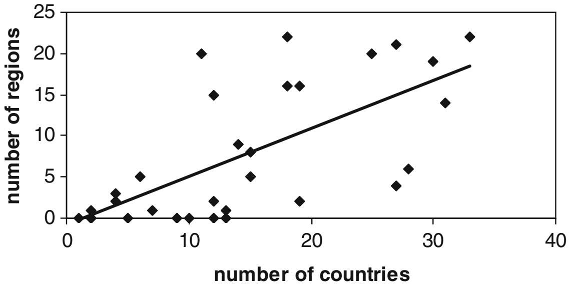

Fig. 3 Relationship between the number of European countries and the number of French regions where alien fungi have been recorded: 33 alien forest tree pathogens recorded in Europe, among which 27 also recorded in France, and 24 in the Forest Health Service database with distributional data

the average annual rainfall, and second the human population, with both having a positive correlation with the number of alien fungi (Table 3). This model ($R^2 = 0.91$; AIC = −76.20) was the only three-variable model out of the 100 best models based on AIC. Among the best 100 models, all included rainfall, and 92 also population. The best model corresponding to the lowest AIC included rainfall and population, and also latitude and longitude and their squares ($R^2 = 0.95$, AIC = −84.95). A seven-variable model slightly different from this one, with agricultural imports in place of population, had close values of goodness-of-fit criteria ($R^2 = 0.94$, AIC = −77.40). The same models were selected when analyses were carried out after removal of Cyprus and Malta (this was checked because of the peculiarity of these two countries: insularity, geographical location, especially for Cyprus, surface area and climate).

In the analysis among French régions, the model selected by stepwise procedure included road imports, with a positive parameter, and longitude, with a negative parameter (Table 4). It was the second best model in terms of AIC ($R^2 = 0.57$, AIC = −80.25) and the only three-variable model among the best 100. It closely followed a model where average annual temperature (with a positive parameter) was also included, in addition to road imports and longitude ($R^2 = 0.61$, AIC = −80.47).

Table 3 Results of stepwise regression for the number of alien fungi species per European country as the dependent variable

Source	*df*	Sums of squares	*F* value	*P* value
Model	3	14.18547	82.00	<.0001
Error	24	1.38398		
Corrected total	27	15.56945		

Variable	Parameter estimate	Standard error	Sum of squares	*F* value	*P* value
Intercept	−5.40503	0.59754	4.71831	81.82	<.0001
Log(area)	0.14349	0.04891	0.49628	8.61	0.0073
Log(population)	0.36320	0.05632	2.39788	41.58	<.0001
Annual rainfall	0.00157	0.00022414	2.81821	48.87	<.0001

Table 4 Results of stepwise regression for the number of alien fungi species per French region as the dependent variable

Source	*df*	Sums of squares	*F* value	*P* value
Model	3	0.31833	7.00	0.0032
Error	16	0.24244		
Corrected total	19	0.56077		

Variable	Parameter estimate	Standard error	Sum of squares	*F* value	*P* value
Intercept	0.30316	0.63740	0.00343	0.23	0.6408
Log(area)	0.20613	0.06264	0.16408	10.83	0.0046
Longitude	−0.02321	0.01175	0.05918	3.91	0.0656
Imports_road	0.00009705	0.00003851	0.09623	6.35	0.0227

The road imports variable was included in all best 100 models, longitude in 80% and average temperature in 77%.

Discussion

This paper presents a consolidated list of 227 fungal species (*sensu lato*) or lower taxa considered as alien in France. Although likely incomplete, this list represents one of the largest inventories of alien fungal species at a national level in Europe and can be considered as a first step towards a more comprehensive inventory to be completed at the European level. Nearly one half of the species in our list (118) had not been included in the lists already published in other European countries. Assembling all available lists, including the present one, now gives a dataset of more than 700 alien fungal species in Europe (Desprez-Loustau 2008).

Some of the difficulties encountered when building this list might be more specific to the French situation, but we highlight them to explain the limits of our inventory and for the benefit of future ones:

(1) There is much more collection and identification effort focusing on mushroom fungi, forming large fruiting bodies, than on microscopic fungi. This is consistent with the over representation of Basidiomycota, especially Agaricales, in our French inventory (Basidiomycota to Ascomycota ratio of 1.2, instead of 0.5 in all described fungal species, Kirk et al. 2008). Founded in 1884 as the first mycological society in the world, the Société Mycologique de France today encompasses more than 100 regional and local mycological societies. Their members are well-trained observers eager to identify and report new species, under the supervision of professional mycologists. Reporting rate and quality have further improved during the last two decades, thanks to the establishment of a national inventory program (Courtecuisse 1992). In contrast, identification of microscopic fungi requires specific methods and equipments, usually only available in laboratories managed by academic (universities, research institutes) and regulation (plant protection services) institutions, and mostly relies on a few professional taxonomic experts. Several new records from the first half of the twentieth century were made in botanical gardens or in agriculture colleges because of the presence of skilful observers with easy access to laboratory facilities. Thus, the Agriculture College of Grignon (south-west of Paris) appears as a "hot spot" of emerging plant pathogens, with first records of species such as *Pseudoperonospora humuli*, the agent of hop downy mildew (Ducomet 1925), *Cumminsellia mirabilissima*, the agent of mahonia rust (Ducomet 1930) and *Kochmania oxalidis,* the agent of oxalis smut (Viennot-Bourgin 1932). Expertise in the identification of several taxa has been lost over the last decades because of the retirement of taxonomic experts.

(2) The culture of reporting is poorly developed in France. Considering only the plant pathogens, there are few reports from France in the dedicated sections of *Plant Disease* and *Plant Pathology* journals. There is no French agency responsible for centralizing, verifying and publishing new microfungal records. The last up-to-date inventory of plant pathogenic fungi is the reference text-book by Viennot-Bourgin (1949), which is a main source of records for alien species. First records of alien fungi are often embedded in grey literature or publications aimed at a very specific audience, and therefore not widely available. Some "first records" are indeed confirmations of earlier records not reported in a formal publication. As an example, *Sphaceloma murrayae*, a foliar pathogen of willows, was mentioned by Morelet in 1967 in the bulletin of a local natural history society (Morelet 1967) and "rediscovered" almost 30 years later as "a pathogen new to Europe" in an international journal (Butin and Kehr 2004).

(3) The alien status of fungi is often ambiguous, with nearly one third of the fungi in our list labelled "cryptogenic", that is of unsure origin (but suspected to be alien). Classical mycological inventories list species but do not address their native or alien status. Most often, mycologists reporting a "first record" did not analyse the novelty of the record (new record and/or new taxon) and did not discuss its relevance in

terms of biological invasion. The species status itself is unclear for several taxa, until more refined analysis will be undertaken. Taxonomic confusions, by pooling different species together, are a source of uncertainty for the presence and distribution of several species, such as *Calonectria kyotensis* (Crous 2005), *Neofabraea perennans* (de Jong et al. 2001), *Hydnangium carneum*, *Laccaria fraterna*/*L. lateritia, Leucoagaricus americanus*/*L. bresadolae*. Some species, such as *Gibberella circinata*, had previously been described as *formae specialis* or varieties (Nirenberg and O'Donnell 1998). Progress in population genetics and phylogeography with the use of molecular tools should help to solve these problems (Taylor et al. 2006). There is rising interest for biogeography of fungi, as demonstrated by a recent special issue of *Mycological Research* (112(4), April 2008).

(4) Most pathogenic fungi are not reported per se but on the grounds of the symptoms they cause, i.e. emphasis is put on the disease rather than on the causal agent in the record. In a number of cases, diseases were described long before the causal agent was identified, particularly for hitherto unknown species. This was the case of the 'wasting disease' which decimated the eelgrass *Zostera marina* meadows along the Atlantic Coast of North America and Europe during the 1930s (Muehlstein et al. 1991). After several decades of speculations concerning the causal agents, the disease was eventually shown in 1991 to be caused by infection with a marine slime mould Heterokonta, *Labyrinthula zosterae*, of cryptogenic origin, which is the single example of a marine organism in our list (Muehlstein et al. 1991). The focus on "new diseases" (as in the recently created online journal "New Disease Reports" of the British Society for Plant Pathology, http://www.bspp.org.uk/ndr/) makes it sometimes difficult to know whether the novelty comes from the first report of the fungus in a particular area or from the first report of the fungus on a new host plant. Furthermore, it can be difficult to distinguish between new diseases arising from the introduction of an alien pathogen or from a change in host and/or environmental conditions leading to a strong increase in populations of an indigenous species. Introductions have been shown to be a major factor of the emergence of diseases, both in animals (Dobson and Foufopoulos 2001) and plants (Anderson et al. 2004). However, climatic changes (even on a local scale) and changes in agricultural practices (e.g. growing susceptible species or cultivars on large spatial scales) have also been considered as important drivers of plant disease emergence (Anderson et al. 2004). For example, *Sphaeropsis sapinea*, included in our list as cryptogenic, might be a European indigenous species which became more "visible" in recent times, by switching from an endophytic to a pathogenic behaviour (causing pine shoot blights sometimes leading to mortality), in relation to several factors (plantation of susceptible species, nitrogen stress, drought stress, etc.: Desprez-Loustau et al. 2006). Studies showing a low genetic variation in this species in Europe (Burgess et al. 2004), indicative of an introduction, were based on a limited number of samples and should therefore be extended. The distinction between the endemic-emerging and the novel pathogen hypotheses deserves more investigation in several cases since it might lead to different mitigation strategies (Storfer et al. 2007; Rachowicz et al. 2005).

The use of diverse sources of information differing in their level of precision and accuracy makes our inventory fragmentary. However, we believe that our list is quite representative of alien fungi in France, allowing us to draw conservative conclusions on some invasion features in fungi and fungal-like organisms. Our European dataset, compiled from heterogeneous lists, was constructed with the aim of enabling analyses of fungal invasions, by using a standardized search procedure assuring a comparable data retrieval for all species and countries (Desprez-Loustau 2008). Interestingly, similar trends relating to factors correlated with invasion success arose from both datasets.

The first determinant factor explaining the spread of alien fungi was the residence time of the species. That the range size of an invasive species is influenced by the time it has had to spread can be considered a trivial expectation; yet, residence time has not always been included in analyses of invasion success. Our study re-emphasizes the need to include this factor, prior to any other analysis of invasiveness (Wilson et al. 2007). For undeliberate introductions, as it is mostly the case for fungi, the difficulty lies in the availability of reliable records of the first date of arrival of the species. Since most alien species arrived as a few individuals, they can remain unnoticed for a period of time, before their populations build up and reach visible levels (Richardson et al. 2000). For pathogenic fungi, which are mostly microscopic organisms requiring specific techniques for identification, this difficulty is even greater. As already mentioned, many diseases were observed long before the identity of the causal organisms was firmly established.

When residence time was accounted for, some factors linked to species characteristics were shown to influence invasion levels. Defining species attributes related to invasion success has received much attention in invasion ecology, especially for plants and birds (Sakai et al. 2001; Pyšek et al. 2004; Hayes and Barry 2008; Lambdon 2008; Moles et al. 2008), but has not been explored for fungi. The analysis of the species diversity within our two datasets suggests that indeed some taxa are more likely to be invasive, considering either/both their introduction and spread potential.

Erysiphales, i.e. fungi causing powdery mildews, are particularly noticeable, since they are over-represented in lists of alien fungi and show a faster spread in European countries than other groups. A high proportion of Erysiphales had already been noticed in the German and England lists of alien fungi (Kreisel and Scholler 1994; Jones and Baker 2007). High rates of introduction, as suggested by a higher representation of Erysiphales among alien fungi than in all described fungal species, are questionable. Since powdery mildew fungi are obligate parasites, the movements of living infected material are assumed to be the most probable pathway of introduction. However, powdery mildew diseases are often characterized by conspicuous and easily recognised symptoms (whitish spots or patches on leaves), which should favour an easy interception by phytosanitary inspection services. It is, however, known that only a small sample of all imported commodities is actually inspected. On the other hand, powdery mildew fungi are characterized by an intense production of airborne spores (conidia), which confer them a high reproduction and dispersal potential (Jarvis et al. 2002). This might far compensate low initial propagule pressures represented by a few inspection escapes. In addition, some introductions might be due to spores carried by travellers (Viljanen-Rollinson and Cromey 2002) or other supports, although conidia in Erysiphales are rather short-lived (Jarvis et al. 2002). Finally, cross continental passive dispersal by spores can not be excluded, for powdery mildew fungi as well as other fungi dispersed by airborne spores (Brown and Hovmøller 2002; Moncalvo and Buchanan 2008).

Whether this should be considered as alien invasions is questionable according to the classic definition of alien species which refers to non natural dispersal. However, these rare “natural introductions” share common traits with human-mediated introductions by suddenly putting into contact host and pathogen populations which have no co-evolution history, leading to severe disease in naïve hosts (Parker and Gilbert 2004). A few examples, mainly involving rusts (Pucciniales) fungi, which have thick-walled, coloured resistant spores, have been documented (Brown and Hovmøller 2002). *Puccinia melanocephala*, the agent of sugarcane rust, was shown with an unusually high level of reliability, to have invaded the Americas following a single introduction event from Cameroon to the Dominican Republic (Purdy et al. 1985). More recently, *Phakopsora pachyrhizi*, the causal agent of Asian soybean rust, invaded North America from a single introduction event, most probably from South America with air currents (Krupa et al. 2006), while the new virulent strain of wheat stem rust (*Puccinia graminis* f.sp. *tritici*) Ug99 invaded step-by-step Uganda, Kenya, Ethiopia, Yemen and Iran (FAO 2008: www.fao.org/newsroom), as predicted by a trajectory analysis model of the prevailing winds (Singh et al. 2006).

Peronosporales, belonging to Oomycota, is another over-represented order in our lists of alien species. Oomycota comprise less than 1,000 described species (to be compared to more than 30,000 in Basidiomycota and 60,000 in Ascomycota) but include many severe plant pathogens, such as *Phytophthora* species (Latijnhouwers et al. 2003). *Phytophthora infestans*, the agent of potato late blight, introduced from South America into Europe via infected tubers, caused the

Great Irish Famine in 1845–1850 and is still a limiting factor for potato production worldwide. *P. cinnamomi* is a threat for natural ecosystems in several parts of the world (Zentmyer 1980). It has to be noted that among the 17 Oomycota species included in the 84 species European dataset five have been described since 1999 in the *Phytophthora* genus, reflecting recent research efforts on this group (Brasier 1999). As for *P. ramorum*, their native area is unknown and their non indigenous status is usually assumed from the low genetic variation of European populations (Cooke et al. 2005). *P. alni* represents a particular case, resulting from hybridization events, probably involving at least one alien species (Ioos et al. 2006). Contrary to Erysiphales, many *Phytophthora* species are soilborne and cause inconspicuous symptoms. Infected soil and asymptomatic plants are therefore most probable pathways, easily escaping phytosanitary inspections. Peronosporales showed an apparent low spread rate in our study (Fig. 2a) but this result should be taken with caution: the R^2 is quite low and the relationship mainly relies on a small number of species of ancient introduction only recorded in a few European countries. The low spread of these species might be explained by specific features, such as sensitivity to frost in the case of *P. cinnamomi*, mainly found in Southern Europe (Marçais et al. 2004).

Our study also suggested the involvement of geographical, climatic and economic factors as explanatory factors of the spread of alien fungi, both within France and across Europe. In both cases, after accounting for the species-area relationship, models explaining the number of species per geographical unit included an economic variable, “human population” or imports, as a significant explanatory variable. “Human population” is an integrative variable which may encompass a wide range of social and economic indicators. Countries and regions with larger populations are more likely to have high levels of trans-continental and terrestrial exchanges, due to the presence of airports and/or harbours, dense road networks, and active economies. The coefficient of correlation between population and imports is extremely high (0.88) at European level. The statistical significance of imports to explain the geographical extent of alien fungi is likely to express a causal relationship. For fungi, most introductions, if not all, are non intentional and are the result of biological contamination (*sensu* Hulme et al. 2008) of various commodities. Higher levels of imports are therefore likely to increase the probability of introduction of fungi and the propagule pressure, which is an important determinant of invasion success (Lockwood et al. 2005). The introduction of *Clathrus archeri* with Australian wool (Parent et al. 2000), of *Erysiphe necator* with contaminated plants from America (Weltzien 1978) and of *Ceratocystis platani* with wood packaging of American troops during World War II landings (Ocasio-Morales et al. 2007) are among a few examples where most probable pathways have been identified. The role of trade routes through nurseries in the movement of *Phytophthora ramorum*, the causal agent of Sudden Oak Death in Californian and European nurseries was also strongly supported by a multilocus genetic analysis (Ivors et al. 2006). The very high proportion of pathogens of crop and ornamental plants among recorded alien pathogenic fungi is consistent with high probabilities of introduction with contaminated plants or plant products. Crop and ornamental plants probably also host higher and more diversified populations of pathogens than wild plants (Zaffarano et al. 2008), which does not exclude a bias linked to greater focus on plants of economic importance than on wild plants. Our results on fungi are in line with many previous studies showing that globalization, especially international trade, is a major driver of biological invasions across taxa and regions (Dehnen-Schmutz et al. 2007; Kobelt and Nentwig 2008; Westphal et al. 2008). Increasing trade volume is likely an important contributing factor to the exponential increase in the number of alien fungi, both in France (result not shown from Appendix 2—Electronic Supplementary Material) and Europe (Desprez-Loustau 2008). Other factors linked to the “human population” might explain the selection of this variable to explain invasion success, such as efforts dedicated to survey, detection and research. Most populated countries and regions are also likely to have a higher level of environmental disturbance, which may favour invasibility (Lake and Leishman 2004). Urban forests and gardens have been shown to be areas especially affected by invasions and sources of alien species for adjacent areas (Alston and Richardson 2006). This holds true as far as the biological support for the fungi (mainly plant communities) has not been dramatically reduced by urbanization and industrialization, as it has been the case in région Nord-Pas de Calais.

Finally, our analyses suggest that climatic factors influence invasion success, with a positive relationship between the number of alien fungi and the average annual rainfall at European level, or the average mean temperature at French level. Such relationships could reflect the importance of bioclimatic constraints, dictating the suitability of regions for the establishment of alien fungal species, as already mentioned for *Phytopthora cinnamomi*. The effects of climatic variables on the distribution of species richness of forest pathogenic fungi in France have been demonstrated (Vacher et al. 2008). Most fungi require free water or high moisture for spore dispersal, germination and infection (Lacey 1986). Dry climates are especially not favourable to foliar pathogens (Desprez-Loustau et al. 2006), which are well represented among alien fungi.

Which species attributes are associated with invasiveness? Which habitat characteristics are associated with invasibility? More generally, what are the correlates of invasion success? are critical questions in invasion biology (Lake and Leishman 2004). Although the numerous studies in this field lead to the conclusion that there are no characteristics common to all invaders or to all invaded communities, some species-level characteristics were shown to be significant within some biological groups (Hayes and Barry 2008). The aim of our study was an exploratory investigation of these questions for alien fungi at two spatial scales. As already well demonstrated for other taxa, factors linked to the introduction process were shown to play a key role. This was reflected by the positive relationship between the time since introduction and the level of imports on one hand, and the level of invasions on the other hand. Factors more specific to fungal invasions were also suggested, with the over representation of Erysiphales and Peronosporales, especially *Erysiphe* and *Phytophthora* genera, and the positive effect of precipitations at European level.

These results are a first step towards a better knowledge of pathways of fungal invasions and of predictors of invasion potential. These informations are urgently needed to improve the efficacy of preventive measures. Current quarantine measures (Schrader and Unger 2003; Brasier 2008) have proved to be ineffective to maintain or slow the pace of introductions with increasing globalization. However, the results obtained in this study on species characteristics related to invasion success are most preliminary. For example, although obligate parasites, including Pucciniales, globally showed a high spread, the poplar rust fungus *Melampsora medusae* was an outlier. Notheworthy this species is heteroecious, i.e. requires an alternate host to complete its biological cycle, which seems to be a limiting factor of its spread in Europe (Pinon 1986). This example clearly points to the need for more refined analyses, based on larger datasets and including biological traits of the species (dispersal/gene flow, reproduction modes, e.g. shift to autocompatibility or purely asexual reproduction, host-specificity/habitat ranges, climatic requirements, etc.) in order to identify key traits related to invasiveness in fungi.

Acknowledgments This study was supported by funding of INRA (Call for Proposals in Epidemiology 2005) and of the European Union within the FP 6 specific targeted research project ‘DAISIE’ (SSPI-CT-2003-511202). We thank Philippe Callac, Jacques Guinberteau, Denis Tourvieille de Labrouhe and Piero Genovesi for sharing data, and Xavier Capdevielle and Annie Yart for data retrieval. The use of the Département Santé des Forêts database is gratefully acknowledged. We thank Pietr Pyšek and two anonymous reviewers for valuable comments on earlier drafts of this manuscript.

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