

Biogeographical patterns and determinants of invasion by forest pathogens in Europe

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Summary

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Key words: alien species, analysis of invasive species variance (ANISVA), biogeographical pattern of invasion, determinants of invasion, emerging infectious disease (EID), invasibility, invasive forest pathogens (IFPs), invasiveness.

- A large database of invasive forest pathogens (IFPs) was developed to investigate the patterns and determinants of invasion in Europe.
- Detailed taxonomic and biological information on the invasive species was combined with country-specific data on land use, climate, and the time since invasion to identify the determinants of invasiveness, and to differentiate the class of environments which share territorial and climate features associated with a susceptibility to invasion.
- IFPs increased exponentially in the last four decades. Until 1919, IFPs already present moved across Europe. Then, new IFPs were introduced mainly from North America, and recently from Asia. Hybrid pathogens also appeared. Countries with a wider range of environments, higher human impact or international trade hosted more IFPs. Rainfall influenced the diffusion rates. Environmental conditions of the new and original ranges and systematic and ecological attributes affected invasiveness.
- Further spread of established IFPs is expected in countries that have experienced commercial isolation in the recent past. Densely populated countries with high environmental diversity may be the weakest links in attempts to prevent new arrivals. Tight coordination of actions against new arrivals is needed. Eradication seems impossible, and prevention seems the only reliable measure, although this will be difficult in the face of global mobility.

Introduction

Over the past 500 yr, the geographic barriers that had maintained an almost static distribution of the world's biota for millions of years have been eroded by human activity, and wild species have consequently moved beyond their natural range (Richardson *et al.*, 2000). Human-driven species expansion has increased tremendously in the last century, as a consequence of the unprecedented growth of international travel and trade, resulting in huge disturbance to ecosystems and severe socio-economic impact (Aukema *et al.*, 2011). In plants, emerging infectious diseases (EIDs) are tightly linked to biological invasions. More than half of the world plant EIDs in the last few decades have resulted from the arrival of previously unrecognized pathogens, including the movement of virulent strains, or the emergence of new aggressive strains (Bandyopadhyay & Frederiksen, 1999; Anderson *et al.*, 2004). Fungal and fungal-like infections have always played a primary role amongst plant EIDs. Disease alerts for plant-infecting fungi in the Program for Monitoring Emerging Diseases (ProMED; <http://www.promedmail.org>) show a 13-fold increase from 1995 to 2010 (Fisher *et al.*, 2012). In forest trees, alien fungal and fungal-like pathogens are the main cause of EIDs, including such striking examples of virulent outbreaks of anthropogenically introduced fungi as Dutch elm disease and chestnut blight (Anderson *et al.*, 2004; Liebhold *et al.*, 2012).

Invasiveness has been defined in several ways, but in all definitions the crucial factor distinguishing an alien (exotic, nonnative, or nonindigenous) from a native organism is human-driven introduction into a new region (Pysek & Richardson, 2006). The definition of 'alien species' given in the Guiding Principles of the Convention on Biological Diversity (2002, CBD Decision VI/23), that is, a species occurring outside of its natural range and dispersal potential, was recently adopted for fungi (Desprez-Loustau *et al.*, 2010). Here we use a slightly modified version of the same definition to better fit forest pathogens. An alien or invasive forest pathogen (IFP) is defined in this paper as a species, subspecies, race, or forma specialis which: (1) is introduced into a country where it was previously unknown (for example, it can be either an alien species to Europe spreading in neighbouring countries or a European species extending its range), (2) behaves as an agent of disease, and (3) threatens the biological diversity of native or exotic forest trees and shrubs.

In the theory of invasion ecology, invasiveness has been associated both with biological traits of the invasive species and with environmental and community features in the naturalized range that render an ecosystem prone to invasion and define invasibility (Goodwin *et al.*, 1999; Mitchell & Power, 2003; Alpert *et al.*, 2000). Social and economic factors are crucial for species introduction (Sakai *et al.*, 2005; Guo *et al.*, 2012), whereas biogeographical and ecological factors are important for naturalization, with evolutionary forces being key mediators of invasiveness (Sax, 2001). The species-energy theory suggests that, in regions with higher biomass productivity, host–pathogen system stability and the pathogen-carrying capacity of an ecosystem are higher (Wright, 1983). Host species persistence is higher in areas with

varied topographical and edaphic conditions, and large ecosystem diversification (Lonsdale, 1999). The invasibility of a country is likely to be related to its geographical extent and number of ecoregions (Omernik, 2004). The pathogen richness of a territory depends on such climatic variables as annual mean temperature and annual total rainfall which affect the pathogen life-cycle (Whittaker *et al.*, 2001; Guernier *et al.*, 2004; Vacher *et al.*, 2008). Temperature especially is a driver of diversity according to the metabolic theory of ecology (Brown *et al.*, 2004), and temperature-dependent kinetics predicts the association of temperature with generation time, mutation frequency and ultimately species diversification (Rohde, 1992).

An assessment of the species features that differentiate successful invaders requires great experimental efforts. For certain species-specific traits, a direct link with invasiveness has been established in some biological groups, but finding traits generally and consistently associated with invasiveness has proved to be very difficult (Alpert *et al.*, 2000; Hayes & Barry, 2008). In plant pathogens, invasiveness is affected by strain virulence, host specificity and mode of action as well as by the host's abundance, demography, phytosociology, and variation in susceptibility (Lovett *et al.*, 2006; Schulze-Lefert & Panstruga, 2011). In fungal pathogens of forest trees, a significant effect on invasiveness has been suggested for residence time (i.e. time since first record), lifestyle and phylogenetic order (Desprez-Loustau *et al.*, 2010). Recently, traits related to mode of reproduction and dispersal, spore shape and size, optimal temperature for growth, and parasitic specialization have been proposed as useful predictors for distinguishing between invasive and noninvasive forest fungal pathogens (Philibert *et al.*, 2011).

In this paper we describe the historical and biogeographical patterns of invasion by forest tree pathogens in Europe since 1800, and we try to explain the observed differences in introduction and spread rates among pathogens and between countries. A large and detailed database of IFPs in 20 European countries was assembled for this purpose through a cooperative effort by the partners of the European Union (EU)-funded project FORTHREATS. Detailed taxonomic and biological information on each invasive species was combined with country-specific data on land use, climate, and the time interval since invasion in order to identify the determinants of invasiveness, and to differentiate the class of environments that share territorial and climatic features associated with a susceptibility to invasion.

Materials and Methods

Data collection, treatment and statistics

Inventory of invasive forest pathogens in Europe A comprehensive database of invasive forest pathogens (IFPs) in Europe in the time period from 1800 to 2008 was assembled in the EU project FORTHREATS and analysed in this paper. Each pathogen was classified on the basis of traits related to fungal biology or to its history of invasion, and relevant for invasiveness according to the literature (Table 1). The national lists of species were compiled by local experts using a common grid of entries. Synonymies were resolved by means of the Index Fungorum (www.indexfungorum.org).

Table 1 Pathogen traits, either biological or related to the history of invasion in Europe, tested as predictors of invasiveness

Pathogen trait	Categories or ranks
Taxonomy	Ascomycota (including Deuteromycota); Basidiomycota; Oomycota
Disease type	Anthraxnose; canker; foliar disease; powdery mildew; rot; root rot; rust; wilt
Extent of invasion per country	0, eradicated by phytosanitary service or replaced by other species; 1, introduced but not spreading; 2, spreading; 3, established in many regions or in the whole country
Host range	Specialist, able to attack only one genus; Generalist, able to attack > 1 genus
Host spectrum	<i>Angiospermae</i> ; <i>Gymnospermae</i> ; both classes
Impact on the host	Dieback, causing dieback of part of the host; reduced growth, causing dwarfing, yellowing, etc.; lethal, causing sudden death of the host
Geographical origin, that is, area where the perfect form of the species is endemic	Africa; Asia; Australasia; Europe; Temperate North America; Tropical North America; South America; unknown; hybrid
Time of arrival in Europe	30-yr classes over the period from 1800 to 2008
Country of first record	Austria; Belgium; Czech Republic; Finland; France; Germany; Greece; Hungary; Italy; Latvia; Lithuania; Norway; Poland; Romania; Slovakia; Slovenia; Spain; Sweden; Switzerland; United Kingdom
Invaded environment	Forest; urban (parks, gardens, and ornamentals); nursery; orchard; other plantations (biomass production, high-quality wood, etc.)
Substrate on which the pathogen arrived in Europe	Bark; living plants; soil; wood; seeds; cuttings; unknown
Pathway of arrival and diffusion in Europe	Trade; tools; tourism; wood packaging; airborne; host range enlargement or host jump
Status in Europe	Alien, clearly introduced into Europe; European, European pathogen expanding beyond its historical range; cryptogenic, probably alien pathogen with uncertain origin; hybrid, new pathogen arisen by natural interspecific hybridization

Estimation of pathogens' invasiveness and countries' invisibility indices In order to classify the pathogens on the basis of their observed invasiveness in Europe, for each species we calculated the annual rate of diffusion from country to country (the spread rate (SR_p)); the yearly rate of linear diffusion from the country first invaded to the extremes of the whole invaded range (the linear spread rate (LSR_p)); and the sum of extent rankings in the invaded territory (the cumulative extent (CE_p)).

In order to classify European countries on the basis of their observed invisibility, for each country we calculated the annual rate of arrival of invasive fungal pathogens (the rate of arrival (RA_c)); the ratio of the spread rate in the country to the overall spread rate in Europe (the relative spread rate (RSR_c)); and the sum of the extent rankings of all pathogens in the country (the prevalence index (PI_c)).

The formulae for the invisibility and invasiveness indices are reported in Supporting Information Methods S1. All data on IFP species, and geographical, socio-economical and climatic variables are reported in the Supporting Information Tables S2, S3.

Statistical analyses

Temporal pattern of invasion The temporal trend of invasion by forest pathogens in Europe was analysed for 30-yr time periods since 1800. The significance of differences between categories of pathogens (classified according to taxonomy, disease, status, origin, and substrate; see Table 1) over time and at any time period was determined using Friedman's nonparametric ANOVA (with k time periods as treatment effects, and n attribute states as blocks), and the χ^2 statistic.

Descriptive analyses of the geographical pattern of invasion In order to determine which countries had similar numbers and

species of invasive pathogens, correspondence analysis (CA) was applied. Principal components analysis (PCA) and hierarchical clustering were applied to determine which countries had similar arrival rates, spread rates and prevalences (i.e. 'status', for instance established or spreading) of invasive species. A similarity matrix was built using the scores of the two principal components, PC1 and PC2, with the highest latent roots, and the resultant clustering was superimposed on a bi-plot graph. Descriptive analyses were performed using the CA module in STATISTICA 6.0 (StatSoft Inc., Tulsa, OK, USA), and the PCA, Hierarchical clustering and Bootstrap resampling modules in GENSTAT 13.2 (VSN Int. Ltd, Hemel Hempstead, UK).

The significance of the clustering obtained through CA and PCA was tested further using a statistical procedure derived from AMOVA (Excoffier *et al.*, 1992), which was applied here for the first time and named 'analysis of invasive species variance' (ANISVA). ANISVA identifies the pattern of invasive pathogens that maximizes the variance amongst previously defined groups of countries, validating the clusters obtained through descriptive analyses (CA or PCA) and providing a simple statistical description of the partitioning inherent in the observed variation. Each group of countries identified by CA or PCA has a unique profile of invasive pathogens, and each pathogen was characterized by a specific geographical profile defined by its geographical occurrence in one to all groups of countries. Based on the squared distances among all pairs of pathogen-specific invasive profiles, the total variance was partitioned through hierarchical analysis into covariance components attributable either to differences among countries within groups or to differences among groups of countries. The significance of the covariance components was determined using nonparametric permutation tests (Excoffier *et al.*, 1992; Weir, 1996; Rousset, 2000). ANISVA was performed in GenAlEx vs 6.4 (Peakall & Smouse, 2006).

The observed variation in invasiveness (SR_p , LSR_p , and CE_p) among pathogens, as well as the observed variation in invisibility (RA_c , RSR_c , and PI_c) between countries, was illustrated by heatmaps accompanied by the dendrograms obtained through hierarchical clustering. Heatmaps and dendrograms were produced with the GPLOTS v2.8.0 package (Warnes, 2010) in R (R Development Core Team, 2011).

Geographical, socio-economical and climatic determinants of invisibility of each country Geographical, climatic and socio-economic factors with a putative effect on invisibility, according to the literature, were collected at a country level from public databases to be tested as predictors of the observed geographical patterns of invasion (Table 2). These factors included, in addition to land area and forest area, an estimate of biomass productivity (above-ground biomass); three indices of territory and ecosystem differentiation (degrees of latitude, number of eco-regions, and the global environmental facility (GEF) benefits index for biodiversity (GBI_{BIO}) (Smith & Martin, 2000; Pandey *et al.*, 2006)), which influence host species abundance and the ecosystem's carrying capacity; a few estimates of human activity, commerce and trade (population, population density, gross domestic product per capita (GDP), stocks traded, and import minus export), which according to the literature are crucial drivers of invasive species spread; and geographical and climatic variables that impact the species life-cycle (midpoint latitude, annual mean temperature, and annual mean rainfall).

The generalized linear model (GLM) was used to test the geographical, socio-economical and climatic variables described above (Table 2) as predictors for each of the indices of country invisibility (RA_c , RSR_c , and PI_c). In addition, nominal regression analysis (the multinomial logit model) was applied to test the same geographical, socio-economic and climatic factors as predictors of the groups of countries obtained on the basis of the frequency of the

presence (CA-based groups) or of the spread rates and extent (PCA-based groups) of the pathogens in a country.

Biological and historical determinants of invasiveness of each pathogen The GLM was used to test the biological and historical pathogen traits described above (Table 1) as predictors for each of the indices of pathogen invasiveness (SR_p , LSR_p , and CE_p). The most parsimonious model was selected on the basis of deviance.

Regression analyses were performed in the GLM module of GENSTAT 13.2 (VSN Int. Ltd) or SPSS v.19 (SPSS, Chicago, IL, USA).

Results

Inventory of invasive forest pathogens in Europe

The database compiled and analysed in this work comprises 123 IFPs (Table S1). Invasive pathogens since 1800 were classified as aliens (42%), species of European origin (28%), cryptogenic species (26%), and hybrids (4%). On average, each invasive pathogen was observed in five countries, but there was large variation among species. Thirty-seven species were observed in one country only, whereas four species (*Erysiphe alphitoides* s.l., *Mycosphaerella pini*, *Rhizoctonia pseudotsugae*, and *Phytophthora cambivora*) were found in > 15 countries.

At present, Ascomycota are the most numerous group (70%) of IFPs in Europe, while Oomycota and Basidiomycota represent 21% and 9% of the total, respectively. Invasive pathogens mainly cause tree dieback (37%) or growth reduction (40%), but almost one-fourth of them can cause death of the host. Invasive pathogens have been most frequently found on ornamental trees in parks and gardens (38%) or in forests (36%). A considerable number have also been found on nursery plants (21%), while 5% have been found in orchards and other plantations.

Table 2 Geographical, socio-economic and climatic factors tested as predictors of invisibility, and respective data sources

Factor	Source database	URL*
Land area (ha); population; population density (population km ⁻²); forest area (ha); above-ground biomass (million tonnes); carbon in above-ground biomass (million tonnes)	The Global Forest Resources Assessments (FRA) [†] by the Forestry Department at FAO	http://www.fao.org/docrep/008/a0400e/a0400e00.htm
Gross domestic product per capita (GDP) (US\$); imports minus Exports [‡] (US\$)	The Conference Board of Total Economy Database	http://www.conference-board.org/data/economydatabase
Midpoint latitude (decimal degrees)	Movable Type Scripts webpage	http://www.movable-type.co.uk/scripts/latlong.html
Eco-regions (<i>n</i>)	Digital Map of European Ecological Regions (DMEER) by the European Environment Agency	http://www.eea.europa.eu/data-and-maps/data/digital-map-of-european-ecological-regions
Annual mean temperature (°C); annual total rainfall (mm)	Worldclim – Global Climate Data	http://www.worldclim.org/
Global Environmental Facility (GEF) benefits index for biodiversity (GBI_{BIO}); stocks traded [‡] (US\$)	The World Bank	http://data.worldbank.org/indicator/ER.BDV.TOTL.XQ/countries

*Last accessed 20 July 2012.

[†]Year 2005.

[‡]Year 2008.

The large majority of IFPs in Europe are specialists (77%). Most species attack Angiospermae (58%), about one-fourth attack Gymnospermae (26%), and a small group (16%) are polyphagous.

Trade and airborne were the most common putative pathways of arrival and diffusion. To our knowledge, all the introductions occurred unintentionally. At present, *c.* 70% of the species are established in Europe, while 9% are spreading and 19% have been recently recorded for the first time. Only 1% of them have been eradicated through sanitary measures (e.g. *Gibberella circinata* in Italy) or replaced by more aggressive species (e.g. *Ophiostoma ulmi* replaced by *Ophiostoma novo-ulmi*).

Temporal pattern of invasion

The number of IFPs introduced has increased exponentially in the past 200 yr (Fig. 1a). The time of introduction of a limited number of species (6.5%) could not be established; these species were therefore excluded from further analyses. The rate of

introduction of ascomycetes continuously increased until now, basidiomycetes appeared at a constant rate over time and the rate of introduction of oomycetes has increased dramatically since the 1990s (Fig. 1b).

Of these IFPs, 27% are European species previously restricted to small areas of the continent, 22% are aliens from temperate North America, and 14% are from Asia. The origins of 25% are unknown. Africa, tropical North America and Australasia were minor sources of invasive pathogens for Europe, but their importance has increased over time, especially in the last 30 yr (Fig. 1c). Spread of endemic species within Europe was the main cause of invasion before the 1940s. The region of origin of alien pathogens was mainly North America from the early 1940s to the 1960s. Hybrids between introduced species were recorded in the 1990s for the first time (Fig. 1c,d).

The exact pathway of introduction was almost unknown for most of the IFPs. However, the most probable pathway was deduced for each IFP based on its biology and host range. Alien

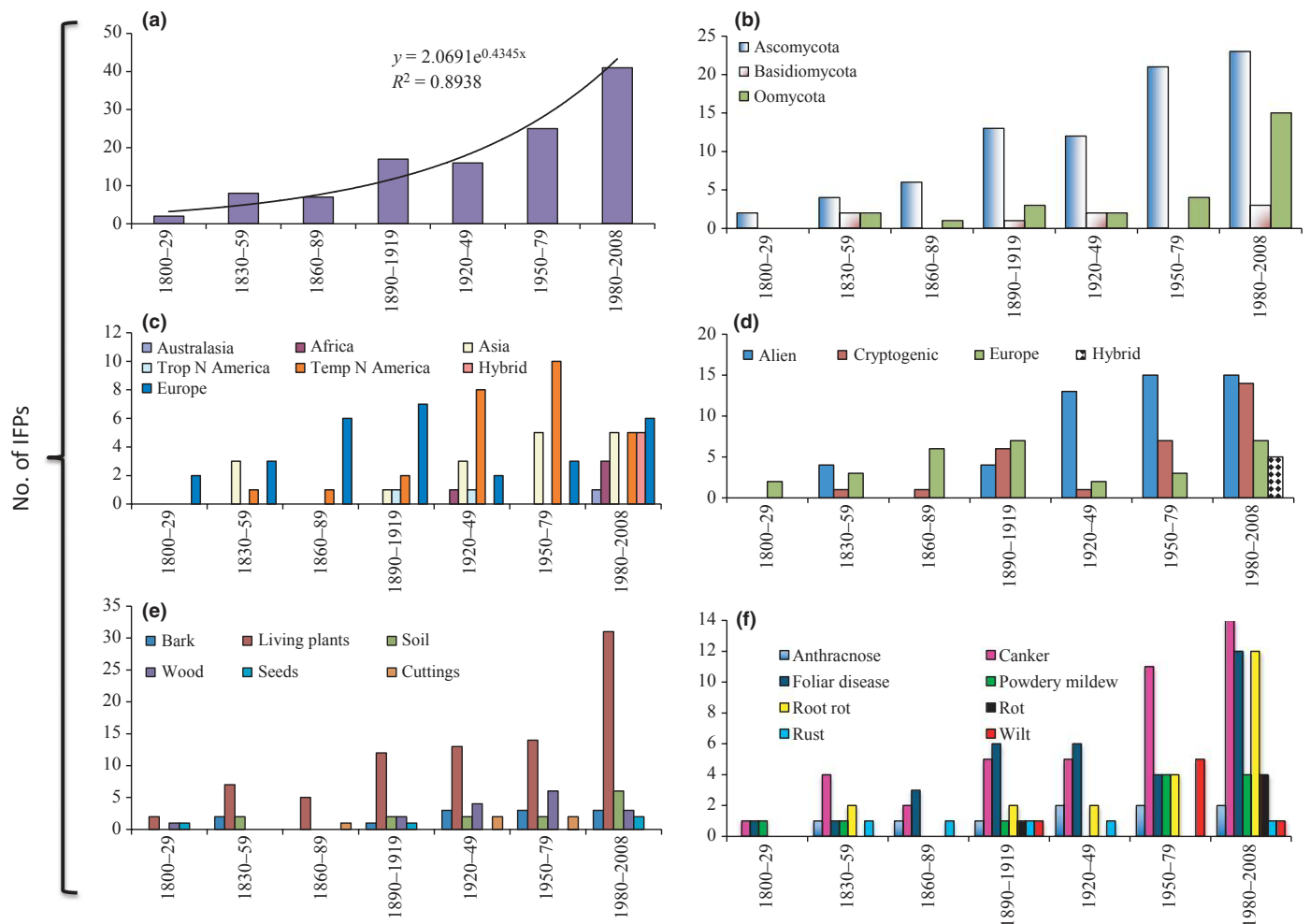


Fig. 1 (a) Total number of alien invasive forest pathogens (IFPs) according to time of arrival in Europe. Friedman's statistic = 12.86; adjusted for ties = 13.33; *P*-value using χ^2 approximation (6 df) = 0.038. (b) Taxonomic order of alien IFPs according to time of arrival in Europe. Friedman's statistic = 11.11; adjusted for ties = 15.90; *P*-value using χ^2 approximation (6 df) = 0.014. (c) Area of origin of alien IFPs according to time of arrival in Europe. Friedman's statistic = 12.64; adjusted for ties = 15.82; *P*-value using χ^2 approximation (6 df) = 0.015. (d) Status of alien pathogens recorded according to arrival in Europe. Friedman's statistic = 15.79; adjusted for ties = 17.86; *P*-value using χ^2 approximation (6 df) = 0.007. (e) Most probable substrate on which alien IFPs arrived in Europe, according to time of arrival. Friedman's statistic = 22.67; adjusted for ties = 24.72; *P*-value using χ^2 approximation (6 df) = 0.000.

pathogens were mainly introduced through living plants (57%) or wood (10%). Less than 10% of the introductions occurred through any of the other pathways (Fig. 1e). In the last 30 yr, the relative importance of living plant and soil pathways has dramatically increased.

IFPs in Europe are agents of cankers (31%), foliar diseases (25%), or root rots and rots (24%). Foliar diseases were common until 1920, whereas after that time canker agents were the most frequent new invaders, and in the last 30 yr the frequency of invasion by agents of root rots and rots has considerably increased (Fig. 1f).

Geographical pattern of invasion

The highest numbers of species (> 40 IFPs since 1800) were found in countries in the central-southern region of Europe (Italy, France, Switzerland, Austria, and Hungary). In Spain, Germany, Slovenia and Sweden, 31–40 species were recorded; in Romania, Slovakia, the Czech Republic, the UK, Norway and Finland, 21–30 species were recorded; and in Latvia, Lithuania, Poland, Belgium and Greece, \leq 20 IFPs were counted (Fig. 2a).

Based on species number and identity, European countries clustered into three macro-groups, illustrating that the incidence of IFPs was related to latitude: Continental (Austria, Belgium, the Czech Republic, Germany, Hungary, Poland, Romania, Slovakia, Slovenia and Switzerland); Atlantic/Mediterranean (France, Greece, Italy, Spain and the UK); and Nordic (Finland, Latvia, Lithuania, Norway, and Sweden) (correspondence analysis; Fig. 2b). The clustering was significant and explained 16% of the among-groups variance (ANISVA; Table 3a).

European countries were divided into two main clusters on the basis of arrival rate (RA_c), relative spread rate (RSR_c), and prevalence (PI_c) of the pathogens in their territory (PCA and hierarchical clustering; Fig. 3). The first cluster includes countries with many long-established invasive species (high PI_c). Within this cluster, Switzerland, Italy, Austria, Hungary and Slovenia have higher arrival rates and lower spread rates than Germany, Sweden and France. The other main cluster includes countries with relatively low arrival rates and prevalences, but generally high spread rates, indicating more recent invasions. The extreme in this cluster is represented by Poland and Latvia, which experienced a few recent and fast invasive events. The clustering was significant and explained 12% of the among-groups variance (ANISVA; Table 3b).

Geographical, socio-economical and climatic determinants of countries' invasibility

Countries' invasibility indices were significantly influenced by environmental, biodiversity and climatic factors as well as by GDP (regression analysis; Table 4). The countries with similar invasive pathogen numbers and species (CA-based clusters) also had similar land area, population, population density, degrees of latitude, GBI_{BIO} , number of eco-regions, and average annual temperature (nominal regression; Table 5a). The countries with comparable estimates of invasibility indices (PCA-based clusters) also had

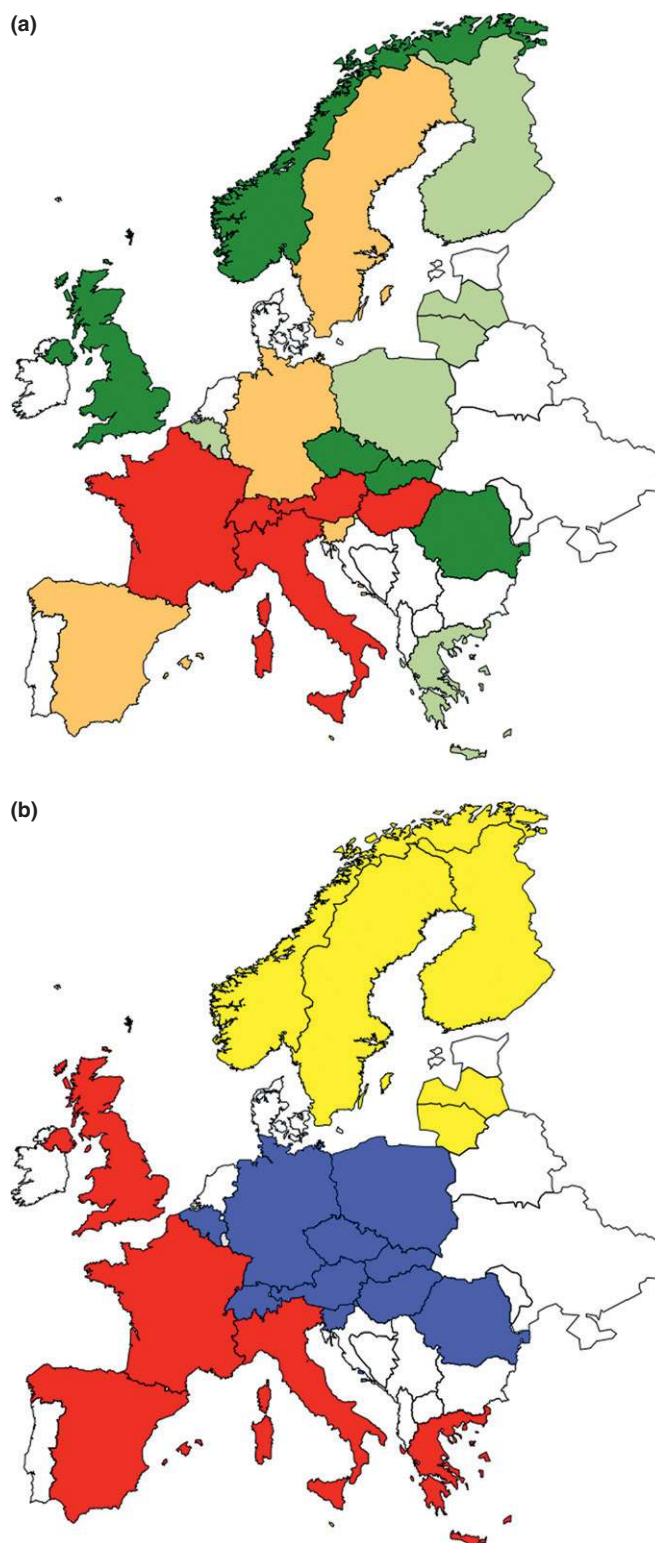


Fig. 2 (a) Numbers of alien invasive forest pathogens (IFPs) in each country. Pale green, 1–20; dark green, 21–30; pale orange, 31–40; red, > 41. (b) Groups of European countries with similar frequencies of IFPs based on correspondence analysis. Similar countries share the same colour.

similar land area, GDP, import-export, above-ground biomass, and average annual rainfall (nominal regression; Table 5b).

Table 3 Analysis of invasive species variance (ANISVA) calculated for the groups of countries obtained using correspondence analysis (CA; a) or principal components analysis (PCA; b)

	Source	df	SS	MS	Est. var.	%
(a)	Among groups	2	66.6	33.3	2.9	16
	Within groups	17	254.9	14.9	14.9	84
	Total	19	321.5		17.9	100
(b)	Among groups	4	93.6	23.4	2.0	12
	Within groups	15	233.2	15.5	15.5	88
	Total	19	326.8		17.6	100

Estimates of pathogens' invasiveness indices

Pathogens clustered into three main groups based on their spreading rates (SR_p and LSR_p), and extent of invasion (CE_p; Fig. 4). The first group consists of a few pathogens that have been recently introduced into many countries, and are spreading at high rates, such as *Hymenoscyphus pseudoalbidus* and *Phytophthora ramorum*. The second group is wider and more heterogeneous. It includes long-established species, such as *Phytophthora cambivora*, and rare species spreading at low rates, such as *Inonotus rickii*. In the third group are included pathogens that are spreading less rapidly than those in the first group, such as *Cylindrocladium buxicola* and *Ophiostoma novo-ulmi* hybrids.

Biological and historical determinants of pathogens' invasiveness

A subset of explanatory variables for each of the invasiveness indices was identified by means of regression analysis (Table 6). Species able to attack both forest and ornamental hosts tended to have higher spread rates. Exotic and hybrid species tended to have higher spread rates than native species. Invasive pathogens of

European or African origin had generally lower spread rates than American or Asiatic species. Spread rates tended to be lower in basidiomycetes than in ascomycetes and oomycetes. Generalist species tended to spread over a larger area than specialized pathogens.

Discussion

This work is based on a detailed database of IFPs in Europe (Table S1), representing the first such analysis carried out. The results show that invasive pathogens, able to cause severe growth reduction and often death of the host, have the potential for widespread harm and pose a substantial threat to forest trees in Europe. A considerable threat remains of pathogens invading European countries, particularly via those member nations that have not long engaged in international trade. The threat is greatest in countries with diverse eco-regions and flora. Epidemics of fungal and fungal-like diseases place plant species in serious danger of extinction world-wide (Fisher *et al.*, 2012). In Europe, the risk of serious genetic depletion as a result of repeated tree losses and offspring reductions is real for many forest tree populations. However, even the most attacked and damaged species still remain in the European landscape, albeit in much reduced numbers, and not even the most aggressive invasive pathogens have yet brought their hosts to extinction (Collin, 2002). Small and scattered populations with limited genetic variability might be especially damaged by invasive generalist pathogens, but in large host populations the spread and establishment of new parasites is predicted to be even more effective (Altizer *et al.*, 2003). Long-term effects of invasion are difficult to forecast, as they are mediated by changes in forest tree species, cascading effects throughout all ecosystem components, and by modifications to forest structure (Lovett *et al.*, 2006). The impact of invasive pathogens causing lethal diseases also depends upon whether or not they attack

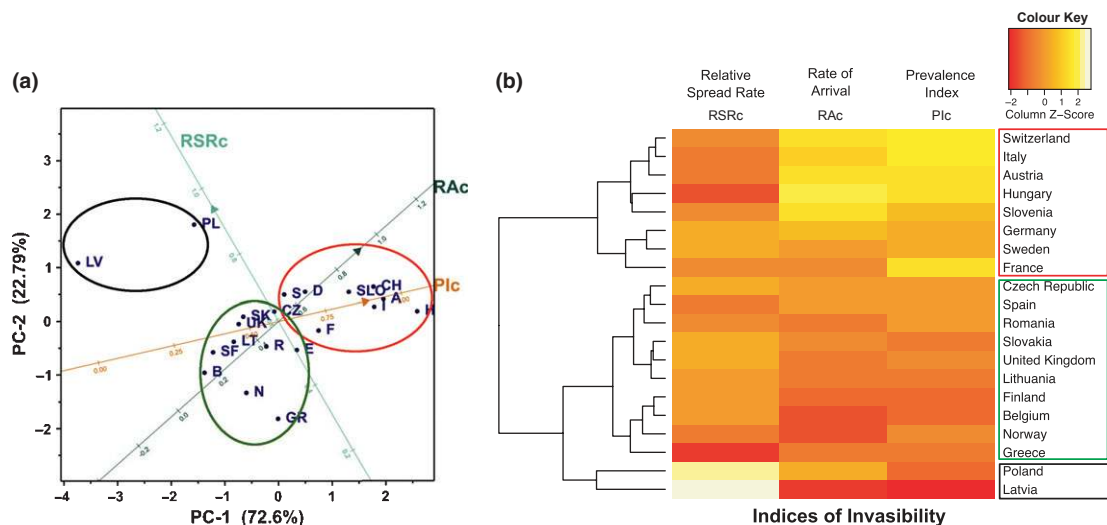


Fig. 3 (a) Clustering of European countries (Austria, A; Belgium, B; Czech Republic, CZ; Finland, SF; France, F; Germany, D; Greece, GR; Hungary, H; Italy, I; Latvia, LV; Lithuania, LT; Norway, N; Poland, PL; Romania, R; Slovakia, SK; Slovenia, SLO; Spain, E; Sweden, S; Switzerland, CH; United Kingdom, UK) according to principal components analysis based on spread rates and extent of invasion (invasibility indices rate of arrival (RA_c), relative spread rate (RSR_c), and prevalence index (PI_c)) of forest pathogens (a) and relative heatmap (b).

Table 4 Summary of generalized linear model and regression analyses for the effect of geographical, socio-economic and climatic factors on each of the country-specific invasibility indexes: (a) rate of arrival (RA_c); (b) prevalence index (PI_c); and (c) relative spread rate (RSR_c)

	Response variable	Explanatory variables	Wald χ^2 (df)	Likelihood ratio χ^2 (df)	R ²	SS (df)	MS	F	P
(a)	RA _c	Degrees of latitude	21.00 ⁽¹⁾						< 0.001
		GBI _{BIO}	6.59 ⁽¹⁾						0.032
		Number of eco-regions	10.01 ⁽¹⁾						0.001
		Mean latitude	29.08 ⁽¹⁾						< 0.001
		Total rainfall	4.19 ⁽¹⁾						0.041
		Average temperature	9.59 ⁽¹⁾						0.002
		Model		22.99 ⁽⁶⁾					0.001
		Regression			0.68	0.85 ⁽⁶⁾	0.14	4.67	0.01
		Residual					0.39 ⁽¹³⁾	0.03	
	Total				1.24 ⁽¹⁹⁾				
(b)	PI _c	Degrees of latitude	19.64 ⁽¹⁾						< 0.001
		Number of eco-regions	11.93 ⁽¹⁾						0.001
		Mean latitude	16.04 ⁽¹⁾						< 0.001
		Total rainfall	7.87 ⁽¹⁾						0.005
		Average temperature	3.85 ⁽¹⁾						0.050
		Model		20.70 ⁽⁵⁾					0.001
		Regression			0.64	0.83 ⁽⁵⁾	0.17	5.08	0.007
		Residual					0.46 ⁽¹⁴⁾	0.03	
			Total				1.30 ⁽¹⁹⁾		
(c)	RSR _c	GDP	3.99 ⁽¹⁾						0.046
		Average temperature	13.39 ⁽¹⁾						< 0.001
		Model		11.73 ⁽²⁾					0.003
		Regression			0.44	0.18 ⁽²⁾	0.09	6.78	0.007
		Residual					0.23 ⁽¹⁷⁾	0.01	
	Total				0.41 ⁽¹⁹⁾				

Table 5 Summary of Nominal Regression analyses testing the effect of geographic, socio-economical and climatic factors on the clusters of countries obtained through Correspondence analysis (CA, a) or Principal components analysis (PCA, b)

Dependent variable	Effect	Pseudo R-Square	Likelihood Ratio Chi-Square (df)	P
(a) CA-based groups	Land area	0.32	6.68 ⁽²⁾	0.035
	Population	0.53	12.34 ⁽²⁾	0.002
	Population density	0.77	22.55 ⁽²⁾	< 0.001
	Degrees of latitude	0.51	11.81 ⁽²⁾	0.003
	GBI _{BIO}	0.77	22.65 ⁽²⁾	< 0.001
	Number of ecoregions	0.54	12.77 ⁽²⁾	0.002
	Average annual temperature	0.93	33.92 ⁽²⁾	< 0.001
(b) PCA-based groups	Land area	0.40	9.56 ⁽⁴⁾	0.048
	GDP	0.42	10.37 ⁽⁴⁾	0.035
	Import-Export	0.56	14.69 ⁽⁴⁾	0.005
	Above-ground biomass	0.63	18.23 ⁽⁴⁾	0.001
	Average annual rainfall	0.41	9.66 ⁽⁴⁾	0.047

foundation species (*sensu* Ellison *et al.*, 2005). However, root rot and canker agents, which tend to produce more severe ecological effects than defoliators (Loo, 2009), have become the most frequent invasive pathogens in Europe in the last 30 yr and now represent one of the key threats to European forests.

Introduction into a new environment offers new evolutionary opportunities to pathogens. The sudden contact between closely related but previously geographically isolated pathogens falls into the category of episodic selection. It presents an opportunity for rapid emergence of new or modified pathogens via interspecific hybridization (Brasier, 1995, 2001). This has been the case with *Phytophthora alni*, a hybrid complex between *Phytophthora cambivora* and *P. fragariae*, which has jumped to new host species (Brasier *et al.*, 2004), and is now spreading in Europe at a very fast rate. Besides host jump, an additional evolutionary gain explaining the success of *Phytophthora* hybrids might be enhanced stress tolerance, which was demonstrated to occur for invasive hybrid plants (Milne & Abbott, 2000). In contrast, the hybrids between *Ophiostoma novo-ulmi* subspecies were shown to spread at average rates and to have moderate extents of invasion. This could be attributable to the fact that they did not change host and did not increase their virulence compared with the parental species (Santini *et al.*, 2005).

Since the beginning of the 19th Century, most invasive pathogens in Europe have been ascomycetes. The amount of introductions of ascomycetes and oomycetes has grown at an increasing rate, while the amount of introductions of basidiomycetes has maintained the same rate over time. The dramatic and recent increment in fungal and fungal-like organisms arrivals, and especially oomycetes, is partly explainable by the development of more effective diagnostic techniques in the last 30 yr (O'Brien *et al.*, 2009). This applies, for instance, to several



Fig. 4 Heatmap and hierarchical clustering of the invasive pathogens based on invasiveness indices, which represent estimates of pathogens' spread rates (spread rate (SR_p) and linear spread rate (LSR_p)) and extent in Europe (cumulative extent (CE_p)), as described in the Materials and Methods section, 'Estimates of pathogens' invasiveness indices'.

Table 6 Summary of Generalized Linear Model analyses for the effect of pathogen-specific biological and historical traits on the pathogen-specific invasiveness indexes, *Spread Rate* (SR_p , a); *Cumulative Extent* (CE_p , b); and *Linear Spread Rate* (LSR_p , c)

	Response variable	Explanatory variable	df	SS	MS	F	P
(a)	SR_p	Regression	5	53.2	10.64	9.08	<0.001
		<i>Status</i>	2	40.6	20.30	17.32	<0.001
		<i>Invaded environment</i>	3	12.6	4.20	3.59	0.016
		Residual	110	128.9	1.17		
		Total	115	182.1	1.58		
		Explained variance %	26.0				
(b)	CE_p	Regression	11	51.4	4.67	3.39	<0.001
		<i>Origin</i>	6	40.6	20.30	17.32	0.001
		<i>Invaded environment</i>	3	12.5	4.17	3.03	0.033
		<i>Taxonomical order</i>	2	5.3	2.66	1.93	0.150
		Residual	103	141.9	1.38		
		Total	114	193.2	1.70		
		Explained variance %	18.7				
(c)	LSR_p	Regression	15	84.7	5.65	5.31	<0.001
		<i>Origin</i>	6	28.86	4.81	4.52	<0.001
		<i>Country of 1st record</i>	3	9.95	3.32	3.12	0.029
		<i>Host range</i>	1	6.15	6.15	5.78	0.018
		Residual	99	105.3	1.06		
		Total	114	190	1.67		
		Explained variance %	36.2				

Phytophthora species nowadays frequently isolated and identified, which are probably indigenous in undisturbed forests, but are new to science (Jung *et al.*, 1996, 2002; Hansen & Delatour, 1999; Balci *et al.*, 2007; Hansen, 2008).

In this work, we classified IFPs into broad groups sharing similar invasive behaviour, a first and critical step towards more focused studies on the mechanisms of invasion. The most dangerous pathogens in Europe, which the national plant protection organizations should try to manage, are exotic or hybrid species, introduced to Europe either from Asia or from temperate and tropical North America; nonspecialized but able to colonize several forest and ornamental trees. Alien species may be more successful invaders because they escape from natural enemies in the introduced range (Wolfe, 2002) and/or attack non-coevolved hosts with no specific defences (Morrison & Hay, 2011). However, the enemy escape hypothesis is controversial (Heard *et al.*, 2006; Parker & Gilbert, 2007), at least for plants. In IFPs, the effect of a temporary lapse of enemies in the new environment has never been tested. However, there is circumstantial evidence for delayed adaptation of natural enemies to two alien invasive pathogens in Europe, that is, hypovirulence in *Cryphonectria parasitica* (Grente, 1965) and d-factor in *Ophiostoma ulmi* s.l. (Brasier, 1983). The success of generalist species is probably attributable to their capability to persist in a wide range of environmental conditions, and to spread long-distance (Brown & Hovmøller, 2002; Evangelista *et al.*, 2008). A clear example of successful invasion by a forest pathogen able to adapt to many new hosts is that by *Phytophthora ramorum* in the UK (Brasier & Webber, 2010). Nevertheless, among forest pathogens there are also several striking examples of successful invaders with high host specificity, such as *O. ulmi* s.l. and *C. parasitica* (Ehrlich, 1934; Ostry, 1995; Ostry & Kastovich, 1997; Schlarbaum *et al.*, 1997; Mc Keen, 1995; Loo, 2009).

Ornamental plantings have proved to be especially susceptible to invasion, probably because they are artificial ecosystems in harsh

conditions, which expose them to the constant risk of being overwhelmed by pathogens. The low incidence of invasions in nurseries could be explained by chemical disease control.

The temporal trend of invasion in Europe reflects European history, as previously suggested by Desprez-Loustau (2009). Until the beginning of the 1920s, most invasive pathogens in Europe were long-established species that simply extended their range across neighbouring countries. After the 1920s, the most invasive pathogens were alien species arriving mainly from North America, Europe's main trading partner at that time. The end of World War I marked a major boundary of this expanding introduction and spread of alien species. In the last 30 yr, the rate of forest pathogen invasions into Europe has escalated exponentially, similarly to that of invasive plants and animals (Genovesi *et al.*, 2009; Hulme *et al.*, 2009; Pysek *et al.*, 2009; Roques *et al.*, 2009). The origin of invasive species has also changed, with a great increase in the number of pathogens from Asia and the appearance of new hybrid species (Brasier, 2000).

Political changes following 1989, when the Iron Curtain fell, opened the doors to globalization, leaving a world without strict borders and few, if any, areas sheltered from invasive species migrations. Globalization and the expanded transport of goods around the planet are the main reasons for the increase in IFPs introductions (McNeely, 2006; Hulme *et al.*, 2008; Hulme, 2009). Rapid transportation and reduced delivery times increase the survival of pathogen propagules, and increase their chances of successful establishment in a new environment (Hulme, 2009).

Nevertheless, the recent rise of IFPs may be partly explained by new and more effective diagnostic techniques and facilities for fungi and chomista, which are generally inconspicuous and hardly visible at most stages of the life cycle (Hawksworth, 2001).

In addition, climatic factors had a significant impact on both country invasibility and pathogen spread and establishment in

Europe. Thus, invasion by forest pathogens could have also been accelerated by climate change, which is known to influence the establishment rates of alien plants and animals (Dukes *et al.*, 2009; Huang *et al.*, 2011).

Invasive pathogens have been most abundant in Italy, France, Switzerland, Austria and Hungary. The high numbers of invasive pathogens in France, Italy, and Switzerland have been previously explained by higher volumes of imports (Desprez-Loustau, 2009). Human population is another recognized predictor of the number of alien fungi in a territory (Desprez-Loustau *et al.*, 2010). We found total population and population density to affect the pattern of invasion. Thus, the high number of invasive pathogens, for instance, in Italy may also be a result of its long history of intense human activity. Their historical role as a bridge between Eastern and Western Europe may partly be responsible for the high number of invasions observed in Hungary and Austria. Italy, France, Switzerland, Austria and Hungary have mainly long-established IFPs, and they experienced high rates of invasion in the past. In contrast, Poland and Latvia are now starting to experience invasions, but were relatively free of them in the past. The small number of invasions in previous members of the Soviet block may partly be the result of commercial isolation during the Soviet era. The unique history of the UK, for example the number of deliberate plant introductions from all over the world by 'plant hunters' (Tyler-Whittle, 1970), is probably the cause of the peculiar pattern of IFPs there.

According to our data, environmental variation and biodiversity richness, in addition to trade considerations, influenced the pattern of invasion of forest pathogens in Europe, as previously reported for plants and animals in other regions of the world (Lonsdale, 1999; Sax, 2001). Establishment of many forest pathogens with different ecological niches has probably been favoured in regions where arrival and spread rates of pathogens were affected by high environmental diversity, as shown here for the first time. For invasive plants and animals, the crucial importance of heterogeneity for the invasibility of the community and on the spread rate of invasive species is known as the 'environmental heterogeneity hypothesis of invasions' (Melbourne *et al.*, 2007).

IFPs have strong economic and ecological implications. The epidemic of chestnut blight in the mountains of southern Europe, for example, aggravated starvation of local human populations and increased migration to urban areas after World War II (T. Turchetti, pers. com.).

In Europe, the impact of biological invasions is reflected in the increasing number of EU-funded LIFE projects devoted to alien species eradication (Vilà *et al.*, 2010).

According to the present survey, a further spread of established IFPs may be expected in countries that have experienced commercial isolation in the recent past. Densely populated countries with high environmental variety and biodiversity have been the main points of entry into Europe for alien species. These countries were historically subjected to rapid invasions and are likely to be the weakest link in attempts to protect against further new arrivals. It has been estimated that the annual monetary impact of alien invasions is close to €10 billion, a figure that is thought to be an underestimate (Hulme *et al.*, 2009). Current European policy has

not adequately addressed the consequences of this reported surge of arrivals. Many policy makers are not completely aware of the threat posed by alien species, and the urgent need for tight coordination of actions against new arrivals, including a rigorous survey of possible pathways through modern diagnostic techniques (Stenlid *et al.*, 2011). Most IFPs have been found on ornamental trees and were associated with the trade of living plants in soil, which became the preponderant pathway of introduction during the last 30 yr. Over this period, the establishment of root-rotters (oomycetes) also increased. At the same time, the origin of the invasive species changed from a prevalent source to many and equally important sources. These observations should serve to focus attention on the risk inherent in the trade of ornamental plants for planting in soil, which also constitutes the main pathway of introduction of pests, as reported by many authors in different countries (Kenis *et al.*, 2007; Smith *et al.*, 2007; Roques *et al.*, 2009; Liebhold *et al.*, 2012). Many forest pathologists throughout the world have expressed their concern about this escalating crisis in the Montesclaros declaration (<http://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration/>). The European rules on trade of plants need to be reformed by taking into account the risk of introduction of noxious organisms through potted living plants from many countries. This pathway is particularly insidious as invasive harmful organisms are not easily detectable in soil, and they are, in addition, almost unknown and neglected in their native ranges.

Eradication seems to be impossible, and so prevention by early detection of new introductions seems the only reliable measure, although it is difficult in the face of global mobility. Strategies to manage the coevolution of invasive pathogens with their new hosts should also be developed (Carroll, 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1 European database of invasive forest pathogens (IFPs)

Table S2 Climatic and geographical parameters used as explanatory variables and country-specific invasibility indexes

Table S3 Number of invasive pathogens per country and socio-economic parameters used as explanatory variables

Methods S1 Formulae used to estimate invasiveness and invasibility indexes.

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