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Simulating the effects of a climate change scenario on geographical range and activity of forest pathogenic fungi

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Abstract

The aim of the study was to explore possible effects of climate change on the geographic range or local impact of several forest pathogenic fungi. To this aim, (1) the parameters of species' responses to climatic variables were determined, in two types of models: specific statistical models and the generic model CLIMEX; (2) these models were used to make simulations under a future climatic scenario, based on a general circulation model of climate, which was regionalized over France. A range of pathogens commonly reported in Europe were studied : *Melampsora larici-populina*, *M. allii-populina* and *M. medusae*, agents of poplar rust, *Mycosphaerella pini* , agent of red-band disease of pines, *Melampsora pinitorqua.*, agent of pine twisting rust, *Cryphonectria parasitica*, agent of chestnut blight, *Phytophthora cinnamomi*, agent of ink disease on chestnut and oaks, *Sphaeropsis sapinea* and *Biscogniauxia mediterranea*, opportunistic pathogens (cortical endophytes) on pines and oaks, respectively. The predicted warming would be favourable to most studied species, especially those for which winter survival is a limiting factor linked to low temperatures (*P. cinnamomi* et *M. medusae*). For some species such as *M. pini*, the favourable effect of warming would be counterbalanced by the negative effect of a decrease in summer rainfall, leading to a stable or decreased impact of these pathogens by the end of the century. Conversely, *B. mediterranea* et *S. sapinea*, favoured by water stress, should have an increased impact.

Interest and limitations of the different models are discussed. Some implications of the projected changes in "forest phytosanitary landscape" are presented in terms of research and management issues.

Key-words : biogeography, climate change, model, epidemiology, forest diseases

Résumé

L'étude a pour objectif d'explorer les effets possibles d'un changement climatique sur la distribution géographique et l'impact local de plusieurs champignons pathogènes forestiers. Pour cela, (1) les paramètres de la réponse des différentes espèces aux variables climatiques ont été définis, dans deux types de modèles : des modèles statistiques spécifiques et le modèle générique CLIMEX; (2) ces modèles ont été utilisés pour faire des simulations sous un scénario de changement climatique, basé sur un modèle de circulation générale du climat régionalisé sur la France. L'étude a porté sur une gamme de pathogènes couramment trouvés en Europe : *Melampsora larici-populina*, *M. allii-populina* and *M. medusae*, agents de la rouille des peupliers, *Mycosphaerella pini*, agent de la maladie des bandes rouges des pins, *Melampsora pinitorqua.*, agent de la rouille courbeuse des pins, *Cryphonectria parasitica*, agent du chancre du châtaignier, *Phytophthora cinnamomi*, agent de la maladie de l'encre des châtaigniers et des chênes, *Sphaeropsis sapinea* et *Biscogniauxia mediterranea*, pathogènes opportunistes (endophytes corticaux) des pins et chênes respectivement. Le réchauffement climatique prédit serait favorable à la plupart des espèces étudiées, en particulier celles dont la survie hivernale est limitante aux basses températures (*P. cinnamomi* et *M. medusae*). Pour certaines espèces, comme *M. pini*, l'effet favorable du réchauffement serait contre-balançé par un effet défavorable de la diminution des pluies estivales, conduisant à une stabilisation voire régression des impacts simulés pour la fin du siècle. Par contre, *B. mediterranea* et *S. sapinea*, favorisés par les stress hydriques, devraient voir leur impact augmenter dans le futur.

L'intérêt et les limites des différents modèles sont discutés. Certaines implications des changements attendus dans le "paysage phytosanitaire forestier" sont présentées en terme de recherche et de gestion.

Mots-clés : biogéographie, changement climatique, modèle, épidémiologie, maladies forestières

Introduction

The influence of climate in explaining the distribution of living organisms has long been recognised, since the pioneering works of von Humboldt and de Candolle in the 19th century, and is a major issue of biogeography. Biogeographical studies have mainly focused on higher plants and animals, and more generally free living organisms. Although parasites and pathogens are primarily dependent on the presence and density of their hosts (resource availability), climate is also an important driver of their distribution patterns (Guernier *et al.* 2004). This applies in particular to plant pathogenic fungi. As poikilothermic organisms infecting poikilothermic hosts, they are heavily influenced by temperature for their growth rate and cold season survival. Climatic variables, especially precipitations, may also affect dispersal (Agrios 2005). The effects of climate on disease include not only direct effects on pathogens, but also indirect effects through host physiology and parasite-associated organisms, such as vectors or hyperparasites (Coakley *et al.* 1999, Harvell *et al.* 2002). A large body of literature is available that deals with the relation between meteorological conditions and disease development, explaining between-year or geographical variation in disease severity (e.g. Houston & Valentine 1988, Jahn *et al.* 1996).

The ongoing climate change, with its high magnitude and speed, is therefore highly likely to induce crucial changes in diseases (Coakley *et al.* 1999, Ayres & Lombardero 2000, Boland *et al.* 2004, Anderson *et al.* 2004). Suggestions that a warmer climate will bring an increase of diseases is supported by positive effects on pathogen and vector growth rates and a greater potential of these species, compared to their hosts, to respond to environmental change, through dispersal, phenotypic plasticity and adaptation (Goudriaan & Zadocks 1995, Coakley *et al.* 1999, Davis & Shaw 2001, Saxe *et al.* 2001, Etterson & Shaw 2001). Also, a dramatic effect of climate change may be the emergence of new

pathosystems, resulting from new encounters between parasite and host species. Indeed, shifts in the distribution of species are most likely impacts of climate change. Expansions or shifts in geographical distributions have been demonstrated in response to climatic changes during the Quaternary period (Davis & Shaw 2001) and recent changes in distributions, associated with changing climate in the last decades, are already visible for many species (Parmesan *et al.* 1999, Parmesan & Yohe 2003). However, rates of range shifts vary greatly among species, which should lead to rearrangements of the assemblages of species in communities (Walther *et al.* 2002), in particular host–parasite interactions. New encounters of parasites with naïve hosts (species or populations), i.e. with no coevolution or coadaptation history, may have the same dramatic consequences as that observed with introduced parasites (Harvell *et al.* 2002). The pine processionary caterpillar, that has showed a recent latitudinal and altitudinal shift together with a host shift (first report on Douglas fir), provides an example of such changes (Goussard *et al.* 1999).

In spite of their high significance, potential range shifts of plant pathogen species in response to climate change have been poorly investigated so far. Due to variation in response to climatic variables among species and spatial variability of climate change, especially in precipitations, no general trend can be expected and there is a need for studies based on meaningful pathogen/disease models and up-to-date regionalized projections of climate change. The aim of our study was to explore possible effects of climate change on the geographic range or local impact of several important forest pathogenic fungi. To this aim, (1) we determined the parameters of species' responses to climatic variables in two types of models: specific statistical models and the generic model CLIMEX; (2) we used these models to make simulations under a future climatic scenario, based on a general circulation model of climate, which was regionalized over France.

1. Materials and methods

1.1 Climatic data and scenario

Past climatic data for the 1961-1990 period come from the Meteo-France network. Future climatic data were extracted from the ARPEGE model (Déqué *et al.* 1994, Déqué *et al.* 1998). This is a global circulation model (GCM) describing the time evolution of the atmosphere by solving fluid dynamics equations. It is used as a meteorological forecast model as well as for climatological simulation. The calculation of radiation includes the effect of 4 greenhouse gases (CO₂, CH₄, N₂O and CFC) in addition to water vapor and ozone, and of 5 aerosol types (land, sea, urban, desert and sulfate) in addition to background aerosols. The model was forced by an effective greenhouse effect corresponding to the provisional IPCC B2 scenario (IPCC 2001). The main assumptions of the emission scenario and the model details can be briefly summed up as follows. A more complete description of the regionalized climate scenario can be found in Déqué *et al.* 1998.

B2 scenario

The IPCC Special Report on Emission Scenarios (SRES) provides 40 different scenarios that are deemed equally likely. These scenarios have been constructed to explore future developments in the global environment with special reference to the production of greenhouse gases and aerosols, from hypotheses on possible demographic, politico-economic, societal and technological future. For the Third Assessment Report, the IPCC facilitated the conversion of two of these emission scenarios (A2 and B2) into concentration scenarios for use in climate simulations. The B2 scenario is a moderate climate change scenario that envisions a 70% increase in the current effective CO₂ concentration by 2100. The B2 scenario envisions a slow population growth (10.4 billion by 2100) with a more rapidly evolving economy and more emphasis on environmental protection. It therefore produces lower emissions and less future warming than the A2 scenario for example (CO₂

emissions in 2100 of 14 and 29 Gt C in A2 and B2, respectively, with whole range including all scenarios between 5 and 29).

The regionalized climate scenario.

Using a coupled ocean-atmosphere GCM at regional scale is currently unrealistic. Two experiments using different experimental set-ups were then performed with the ARPEGE model in order to allow downscaling. The first consisted of a pair of coupled coarse-resolution 150-year simulations corresponding to 1950-2100. The atmospheric model was run with a uniform T63 truncation (which is roughly equivalent to a 280 km regular mesh) and a high vertical resolution with 45 levels. The first simulation was a control simulation in which the greenhouse gas concentrations remained constant (1950 radiative forcing). For the second simulation greenhouse gas concentrations were prescribed to the models according to IPCC historical data (for the period 1950 to present) and scenarios (for the second half of the simulation). In a second step, several time-slice simulations were performed with a variable resolution model corresponding to 1960-2099. From 1960 to 1999, Sea Surface Temperature (SST) boundary conditions were prescribed to the model according to monthly mean observed SST (Smith et al. 1996). From 2000 through 2099 artificial monthly SSTs were created by adding anomalies from the above-described coupled scenario to observed SSTs. The variable resolution configuration had a T106 truncation instead of T63 and 31 vertical levels. The variable resolution allowed simulation of fine-scale information over a regional area. The stretching factor was 3 and the pole of stretching was approximately at the center of the Mediterranean basin (40°N, 12°E) (Gibelin and Déqué, 2003). As a result the mesh size is about 50 km over France (a 0.5° x 0.5° resolution) and about 500 km over the Pacific Ocean. This version uses semi-lagrangian advection and a two time-level discretization. Vertical discretization uses hybrid coordinates (Simmons and Burridge 1981). The time step is 30 min. Most output data are daily but some parameters are provided every 6 hours.

Integration of simulated climatological data in the epidemiological models.

Simulated climatological data were used for the period 2070-2099. The choice of a 100 year time span between the two study periods was dictated by the low frequency variability of local climate. Although the global mean temperature increases slowly and regularly along the 21st century in the model, regions like Europe experience fluctuations due to natural processes involving oceanic circulation. In order to study the response of the 2020's or 2040's, ensembles of coupled scenarios, which do not yet exist, would be necessary to filter out internal variability. Beyond 2060, the signal due to radiative forcing is larger than the noise due to natural variability.

The limiting ability of current GCMs, including the model we used, to reproduce the natural variability of climate made it difficult in turn to compare the 2070-2099 study period with the 1961-1990 reference period. To cope with this difficulty, the anomaly method was used. This method mitigates the limitations of the model by keeping the present natural variability of climate whilst taking into account the global climate change at a regional and temporal scale. Monthly mean anomalies of climatic variables were computed for each mesh point by calculating differences between monthly mean values extracted from the 1961-1990 and 2070-2099 variable resolution simulation, respectively. These anomalies were then interpolated to the coordinates of the meteorological stations with a $1/r^2$ interpolation using the five closest grid points. Adding these mean monthly anomalies to the observed climatological data in the 1961-1990 period created simulated data for the 2070-2099 period.

1.2 Selected species

Several species of forest pathogenic fungi were selected among the most frequently encountered in France (database of the French Forest Health Department, Département

Santé des Forêts= DSF), and more generally in Europe (Butin 1995), on various host species, representing a range of disease types:

- foliar and shoot diseases: *Melampsora larici-populina* Kleb. *M. allii-populina* Kleb. and *M. medusae* Thüm., agents of poplar rust, *Mycosphaerella pini* Rostr. (= *Scirrhia pini*, anamorph = *Dothistroma septosporum* or *D. pini*), agent of red-band disease of pines, *Melampsora pinitorqua* Rostr, agent of pine twisting rust
- canker diseases : *Cryphonectria parasitica* (Murrill) M.E. Barr, agent of chestnut blight
- root diseases : *Phytophthora cinnamomi* Rands., agent of ink disease on chestnut and oaks
- opportunistic pathogens (cortical endophytes) : *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton on pines, *Biscogniauxia mediterranea* (De Not.) Kuntze (= *Hypoxylon mediterraneum*, anamorph : *Nodulisporium* sp, or *Periconiella*) on oaks.

1.3 Specific statistical models of pathogen response to climate

A few forest pathogenic fungi have been the subject of extensive systematic surveys in France : *P. cinnamomi*, *C. parasitica*, *M. medusae*, introduced species for the three of them, submitted to European quarantine regulations for the two latter. Survey data of *P.cinnamomi* have already been used to develop a model of pathogen survival and disease development in relation to winter temperature (Marçais et al 1996, 2004). This model was used to map disease risks under current and projected climate (Bergot et al 2004). In the present study, we used *Cryphonectria* and *Melampsora* data to develop statistical models of species occurrence.

M. medusae and *M. allii-populina* on poplars

Within the scope of the quarantine survey of *Melampsora medusae*, systematic observations were conducted by the Plant Health Service (SPV) in 311 French nurseries from 1993 to 2003. Ten leaves were harvested for each poplar clone. The identification of species was based on microscopical observations of one urediniosore per leaf, on the abaxial surface. For our study, only reports on non discriminant clones, i.e. susceptible to all rust species, were taken into account (one to seven in each location and year). *M. larici-populina*, which is widely distributed in the whole study area, was used as reference for the two other species, assuming that the presence of *M. larici-populina* is a good indicator of occurrence of poplar rusts in a nursery (poor control). Results were therefore expressed for *M. allii-populina* and *M. medusae* as the ratio of infected clones by either species to the number of clones infected by *M. larici-populina*. In the absence of any reference data, no analysis could be done for *M. larici-populina*.

Cryphonectria parasitica on chestnuts

A systematic survey of chestnut blight was carried out by the Forest Health Department (DSF), in 1996-1997 in 1100 chestnut plots, corresponding to a sampling rate of one plot per 1000 Ha in the affected area (South) and one plot per 500 Ha in the zone considered as disease-free at that time (northern part of the country) (de Villebonne 1998). In each plot, the proportion of infected trees among 50 to 100 observed trees (PIT) was recorded. The data used to fit the model were a random sub-sample (432 points) of the 586 "positive" points (i.e. plots affected by disease), the remaining points being used for validation.

Statistical analyses

The dependent variable (proportion of clones affected by *M. allii-populina* or *M. medusae* in each nursery, percentage of infected chestnuts by *C. parasitica* in each plot) was analysed by a logistic regression, with a logit link (SAS Logistic procedure). Climatic variables tested were the trimestrial means over the 1961-1990 period of : minimum,

maximum and mean daily temperatures (in °C), sum of precipitations (in mm), water deficit = evapotranspiration minus sum of precipitations (in mm), and the annual numbers of days with a minimum temperature below 0°C, -5°C and -10°C. Climatological variables from the Meteo-France network were interpolated on a 1km x 1km grid using a kriging analysis taking topography into account (AURELHY model, for Analysis Using the RELief for HYdrometeorology).

Table 1: Main references used for selecting initial values of parameters and parameter-fitting in Climex

Species	Map *	References
<i>Melampsora larici-populina</i>	569 (1986)	Somda & Pinon 1981
<i>M. allii-populina</i>		
<i>M. medusae</i>	547 (1991)	
<i>Cryphonectria parasitica</i>	66 (1994)	Anagnostakis & Aylor 1984 Gao & Shain 1995 Guérin & Robin 2003 Guérin <i>et al.</i> 2001 Robin & Heiniger 2001
<i>Melampsora pinitorqua</i>	389 (1961)	Desprez 1983 Kurkela 1969, 1973a, b Siwecki 1974
<i>Mycosphaerella pini</i>	419 (1997)	Evans 1984 Ivory 1994 Gadgil 1984 Gibson 1972, 1974 Peterson 1973
<i>Sphaeropsis sapinea</i>	459 (1992)	Blodgett <i>et al.</i> 1997 Keen & Smits 1989 Stanosz <i>et al.</i> 2001
<i>Biscogniauxia mediterranea</i>		Vannini & Valentini 1994 Vannini <i>et al.</i> 1996
<i>Phytophthora cinnamomi</i>	302 (1991)	Benson 1982 Gisi <i>et al.</i> 1980 Grant & Byrt 1984 Marçais <i>et al.</i> 1996 Phillips & Weste 1985 Shew & Benson 1983 Sterne <i>et al.</i> 1977 Zentmyer 1981 Zentmyer <i>et al.</i> 1976, 1979

* Commonwealth Mycological Institute, then CABI Publishing : Distribution Maps of Plant Diseases.

All models using one, two or three variables were tested. Those associated with the highest deviance decrease were studied in more detail (residuals and influential points). The best model with the least variables was selected. Maps of current and future disease variables were obtained by plotting the calculated percentage values on the 1km x 1 km grid.

1.4 The Climex model

1.4.1 General description

Climex is a dynamic simulation model developed by the CSIRO (Sutherst *et al.* 1999) to predict the potential geographical distribution, or bioclimatic envelope, of a given species, i.e. the locations where the target species can develop according to its climatic requirements. The specific values for parameters that describe the organism's response to temperature and moisture are inferred from the known geographic distribution and seasonal phenology of the species; laboratory data can also be used to fit some parameter values.

The main model output is an ecoclimatic index (EI) which gives an overall measure of suitability of locations for permanent occupation of the target species. This index is calculated from the combination of two indices: the annual growth index (GI) and the annual stress index (SI). Annual indices are the sum of weekly indices, combining temperature and moisture indices, as follows:

$$EI = GI * SI,$$

$$GI = 100 \sum_{w=1}^{52} \frac{GI_w}{52},$$

$$GI_w = TI_w * MI_w,$$

with TI_w = Weekly Temperature Index, scaled from 0 to 1, using four parameters : DV0 (lower temperature threshold), DV1 (lower optimum temperature), DV2 (upper optimum temperature), DV3 (upper temperature threshold) to describe the non-linear response of growth to temperature, MI_w = Weekly Moisture Index, scaled from 0 to 1, using four parameters SM0, SM1, SM2, SM3, defined as above.

The annual stress index (SI) is also calculated from weekly indices for each of four primary stresses : heat stress, cold stress, wet stress and dry stress, and their interactions. A threshold value and an accumulation rate defines all stresses. In the case of cold stress, two types of stress are defined : a lethal stress at low temperatures and a chronic stress, when thermal accumulation is too low to maintain metabolism. In all cases, it is assumed that the accumulation of stress is exponential during the year.

1.4.2 Application

For all selected species, a thorough analysis of literature dealing with the response to climate (including seasonal variation of susceptibility to the disease) and world geographical distribution was performed (Table 1). Geographical distributions derived from the DSF database were used for France.

The parameter values relating to species responses to temperature were defined from a laboratory experiment. For each species, three isolates from different geographic areas of France were used to establish mycelial growth-temperature curves. Isolates were sub-cultured on malt-agar or PDA media, with 5 Petri dishes per isolate and temperature. After an initial growth period at 22°C (first growth assessment), Petri dishes were distributed in growth chambers at 2°C, 6°C, 10°C, 14°C, 18°C, 22°C, 26°C, 30°C, 34°C, 38°C. The second growth assessment was performed when cultures had reached approximately half of the diameter of dishes. Daily linear growth rate was calculated for each temperature. The four temperature parameter values used in Climex were defined as follows: DV0 = lowest temperature with growth = 10% of maximal growth, DV1 = like DV0 with 70%, DV2 = highest temperature with growth = 70% of maximal growth, DV3 = like DV2 with 10%. Mean values over the three isolates were used for each species (Table 2). Literature data were used for rust species (Table 1).

For all other parameters, initial values were chosen from the templates provided with CLIMEX (temperate, mediterranean, wet tropical) according to the knowledge on species origin and distribution (Table 2). A lethal stress at cold temperatures was defined for

Table 2 : CLIMEX parameters

Factor	Parameter	Climex templates					Parameters defined in this study								
		Wet tropical	Mediterranean	Temperate	Semi-arid	Desert	<i>P. cinnamomi</i>	<i>P. cinamomi</i> (root)	<i>P. cinamomi</i> (stem)	<i>M. pinitorqua</i>	<i>C. parasitica</i>	<i>M. pini</i>	<i>S. sapinea</i>	<i>B. mediterranea</i>	
Temperature	DV0	15	10	8	14	15	5	8	8	5	6	2	8	10	
	DV1	26	16	18	28	25	23	22	22	12	20	17	21	24	
	DV2	33	24	24	36	40	28	32	32	20	30	28	31	30	
	DV3	36	28	28	40	44	32	34	34	25	37	33	34	38	
Moisture	SM0	0,3	0,1	0,25	0,05	0	0,4	0,4	0,4	0,5	0,1	0,3	0,1	0,05	
	SM1	0,5	0,4	0,8	0,1	0,001	0,7	0,7	0,7	0,8	0,5	0,7	0,2	0,1	
	SM2	1,75	0,7	1,5	0,4	0,2	1,3	1,3	1,3	1,5	1,5	1,75	0,7	0,4	
	SM3	2	1,5	2,5	0,6	0,3	3	3	3	2,5	2,5	2	1	0,6	
Cold stress	TTCS	0	0	0	6	2	0	0	2	0	0	0	0	0	
	THCS	0	0,005	0	0,01	0,001	0	0,005	0,1	0	0	0	0	0	
	DTCS	25	15	15	15	15	10	10	10	0	15	15	15	15	
	DHCS	0,0015	0,001	0,0001	0,0002	0,0005	0,0007	0,0001	0,0001	0	0,0001	0,0001	0,00015	0,0003	
Hot stress	TTHS	36	30	30	40	44	30	34	34	25	37	33	34	38	
	THHS	0,001	0,002	0,005	0,002	0,001	0,005	0,002	0,002	0,005	0,005	0,005	0,005	0,002	
	DTHS	0	0	0	0	0	0	0	0	0	0	0	0	0	
	DHHS	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dry stress	SMDS	0,3	0,02	0,2	0,05	0	0,1	0,1	0,1	0,5	0,1	0,3	0,02	0,05	
	HDS	0,006	0,05	0,005	0,005	0	0,05	0,05	0,05	0,005	0,005	0,01	0,05	0,005	
Moisture stress	SMWS	2	0,6	2,5	0,6	0,3	0	0	0	0	0	2,5	1	0,6	
	HWS	0,002	0,0015	0,002	0,005	0,1	0	0	0	0	0	0,002	0,005	0,005	
Dry * Hot stress	TTHD						32								
	MTHD						0,05								
	PHD						0,005								
Wet * Hot stress	TTHW		23									23	23		
	MTHW		0,5									0,5	0,5		
	PHW		0,075									0,01	0,075		

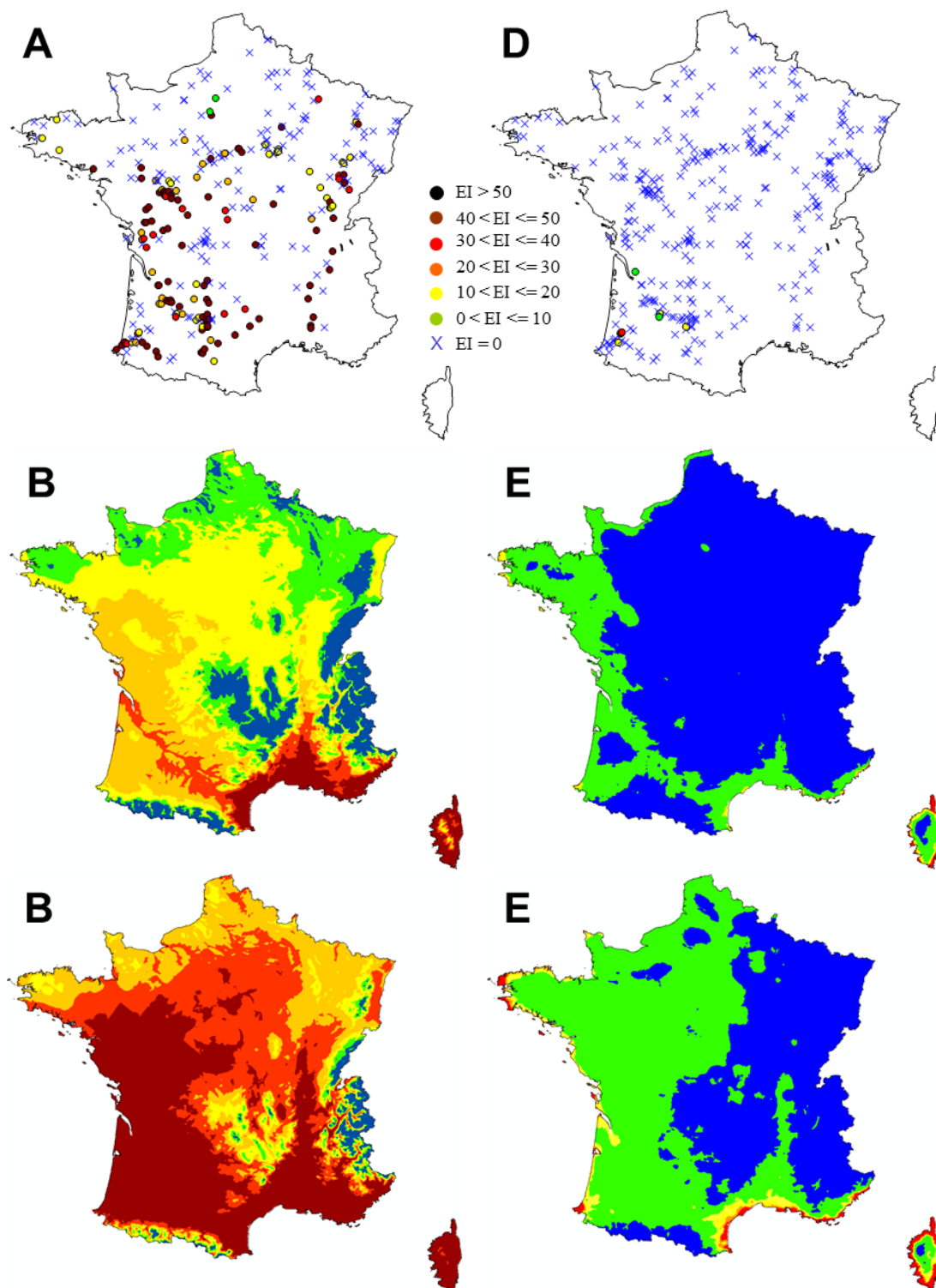


Fig. 1: Distribution from survey data (PHS 1993-2003) of *Melampsora* rusts of poplars (*M. allii-populina* : A, *M. medusae* : D) and predicted range based on simulated prevalence (p) by a logistic regression with climatic variables, for *M. allii-populina* (B, C) and *M. medusae* (E, F), under current (1961-1990: B, E) and future climate projected under the Arpege-Climat scenario (2070-2099: C, F).

P. cinnamomi, in agreement to its known sensitivity to frost (Benson 1982, Zentmyer 1980, Marçais et al 1996, 2004), although only a chronic cold stress is considered for *P. cinnamomi* in Climex (Table 2). Higher values of parameters of lethal cold stress (threshold and rate) were selected when *P. cinnamomi* was considered as a canker agent compared as a root pathogen, due to lower temperature buffering capacity of trunks compared to soils. Final values of moisture and stress parameters were obtained by an iterative parameter-fitting process until a good fit to geographical distribution and seasonal variation data was obtained.

Climatological data from 65 stations of the Meteo-France network were imported in the meteorological data file (instead of the 29 provided in CLIMEX) to improve resolution to a mean 90km x 90 km.

2 Results

2.1 Specific statistical models

2.1.1 *Melampsora spp on poplars*

The main explaining variables for *M. allii-populina* relative frequency (p), derived from the logistic analysis, were the mean summer temperature and water deficit : $\text{logit}(p) = -10,34 + 0,471 T_s + 0,007 WDs$ (Wald Chi2 = 37.93 P<0,0001 and 11.52 P=0.0007, for T_s and WDs, respectively). The odds ratio, 1.6 for each 1°C increase and 1.1 for each 10mm increase in summer water deficit, indicate that *M. allii-populina* occurrence is favoured by warmer summer climate and slightly by water deficit in the same months. The spatial distribution simulated by this model with current climatic data showed higher frequencies in the West and in the Rhone valley, in good agreement with observed data from the SPV survey (no data for the Mediterranean area) (Figure 1). Under the climatic scenario for the 2070-2099 period, *M. allii-populina* would be highly favoured in most parts of the country. Only restricted zones in mountainous areas would keep low values. The situation in the North in 2100 would be similar to that in the South-West nowadays.

Contrary to *M. larici-populina* and *M. allii-populina*, which are indigenous to Europe, *M. medusae* originates from North America and was first observed in Europe in Spain in 1925 (Fragoso 1925) and in France in 1943 (Dupias 1943). Its distribution in France, as revealed by the SPV survey, is still restricted to a small area in the South-West. The logistic regression of the relative frequency of occurrence of *M. medusae* in relation to climatic variables produced a highly significant model where frequency was explained by the mean minimal winter temperatures ($\text{logit}(p) = -7.27 + 1.04 TNw$; Wald Chi2 = 11.54 P=0.0007), with an odds ratio of 2.8 for each 1°C increase. In the distribution map produced by this model with climatic data for the 1961-1990 period, coastal zones along the Mediterranean Sea and Brittany appeared as potentially favourable zones in addition to the observed range, but few nurseries had been sampled in these areas, where poplar plantations are rare (Figure 1). Using the climatic data simulated for 2070-2099 with the same model led to an expansion of favourable zones inward from the coasts. However, the simulated relative frequency would keep at low levels in most areas.

2.1.2 *Cryphonectria parasitica*

C. parasitica was first reported in France in 1956 (Darpoux 1956) from the South-East (Rhone valley) and shortly after in the South-West (Basque country), although it was probably introduced before and remained unnoticed because of ink disease damage on chestnuts. Chestnut blight is still expanding northwards. Since the survey completed in 1996-1997 (Figure 2), new disease records have been made especially in Brittany (north-west).

The main explaining variables for *C. parasitica* prevalence (p) derived from the logistic analysis were the mean summer minimum temperature, spring precipitations and summer water deficit:

$\text{logit}(p) = -10,478 + 0,248 \text{ TNs} + 0.020 \text{ Psp} + 0,014 \text{ WDs}$ (Wald Chi² = 477, P<0,0001; 2080, P<0.0001; 825 P<0.0001 for the 3 variables, respectively).

The model showed a satisfactory level of external validation (correlation predicted-observed values in the validation data set = 0.6 df = 152). The odds ratio, 1.3 for each 1°C increase, 1.2 for each 10mm increase in spring precipitations and 1.15 for each 10mm increase in summer water deficit, indicate that *C. parasitica* occurrence is favoured by increased spring precipitations and warmer and drier summer climate. The map produced from this model with current climatic data fitted well with observations, especially for high disease incidence in the South (Figure 2). The model indicated moderate suitability of climate (0.1<PIT<0.2) in northern part areas where the disease had not been detected in the first survey but was reported since then (Brittany and Alsace-North East). Under the climatic scenario simulated by Arpege-Climat for the end of this century, an increased in PIT was predicted in most locations, the whole country becoming moderately to highly climatically suitable to the disease.

2.2 Climex simulations

2.2.1 *Melampsora* spp on poplars

M. larici-populina and *M. allii-populina* are widely distributed in Europe but their ranges only partly overlap, only *M. larici-populina* is encountered in Northern Europe (Somda & Pinon 1981). In France, *M. larici-populina* predominates, *M. allii-populina* being mainly encountered in southern regions. Climex simulations were performed using available knowledge on the ecophysiology of both species. However, no satisfactory model (set of parameters) could be fitted to be consistent with the differences in distribution between the two species (unshown results).

2.2.2 *Cryphonectria parasitica*

A set of parameters compatible with the known biology and world distribution of the fungus and disease (especially in China, in the native range and North America, the other area of introduction) could be defined (Table 2). Ecoclimatic indices (EIs) in France (from 17 to 52, mean value = 28) were much lower than in the region of origin of the fungus in China and in North America (up to > 80 in both areas) but the whole country was classified as climatically suitable (Figure 2). The highest predicted values of EIs were obtained in the South, in agreement with the observed distribution and that simulated with the logistic model, but also along the Atlantic coast, up to Brittany. Moderate values of EIs were observed in a large part of the country. Under the climatic scenario simulated by Arpege-Climat, very little change in EIs was predicted (mean values of 28 and 29, for the reference and future periods, respectively). The stability of EIs is the result of increased temperature-growth indices (mean TI values of 43 and 53, respectively, with positive anomalies for all locations) counterbalanced by decreased moisture-growth indices (mean MI values of 87 and 76, respectively, with only negative anomalies).

2.2.3 *Melampsora pini*

M. pini is a common pathogen of pines (*Pinus sylvestris*, *P. pinaster*) in many European countries but is assumed to be better adapted to a cool and humid sub-boreal climate (Kurkela 1973a, b). A set of parameters matching the known biology and the European distribution of the fungus could be defined (Table 2). The resulting map for France is in good agreement with the observed distribution of the disease, especially for the absence in the Mediterranean area (Figure 3). The simulation with climatic data for the 2070-2099 period indicates a general decrease in climatic suitability for the development of the fungus in the whole country as compared to the reference period (Figure 3, mean anomalies in EIs, Tis and MIs = -15, -4, and -10, respectively). Nearly all the southern part of the country would become unfavourable to the disease.

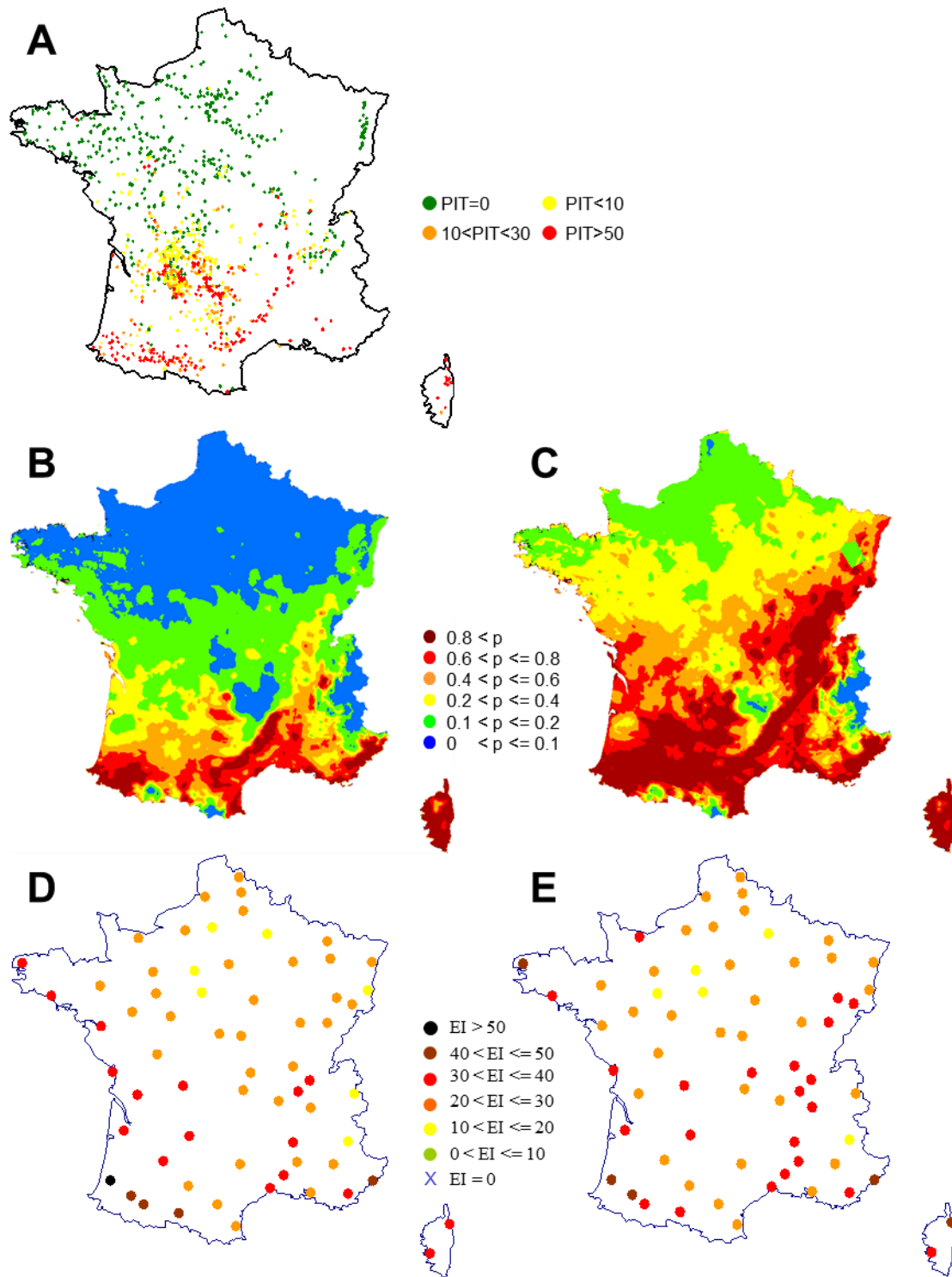


Fig. 2: Distribution from survey data (DSF 1996-1997, PIT = percentage of infected trees) of *Cryphonectria parasitica* (A), and predicted range based on simulated prevalence (p) by a logistic regression with climatic variables (B, C) or ecoclimatic indices (EI) by the CLIMEX model (D, E), under current (1961-1990: B, D) and future climate projected under the Arpege-Climat scenario (2070-2099: C, E).

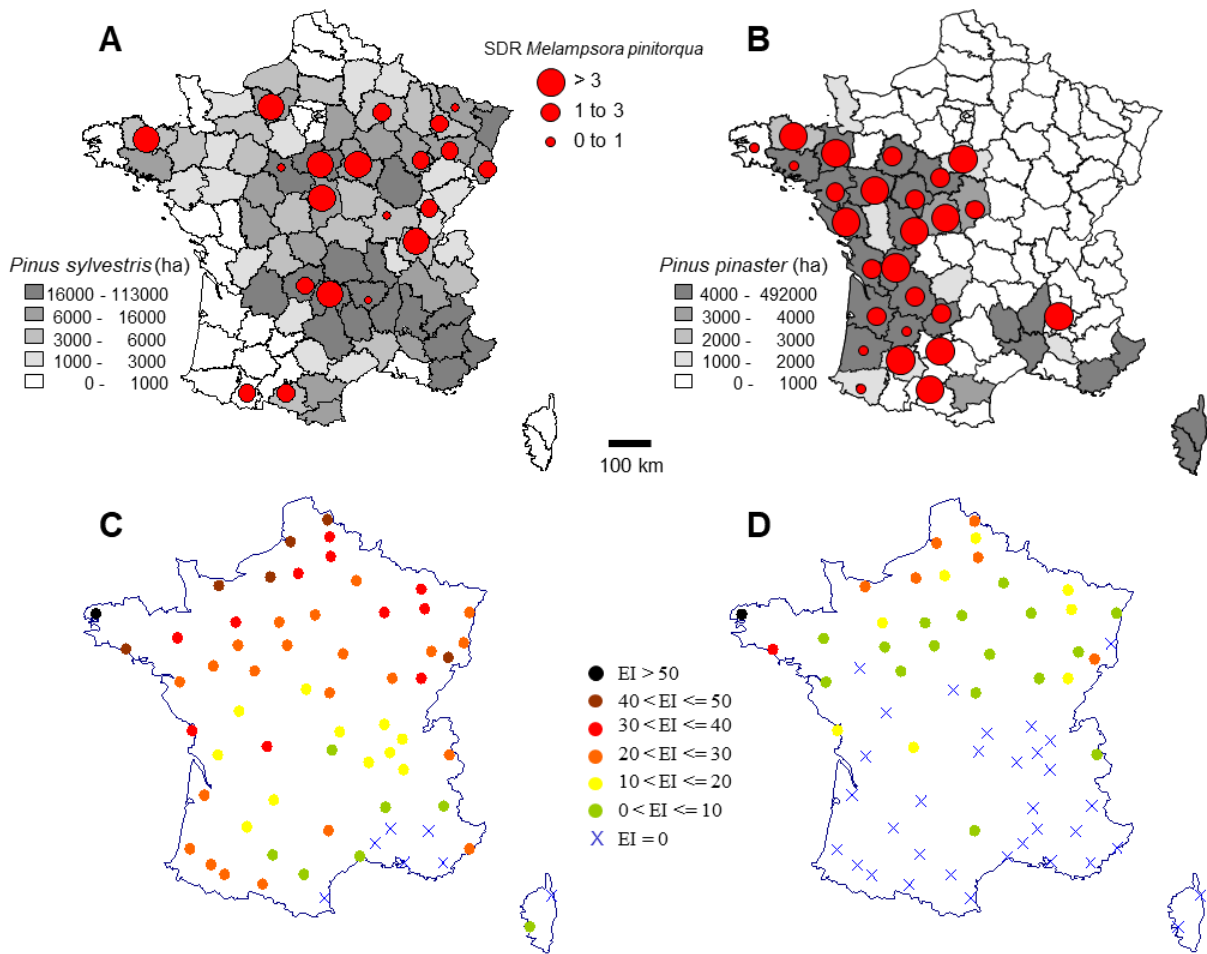


Fig. 3: Distribution of standardized disease rates (SDR) from observed reports (DSF 1989-2004) of *Melampsora pinitorqua* (A, B), and predicted range based on ecoclimatic indices (EI) estimated by the CLIMEX model (C, D), under current (1961-1990: C) and future climate projected under the Arpege-Climat scenario (2070-2099: D).

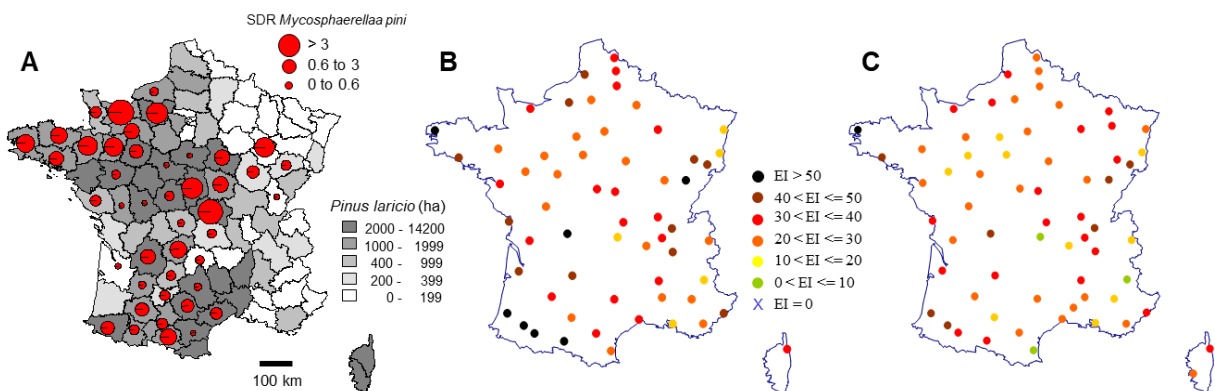


Fig. 4: Distribution of standardized disease rates (SDR) from observed reports (DSF 1989-2004) of *Mycosphaerella pini* (= *Dothistroma septosporum*) (A), and predicted range based on ecoclimatic indices (EI) estimated by the CLIMEX model (B, C), under current (1961-1990: B) and future climate projected under the Arpege-Climat scenario (2070-2099: C).

2.2.4 *Mycosphaerella pini*

M. pini, the causal agent of red band disease of pines, was first described in France in 1966 (Morelet 1967). Disease impact was relatively low in subsequent years (Lanier *et al.* 1976) but has been on an increasing trend in the recent period, both in France (de Villebonne & Maugard 1999) and in other European countries (Brown *et al.* 2002). In the DSF database, 92% *M. pini* reports occurred on *P. laricio*.

A set of parameters consistent with the known biology and the world distribution of the fungus (especially in North America and Europe) could be defined in Climex (Table 2). The resulting map for France in simulations for the 1961-1990 period suggests that most areas should be climatically suitable for *M. pini* development, although in the actual distribution *M. pini* is poorly encountered in the eastern part of the country (Figure 4). Slightly less favourable conditions may result from climate change in the 2070-2099 period, in relation to precipitation decrease during the growing season (mean anomaly in EI= -5, TI =+5, MI = -12)(Figure 4).

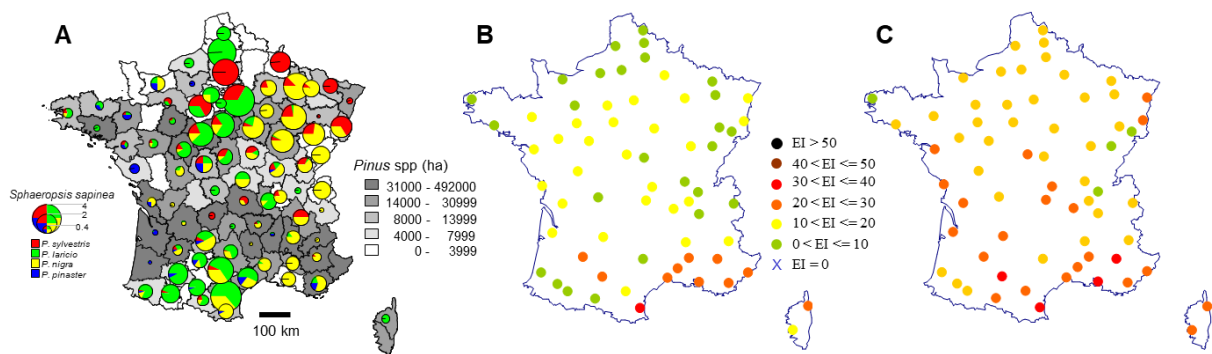


Fig. 5: Distribution of standardized disease rates (SDR) from observed reports (DSF 1989-2004) of *Sphaeropsis sapinea* (A), and predicted range based on ecoclimatic indices (EI) estimated by the CLIMEX model (B, C), under current (1961-1990: B) and future climate projected under the Arpege-Climat scenario (2070-2099: C).

2.2.5 *Sphaeropsis sapinea*

S. sapinea was not considered as a major pathogen in France in the 1970s (Lanier *et al.* 1976), yet this parasite has been one of the most commonly reported in the DSF database during the last 15 years (Piou *et al.* 1991).

Simulations of *S. sapinea* climatic envelope with Climex, using available knowledge on the parasite ecophysiology and past climatic data, showed a high potential development of the disease in the southern part of the country, in accordance with observations. However, low to moderate values of EIs were observed in the North-East in simulations, whereas high disease rates were also observed in this region (Figure 5). A general increase in parasite activity was simulated for the 2070-2099 period under the Arpege-Climat scenario.

2.2.6 *Biscogniauxia mediterranea*

B. mediterranea is the causal agent of charcoal disease of oaks and so far has been described mainly in the Mediterranean area, in Spain, Portugal, North Africa, and in the southern United States and central America (Desprez-Loustau *et al.* 2006). There are only five reports in the DSF database, all in the Mediterranean area, one in Corsica and four closely located in the Var department (Figure 6). *B. mediterranea* is a highly thermophilic species (Table 2). Climex simulations showed a very restricted bioclimatic envelope and low ecoclimatic indices in France under current climate (Figure 6). Under the scenario used for

the 2070-2099 period, a quite large expansion, from the Mediterranean region to the Atlantic coast is anticipated, but ecoclimatic indices remain low.

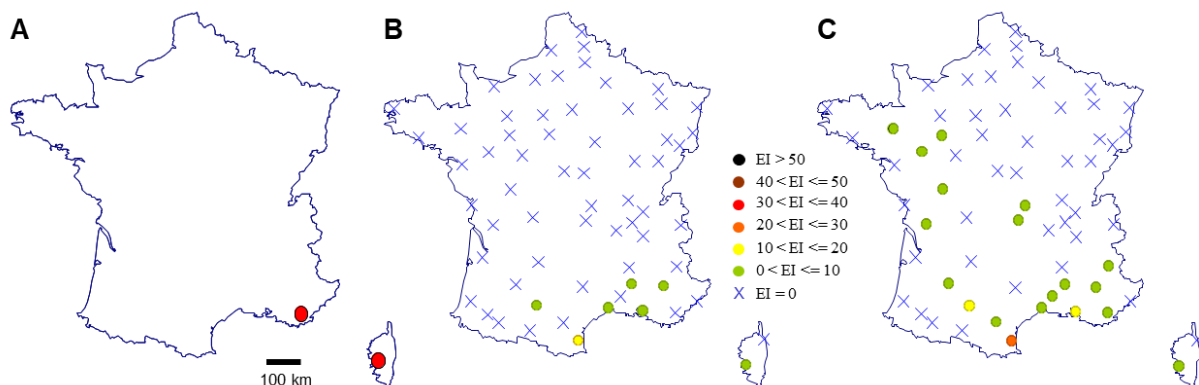


Fig. 6: Distribution of observed reports (DSF 1989-2004) of *Biscognauxia mediterranea* (A), and predicted range based on ecoclimatic indices (EI) estimated by the CLIMEX model (B, C), under current (1961-1990: B) and future climate projected under the Arpege-Climat scenario (2070-2099: C).

2.2.7 *Phytophthora cinnamomi*

Phytophthora cinnamomi was first reported in France in 1860 as the causal agent of ink disease of chestnuts, with primary symptoms of root necrosis leading to tree decline. Most chestnut grove areas were affected within 40 years after this first disease record (Grente 1961). The first report of *P. cinnamomi* on oaks (red oak, *Q. rubra* and pedunculate oak, *Q. robur*), causing a bleeding trunk canker, also called “ink disease”, is much more recent (Moreau et Moreau 1952). *P. cinnamomi* has also been found on mediterranean oaks (Brasier et al 1993, Robin et al. 1998). In Europe, *P. cinnamomi* has been reported as a chestnut or oak pathogen in Spain, Portugal, Italy, Switzerland, United Kingdom, Slovakia and Romania (Delatour et al. 2003, Vannini & Vettraiño 2001, Vettraiño et al. 2005). *P. cinnamomi* distribution in nurseries is much wider than in forest stands, both in France (Vegh & Bourgeois 1975) and in Europe (Themann et al. 2002).

Results of Climex simulations showed three areas with higher suitability for *P. cinnamomi* as a stem disease: the mediterranean coast, South-West and Brittany, whereas climate would impede *P. cinnamomi* development in a large part of the country, in good agreement with reports of *P. cinnamomi*-associated oak disease, except that Brittany has not been affected so far (Figure 7). A much wider range was obtained for the root disease due to lower cold stress values (Figure 7), consistent with a wider geographic range for disease reports on chestnuts than on oaks. The change predicted for the root disease between the two periods is less important than for the stem disease, with mean anomalies in EI = 1 and 3, respectively, and a much smaller expansion. For both diseases, positive changes associated with warming (mean anomaly in TI = +11) are counterbalanced by a decrease in parasite development potential in many locations, resulting from a decreased moisture-growth index (mean anomaly = -11), due to higher water constraints.

3 Discussion

For all selected forest pathogenic fungi, biogeographical models could be fitted to distribution data. These results support the assumption that climate is an important determinant of geographic range and spatial variation in activity of these fungi. It has to be mentioned that mainly foliar and shoot/stem pathogens had been selected since direct

effects of climate are more likely to be important than for root pathogens. Variables selected in statistical models have ecological significance and can usually be explained by the biology of organisms. For example, the significant positive effects of minimum temperature, spring precipitations and summer water deficit on *C. parasitica* prevalence might be explained by the thermophily of this species, favourable conditions for ascospore dispersal and for canker

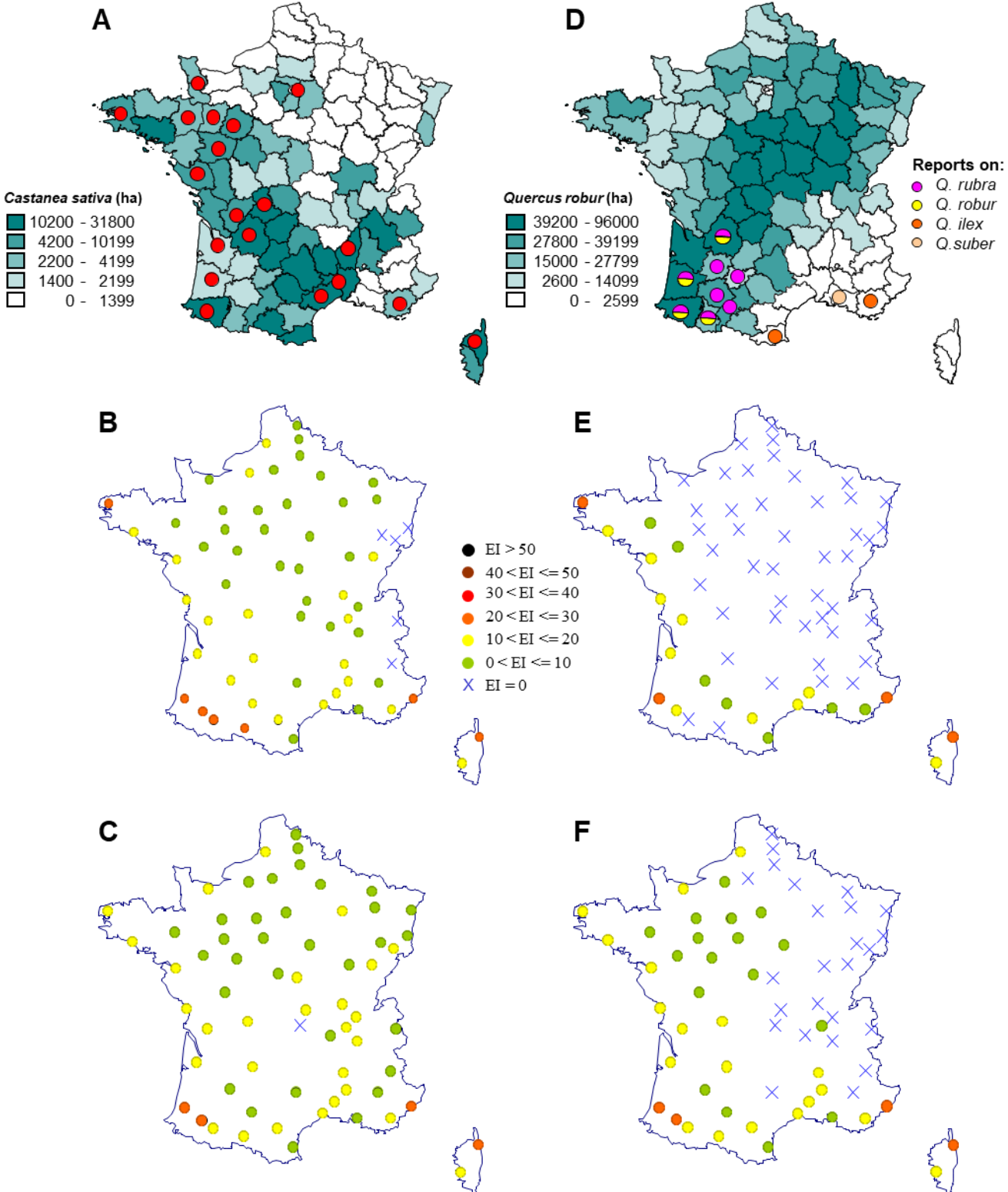


Fig. 7: Distribution of observed reports (INRA and DSF 1989-2004) of *Phytophthora cinnamomi* (A, D), and predicted range based on ecoclimatic indices (EI) estimated by

the CLIMEX model for a root rot (B, C) or a stem canker agent (E, F), under current (1961-1990: B, E) and future climate projected under the Arpege-Climat scenario (2070-2099: C, F).

development (Gao & Shain 1995, Guérin *et al.* 2001), respectively. The high positive effect of minimal temperatures on *M. medusae* distribution strongly suggests that winter survival of the pathogen may be a limiting factor for the development of the disease in France. Although teliospores, the sexual, thick-walled resting spores of most rust species, were observed in the affected area, their functional significance might be low due to a low abundance of alternate hosts (larch trees) in these areas. Between-season survival would then rely on urediniospores, more sensitive to frost than teliospores (Pinon 1986). The overwintering of *M. medusae* as urediniospores has been demonstrated in the South of United States (Sinclair *et al.* 1987). Conversely, in the northern part of the natural range in Canada, larch infection by basidiospores (produced from teliospores) is functional, enabling the parasite to complete its biological cycle and to survive in cold areas.

The choice of one type of simulation model for a given species is mainly dictated by available data for this species. When focused extensive surveys, producing large sets of distribution data, are available, specific statistical models based on multiple regression offer a powerful tool to explore quantitative relationships between pathogen occurrence and local climatic variables (Venier *et al.* 1998, Mila *et al.* 2004). A main limitation of this approach occurs if the potential distribution of the species has not been realized, because of a non equilibrium situation for example (Thuiller *et al.* 2005). This is probably the case for *C. parasitica* in France, explaining the discrepancy in northern areas between the logistic model outputs (based on observed distribution) and Climex simulations (with parameters derived from native range in Asia and distribution in the American area, invaded before France and much more rapidly even in northern cold areas, Anagnostakis 1987).

Process-based models should be more satisfactory in the aim of prediction, but they require a deeper knowledge on the ecophysiology of pathogen and disease. There are still very few for forest diseases. A process-based model was only available for *P. cinnamomi* in this study (Marçais *et al.* 2004). This model where disease severity is mainly explained by pathogen survival across years as a function of temperature, needs further improvement to take into account the whole epidemiological cycle, including the potential effect of temperatures during the growing season and the effects of moisture (Sterne *et al.* 1977, Weste & Marks 1987, Zentmyer 1980, Gisi *et al.* 1980).

When distribution and ecophysiological data are more scarce, the generic Climex model proved to be a valuable alternative. The very good consistency between Climex simulations and outputs from the mechanistic model of *P. cinnamomi* (Bergot *et al.* 2004) further confirmed its interest. CLIMEX had previously been used for risks assessments of plant pathogens on a spatial basis (Yonow *et al.* 2004, Pivonia & Yang 2004, Venette & Cohen 2006). Replacing the standard meteorological data base with climate information from the regionalized Arpege-Climat model allowed us to explore effects of climate change. The sets of parameters defined in our study might be used as new templates for fungal species. Most species included in this study showed a wide temperature range allowing growth, covering 25 to 30°C, which reflects the great plasticity of fungal species and differs notably from parameter templates provided with CLIMEX, mainly for animal and plant species (Table 2). However, the use of Climex for fungal pathogens suffers from several limitations. First, it may be problematic for some fungal species with a high degree of pleomorphy. Pleomorphy, i.e. the occurrence of different morphological and functional stages in the biological cycle, is a common trait in fungi, best exemplified by macrocyclic rusts, with different spore types (basidiospores, eciospores, urediniospores and teliospores) showing different responses to climatic variables (Kurkela 1973a, b). Furthermore, climate effects on some pathosystems

may be more important on the host physiology than directly on the fungus (Desprez-Loustau *et al.* 2006). This is especially the case for opportunistic fungi, such as *S. sapinea* or *B. mediterranea*, which turn from endophytes to pathogens in drought stressed hosts (Vannini & Valentini 1994, Blodgett *et al.* 1997, Stanosz *et al.* 2001). This may explain the discrepancy between the climatic envelope simulated for the current period and the actual disease reports of *S. sapinea*: the fungus might be present in a latent form in wide areas, under various climates, but becoming visible (i.e. causing symptoms) only occasionally and/or locally in response to favouring factors (drought, hail). Effects of climate on host-parasite interaction may also include impact on phenological synchrony, in the case of a susceptibility window for the host and a limited period of infection for the parasite (Desprez-Loustau & Dupuis 1994).

Finally, for all types of model, a basic difficulty with fungi may stem from the definition of the species itself (Harrington & Rizzo 1999). Several recent studies demonstrated the existence of cryptic species lumped under the same pathogen and/or disease name. For example, red band disease of pines was recently shown to be caused by two different species : *D. septosporum* and *D. pini* (Barnes *et al.* 2004).

Simulations with regionalized climatic data allowed us to analyse the response of pathogens and diseases to a climatic change scenario. As expected from the different ecological requirements of the various pathogen species, no general unidirectional trend in the evolution of diseases, both in geographical extension and severity, could be predicted. For the only species typical of cool humid temperate climate included in the study, *M. pinitorqua*, an important regression of potential range was simulated. Conversely, increased ranges were simulated for more thermophilic species, due to the release of temperature constraints. This is particularly the case for species for which winter survival is a critical stage limited by low temperatures in their introduced areas, such as *P. cinnamomi*. However, the climate change scenario did not always lead to range expansions or enhanced activity, even for rather thermophilic species. In the case of *C. parasitica* for example, causing chestnut blight, positive effects of warming might be counterbalanced by negative effects of water constraints. The same trend was observed for *M. pini* and *P. cinnamomi*. Only *B. mediterranea* and *S. sapinea*, which are clearly favoured by water stress showed higher moisture-growth indices in Climex simulations under future simulated climate. As a whole, the predicted change in temperatures, characterized by warming, should be favourable for most species whereas the change in rainfall patterns, with lower precipitations during the growing season, will affect species very differently according to their biology. The response of parasites to water factors is therefore likely to be a determining process in their response to climate change (Woods *et al.* 2005). However, precipitation and moisture variables are highly affected by local trends and effects of water factors on parasites and the diseases they cause are much more complex and less finely documented than temperature effects, which dramatically limit our ability to predict changes linked to them. This confirms the need to work with fine-scale regionalized climate scenarios (Seem 2004) and to improve knowledge on pathogen responses to hydric variables.

The biogeographic approach used in this study only gives indication on the potential range of pathogens based on their climatic envelope, on a long-term trend. The realized range will depend on a variety of other factors.

The first one is related to species migration capacities. As already mentioned, the recent northwards expansion of *C. parasitica* distribution in France might be interpreted not only as a response to warmer climate but also as the progressive colonisation of the potential climatic envelope. This slow progression from initial southern introductions in France may be explained by the lower susceptibility to disease of European compared to American chestnuts (Anagnostakis 1987), the occurrence of hypovirulence (Heiniger & Rigling 1994, Robin & Heiniger 2001) and application of quarantine regulations (existence of a phytosanitary passport within the country, until recently), limiting spreading.

A further important limitation of bioclimatic models in the case of parasites stems from the filter effect of host distribution, which is all the more important that parasites are more specific. *M. pini* is a good example of the determining effect of susceptible host distribution on parasite distribution. The absence of reports of the fungus in eastern regions might be primarily explained by the low occurrence of susceptible hosts (*Pinus laricio*) more than climatic constraints (Figure 4). The host distribution effect is even more important for heteroecious rusts, biotroph parasites alternating on two hosts species during their life cycle. In particular, the distribution of the host harbouring the sexual stage (acting as a cold resistant stage) is likely to be a determinant factor in the overall distribution of the pathogen, as suggested in our study for *M. medusae*. Similarly, the distribution of pine twisting rust might be essentially dependent on the distribution of aspens, which could explain the absence of the disease in the Mediterranean area where their occurrence is very low. The difference in alternating hosts between *M. larici-populina* and *M. allii-populina* might also explain the different ranges of the two species and why they could not be differentiated in Climex, using only fungal responses to temperature. For these pathogens with narrow host range, potential changes in host distributions induced by climate change will have to be considered to predict changes in diseases. Conversely, for generalist parasites with wide host ranges, such as *P. cinnamomi*, the distribution may be more directly related to climatic effects since host availability is not limiting.

Human activities, by promoting parasite transport as well as affecting host distribution and susceptibility, have been and will be major factors potentially favouring diseases. Many emergent diseases of plants have been related to introduction of exotic parasites or farming practices (Anderson *et al.* 2004). The devastating epidemics caused by the introduction of *P. cinnamomi* in Australia and *C. parasitica* in North America are well documented examples (Weste & Marks 1987, Anagnostakis 1997). In the introduced areas, parasites were put in contact with very susceptible species, *Eucalyptus marginata* and many herbaceous species in Australia, *Castanea dentata* in North America. Conversely, in endemic zones, a long co-evolution between parasites and hosts has led to a dynamic equilibrium between virulence and resistance (Asian chestnuts resistant to the *Cryphonectria* canker, Anagnostakis 1992). Pine twisting rust is an example to illustrate the effects of silviculture. Before the 1950s, the disease was almost exclusively reported on *P. sylvestris* (Hariat 1908, Dupias 1965) whereas *P. pinaster* is now the most frequently reported host in the DSF database (0.073 and 0.122 reports/1000 ha for *P. sylvestris* and *P. pinaster*, respectively, with similar surface areas for both species). The increase of maritime pine plantations in areas favourable to the disease (due to climatic factors and alternate host abundance), associated with silvicultural practices promoting pine growth and resulting in higher susceptibility, may explain such patterns (Desprez-Loustau & Wagner 1997).

Finally, biogeographical simulations assume similar ecological requirements of species under present and future climate, i.e. do not take into account potential adaptive responses to climate change (Davies & Shaw 2001, Jump & Peñuelas 2005). Although this assumption has been supported by several studies demonstrating conservatism of the climatic niche in various species (Peterson *et al.* 1999, Martinez-Meyer and Peterson 2005), the adaptation of fungal pathogens to climate is a largely unexplored field that needs further investigations.

In spite of these limitations, a sound result of this study is the demonstration of the high but variable sensitivity of most pathosystems to climate change at a regional scale (even for a moderate change scenario). This strongly suggests not necessarily a future increase in disease but most probably important changes of future “forest phytosanitary landscape” in France, and more generally Europe (since France represents a wide variety of climates). The *Melampsora* complex of poplar rusts illustrates such projected changes. Whereas under the current situation *M. larici-populina* is the dominant species, the relative frequency of *M. allii-*

populina is expected to rise in the future, possibly dictating a change in priorities in disease resistance breeding programmes. In most south-western Europe regions, climate change will be characterized by warming and decreased precipitations during the vegetative season. This should favour pathogens such as *S. sapinea* (as already observed) or *B. mediterranea*, which are typical opportunistic parasites, affecting stressed hosts, especially after drought (Desprez-Loustau et al 2006). These organisms are commonly found in a latent form as endophytes, which favours their anthropogenic dissemination in infected but symptomless plants or seeds (Burgess & Wingfield 2002). Progress has recently been made in the knowledge of such fungi (Smith & Stanosz 1995, deWet *et al.* 2002, 2003, Blodgett & Bonello 2003) but the diversity of endophytes, both at inter- and intra-specific levels, and their significance in relation to tree physiology (from mutualism to parasitism) clearly requires further research.

The fact that changing disease patterns are projected has several implications for management. First, the availability of indicators is a prerequisite for any kind of decision taking. Even more than for crops, disease management in forest ecosystems has to rely on an anticipatory and preventive approach, based on risk analysis. Surveillance networks, providing spatialised and quantified data are required in order to assess spatial and temporal evolution of diseases, and will help improve epidemiological models. The DSF database used in this study proved to be very valuable; improvement could come from the combination of two types of data collection : (i) "spontaneous" reports as in most of the current DSF database and (ii) monitoring on systematic networks, which has been initiated for some diseases at European level. This would allow both the detection of new emerging diseases and of increasing trends for established diseases. The other main issue relates to the dispersal of parasites, allowing them to establish in their increased potential climatic envelopes. Dispersal of parasites is greatly favoured by anthropic activities (long-distance transport). This points to the general need of strict hygiene measures, based on the most probable dissemination pathways of organisms (in seeds, wood, plants) in order to avoid dissemination of parasites in climatically favourable zones where they could find naive host populations with potentially high susceptibility.

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