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Ecological integration of alien species into a tree-parasitic fungus network

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Abstract The diversification of species and their interactions during the course of evolution has produced ecological networks with a complex topology. This topology influences the current functioning of ecosystems. It is therefore important to investigate whether the species introduced recently by human activities have merged seamlessly into recipient ecological networks by developing interactions quantitatively and qualitatively similar to those of native species, or whether their establishment has altered the topology of the networks. We tackled this issue in the case of a well resolved interaction network between 51 forest tree taxa and 154 pathogenic fungal species. We found that alien and native species with similar phylogenetic histories and life-history strategies had similar types and numbers of interactions. Our results also suggest that the clustered architecture of the network has not been altered by the integration of alien species. It therefore seems that a few centuries have been sufficient for the network to assimilate the newly introduced species. This rapid integration was unexpected for a plant-pathogen network, because selection acts continually on plants, favouring the emergence of defences against new pathogens and impeding the development of new interactions. However, it was recently shown that perturbation of the structure of ecological networks might be overlooked if species interactions are not quantified. The tree-parasitic fungus network considered in this study is binary. We might therefore end up with different results by using quantitative data.

Keywords Alien species · Host-parasite interactions · Trees · Fungi · Ecological networks · Random graphs

Introduction

According to the World Conservation Union (IUCN; http://www.issg.org), alien species—also called non native, exotic, non indigenous or foreign species—are

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species occurring outside of their natural range and dispersal potential. Their number has increased dramatically in recent decades, due to the intensification of transportation and trade at the global scale (Desprez-Loustau et al. 2010; Hulme 2009). Some alien species seem to have no significant ecological or economic impact after their establishment in semi-natural or natural ecosystems or habitats. For example, *Clathrus archeri*, a saprophytic fungus introduced into Europe at the beginning of the twentieth century has as yet had no major impact (Desprez-Loustau 2009). By contrast, other alien species promote change and threaten native biological diversity (Clavero and Garcia-Berthou 2005; Vitousek et al. 1996). Such species are described as “invasive”. Given the considerable negative impact of certain alien invasive species (Pimentel et al. 2000), one of the major challenges facing ecologists is the prediction of future biological invasions (Thuiller et al. 2005; Worner and Gevrey 2006) and the development of strategies to reduce their likelihood and mitigate their impact (Hulme 2006; Hulme et al. 2008). Another, more fundamental approach to biological invasions is to consider alien species as providing us with an opportunity to study the assembly of biotic communities and their evolution over time (Callaway and Maron 2006; Wilson et al. 2000).

This approach was adopted by Geerat J. Vermeij in his research framework for invasion biology: ‘Invasion biology has much to offer ecologists and evolutionary biologists in probing the integrity and orderliness of recipient biotas’ (Vermeij 1996). After defining a biological invasion as the geographical expansion of a species into an area not previously occupied by that species [the use of the impact criterion for defining an invasion remains a matter of debate (Valéry et al. 2008)], Vermeij suggested that all invasions occur through three successive stages: (1) arrival of the new individuals in the recipient region, (2) establishment, through the formation of self-sustaining populations, and (3) integration, through the development of ecological links with the other species of the recipient region. He invited the scientific community to investigate the third stage of invasion further, to determine whether there are rules governing the ecological and evolutionary integration of invaders into recipient communities.

In this study, we used recent advances in network theory to tackle this issue. We investigated whether the species establishing themselves in new geographic areas tended to merge seamlessly into the existing ecological network by developing interactions quantitatively and qualitatively similar to those of native species, or whether the establishment of these species altered the architecture of the network. Two specific questions were addressed: (1) Do aliens and native species differ in terms of their numbers of interactions? (2) Do aliens and native species differ in terms of the species with which they interact? We addressed the first of these questions, by using logistic regression models to investigate whether the probability of recording an interaction between two species with given phylogenetic origins and given ecological features was significantly different if one of the species was alien. We addressed the second question using the probabilistic random graph model MIXNET [MIXture for NETworks; (Daudin et al. 2008; Picard et al. 2009)] to group together species with similar interaction patterns. We then investigated whether the introduction status of the species accounted for the clusters obtained. All our analyses were based on a well resolved interaction network between tree species and their fungal pathogens (Vacher et al. 2008a), generated by 30 years of forest health monitoring throughout France.

Materials and methods

Tree/fungus interaction records

The ecological network considered here consisted of 543 interactions between 51 forest tree taxa (all but six being true species or groups of cultivars belonging to the same genetic continuum) and 154 parasitic fungal species. The network is binary. The presence of an interaction between a given fungal species and a given tree species means that the fungal species was reported on diseased trees belonging to the tree species and was considered to be involved in the disease symptoms. All the observations of tree-fungus interactions originated from the database of the French governmental organization in charge of forest health monitoring (the *Département Santé des Forêts* (DSF)) for the 1972–2005 period. The methods used for data collection have been described in more detail in previous analyses of the DSF database (Vacher et al. 2008a, b).

Introduction status of tree species

The definition of tree species as aliens or species native to France was not an easy task, because the composition of European forests has been profoundly modified by human activities. A species is considered to be native (in the strict sense of the term) to a given territory if it arrived there unaided before humans started to have a major impact (Petit et al. 2004). However, some tree species were spread by humans many centuries ago, and their natural range is now difficult to ascertain (Petit et al. 2004). These species are known as *archeophytes* and were considered to be native for the purposes of this study. Many other tree species have been deliberately introduced by humans over the last few centuries, particularly for food and timber production. This is the case, for example, for *Quercus rubra*, which was first planted in botanic gardens as an ornamental plant and has subsequently been used for wood production in forests (Petit et al. 2004). In this study, we considered a tree species to be alien if it was introduced into France after the beginning of the modern era (which we define as the discovery of the New World by Columbus). Such recently introduced species are known as *neophytes*.

Introduction status of fungal species

As for the tree species, it was not a straightforward task determining which fungal species were aliens (Desprez-Loustau 2009; Desprez-Loustau et al. 2010). Indeed, knowledge of the diversity of fungal species at a given site is often scarce, even for well studied, temperate regions (Hawksworth and Rossman 1997). Moreover, little is known about the biogeography of most fungi (Desprez-Loustau et al. 2007). In this context, alien status can be assigned with certainty to only a few recently introduced fungal species, the introduction of which is documented in the scientific literature. In this study, we considered a fungal species to be alien if there was documentary evidence that this species was first described in France after 1850 and good evidence that it was introduced from elsewhere.

Other descriptors of tree species

We characterized each tree species by phylum (Magnoliophyta or Conipherophyta) in addition to introduction status. An estimate of the area covered by each tree species was also available (*Inventaire Forestier National*, 2000 census report). An estimate of the total number of times each tree species had been encountered and examined by foresters during their daily work was also available from the DSF database. This variable is called “sampling intensity” and is positively correlated with area, because foresters encounter abundant tree species more frequently than rare species during their daily work (Vacher et al. 2008a). We chose to include both variables in the analyses, despite their correlation, because they reflect very different processes. The current area of a tree species depends on ancient climatic events and on human activities over the last centuries, whereas sampling intensity only reflects the recent activity of foresters.

Other descriptors of fungal species

Each fungal species was characterized by phylum (Ascomycota or Basidiomycota) and life-history strategy in addition to introduction status. As suggested by Garcia-Guzman and collegues (Garcia-Guzman and Morales 2007), life-history strategies were described in terms of the parasitic lifestyle (biotrophic versus necrotrophic) and the plant organs and tissues attacked: (1) strict foliar necrotrophic parasites, (2) canker agents, (3) stem decay fungi, (4) obligate biotrophic parasites, (5) root decay fungi, (6) other foliar and twig necrotrophic parasites, (7) stem blue stain agents, (8) parasites of fine roots, (9) wilting agents and (10) other root fungi. The first five strategies accounted for 87% of the fungal species.

Statistical analyses

We first considered all the potential interactions between tree species and parasitic fungal species and analyzed the impact of the various species descriptors (Table 1) on the probability of an interaction occurring. A few species with under-represented values for some descriptors were removed from the dataset: two tree species and one fungal species for which introduction status was uncertain were removed; moreover, only fungal species displaying one of the five major life-history strategies described above were considered. Species removal facilitated statistical analyses by reducing the number of combinations

Table 1 List of variables used to characterize tree species and parasitic fungal species

Abbreviation	Description
Intro_T	Introduction status of tree species
Phylum_T	Phylum of tree species
Area_T	Area covered by tree species
Sampling_T	Sampling intensity of tree species
Intro_F	Introduction status of fungal species
Phylum_F	Phylum of fungal species
Strat_F	Life-history strategy of fungal species

of descriptors values absent from the dataset. The probability of recording an interaction between two species (logit-transformed) was modeled as a function of seven fixed effects and all their pairwise interactions, with SAS/STAT software (SAS/STAT 2000). The seven fixed effects were: Intro_T, Phylum_T, Area_T (log-transformed), Sampling_T (log-transformed), Intro_F, Phylum_F and Strat_F (Table 1). An initial model was generated without random effects (SAS, LOGISTIC procedure). We then introduced species names as random effects (SAS, GLIMMIX procedure), because the ecological interactions of a given species might not be independent.

We then used a probabilistic model for random graphs called MIXNET (MIXture for NETworks; available at http://stat.genopole.cnrs.fr/software/mixnet/; Daudin et al. 2008; Picard et al. 2009) to classify the species into clusters as a function of their interaction patterns. The full dataset was used to construct a bipartite graph with species as vertices and interactions as edges. The graph had three isolated edges and a large connected component (Vacher et al. 2008a). This connected component was analyzed with MIXNET, which assumes that the graph vertices form a finite number of clusters. The software calculates algorithms for estimating the probabilities of particular vertices belonging to the various clusters and the probabilities of connections between clusters (i.e. the probability of a vertex belonging to one cluster being connected to a vertex belonging to another cluster).

Having assigned each vertex to the cluster to which it had the highest probability of belonging, we validated the clusters statistically by testing whether element similarity (i.e. similarity between parasitic fungal species as a function of host tree species and similarity between tree species as a function of their parasites) was significantly greater within than between clusters. We used the multiresponse permutation procedure (MRPP), a non parametric test of differences between predefined groups (Mielke and Berry 2001). The MRPP statistic δ is the weighted mean of within-group means of pair-wise dissimilarity between group elements. As previously described (Prado and Lewinsohn 2004), dissimilarity was calculated as a Jaccard distance and group size was taken as the group weight. We used the *mrpp* function of the R vegan package (Oksanen et al. 2006) to calculate the expected statistic $E(\delta)$ if the groups were assembled at random. The within-group chance-corrected agreement (A), defined as $1- \delta/E(\delta)$, has a maximum of 1 when there is no dissimilarity between the elements of any group. The *P*-value is the probability of obtaining, by chance, a value of A greater than or equal to the observed value.

Finally, we used logistic regression (SAS, LOGISTIC procedure) to investigate whether the introduction status of a species had an effect on its belonging to a cluster. As in the analysis described above, the two tree species and the one fungal species for which introduction status was uncertain were removed from the dataset and we considered only fungal species with one of the five major life-history strategies. Statistical analyses were conducted separately for tree species and fungal species. The model for tree species had Intro_T, Phylum_T, Area_T (log-transformed) and Sampling_T (log-transformed) as fixed effects (Table 1). The model for fungal species had Intro_F, Phylum_F and Strat_F as fixed effects (Table 1). Pairwise interactions were not included, because the dataset was too small to estimate such interactions. A forward selection procedure was used to select the best combination of explanatory variables.

Results

Aliens accounted for 16% of the species. Of the 51 tree species (Table S1), 33 were native, 16 were alien and the status of 2 species was uncertain. Of the 154 parasitic fungal species (Table S2), 135 species were native, 18 were alien and 1 had an uncertain status. We recorded a total of 489 host-parasite interactions between the tree species and the fungal species for which introduction status was known. Alien species were involved in 37% of these interactions.

Quantitative comparison of interactions between alien and native species

Logistic regression models showed that the probability of recording an interaction between a parasitic fungal species and a tree species depended on the phylogenetic origin of both the tree and the fungus (Phylum_T and Phylum_F), the current area of the tree species (Area_T) and its sampling intensity (Sampling_T), the life-history strategy of the fungal species (Strat_F) and its introduction status (Intro_F). Indeed, all these variables were significant main effects or were involved in a significant interaction, in both the model without random effects and the mixed model (Table 2). Only the introduction status of tree species (Intro_T) was not significant either as a main

Table 2 Type 3 tests of fixed effects for two logistic regression models predicting the probability of recording an interaction between a tree species and a parasitic fungal species

Fixed effect	Simple model			Mixed model				Summary
	df	Wald's χ^2	*P* value	*df* (num)	*df* (den)	*F* value	*P* value	
Intro_T (IT)	1	1.0999	0.2943	1	56.69	0.92	0.3424	
Intro_F (IF)	1	3.8595	0.0495	1	2702	3.48	0.0623	*/mS
Phylum_T (PT)	1	4.6249	0.0315	1	36.07	3.79	0.0595	*/mS
Area_T (AT)	1	0.0184	0.8922	1	115.3	0	0.9607	
Sampling_T (ST)	1	8.7496	0.0031	1	211.7	8.32	0.0043	**/**
Phylum_F (PF)	1	0.3414	0.559	1	3585	0.01	0.9102	
Strat_F (SF)	4	7.1817	0.1266	4	6410	1.58	0.1776	
IT*IF	1	1.0394	0.308	1	6470	1.11	0.2927	
IT*PT	1	0.1738	0.6767	1	33.85	0.11	0.7472	
IT*AT	1	2.3672	0.1239	1	52.48	1.83	0.1814	
IT*ST	1	2.3132	0.1283	1	45.46	1.93	0.1721	
IT*PF	1	2.4363	0.1186	1	6470	2.57	0.109	
IT*SF	4	2.2039	0.6983	4	6470	0.57	0.6858	
IF*PT	1	0.5899	0.4424	1	6470	0.64	0.4237	
IF*AT	1	2.807	0.0939	1	6470	2.94	0.0866	mS/mS
IF*ST	1	8.8595	0.0029	1	6470	8.88	0.0029	**/**
IF*PF	1	7.295	0.0069	1	222.3	4.05	0.0454	**/*
IF*SF	2	16.0934	0.0003	2	151	3.31	0.0392	***/*
PT*AT	1	6.6833	0.0097	1	34.85	5.37	0.0265	**/*
PT*ST	1	7.8747	0.005	1	29.3	6.21	0.0186	**/*
PT*PF	1	10.1483	0.0014	1	6470	10.42	0.0012	**/**
PT*SF	4	44.2852	<.0001	4	6470	11.27	<.0001	***/***
AT*ST	1	0.04	0.8415	1	42.59	0.14	0.712	
AT*PF	1	0.8508	0.3563	1	6470	0.86	0.3533	
AT*SF	4	2.4277	0.6576	4	6470	0.66	0.6222	
ST*SF	4	2.2148	0.6963	4	6470	0.58	0.6786	
ST*PF	1	0.2064	0.6496	1	6470	0.17	0.6835	
PF*SF	3	16.1749	0.001	3	320.3	3.48	0.0162	**/*

The simple model included only fixed effects, whereas the mixed model included species names as random effects. The general Satterthwaite approximation was used to calculate the degrees of freedom for the denominator in the mixed model. Significant effects, for both models, are reported in the last column: * $P < 0.05$,** $P < 0.01$, *** $P < 0.001$; mS: $P < 0.10$

effect or as part of a significant interaction. By contrast, the introduction status of fungal species (Intro_F) was significant in interaction with the phylogenetic origin of fungal species (Phylum_F) and their life-history strategy (Strat_F). However, these significant interactions arose from groups containing few observations: only one alien species (*Cronartium ribicola*) belonged to the Basidiomycota (Fig. 1a) and only two alien species (*Cronartium ribicola* and *Microsphaera alphitoides*) were obligate biotrophs (Fig. 1b).

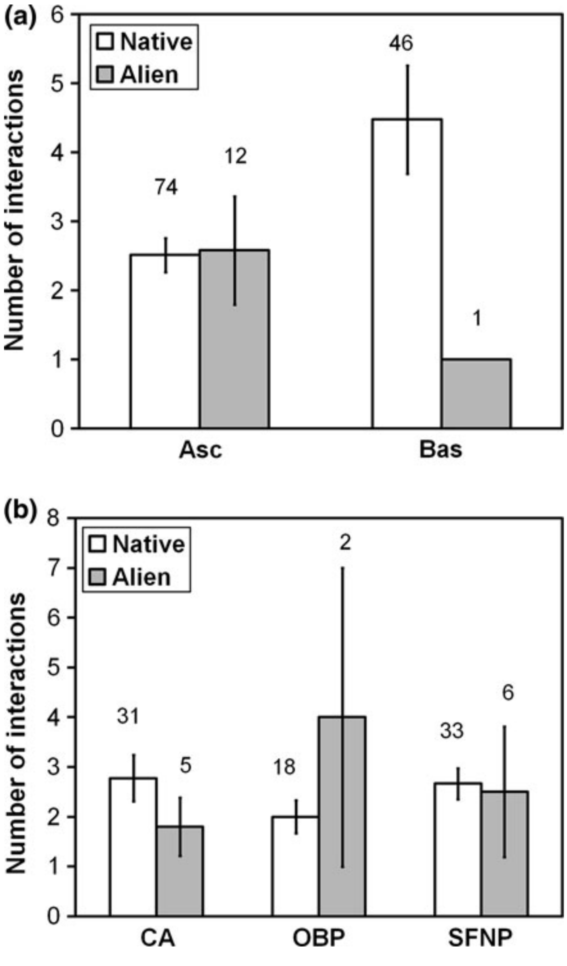

Fig. 1 Mean number of interactions for native and alien fungal species, as a function of **a** phylogenetic group (Asc: Ascomycota; Bas: Basidiomycota) and **b** life-history strategy (*CA* canker agent, *OBP* obligate biotrophic parasite, *SFNP* strict foliar necrotrophic parasite). Standard errors of the mean and the number of species in each category are indicated above the bars

Qualitative comparison of interactions between alien and native species

The integrated completed likelihood (ICL) criterion indicated that the optimal number of network clusters was 6 (Fig. 2). Three clusters of tree taxa (T1, T2 and T3) and three clusters of parasitic fungal species (F1, F2 and F3) were identified and validated statistically ($A = 0.069$, $P < 0.001$ for both tree and fungal species). Alien species were found in almost all the clusters (Fig. 3) and logistic regression confirmed that the introduction status of a species was not a major determinant of its belonging to a cluster. The logistic regression model for tree species was highly significant according to the likelihood-ratio test ($df = 4$, $\chi^2 = 87.2159$, $P < 0.0001$), with phylum and sampling intensity identified as the best combination of explanatory variables. A close look at the composition of each cluster (Table 3) confirmed that the tree species were not randomly distributed as a function of these two variables. T1 included only tree species belonging to the Magnoliophyta, whereas T3 consisted exclusively of tree species belonging to the Conipherophyta. T1 and T3 clustered frequently sampled tree species, whereas T2 did not. The model for fungal species was also highly significant according to the likelihood-ratio test ($df = 8$, $\chi^2 = 33.6060$, $P < 0.0001$) and identified the life-history strategy of fungal species as the sole explanatory variable. A close look at the composition of each cluster (Table 4) confirmed this effect. F1 and F2 were large clusters of fungal species including all five main life-

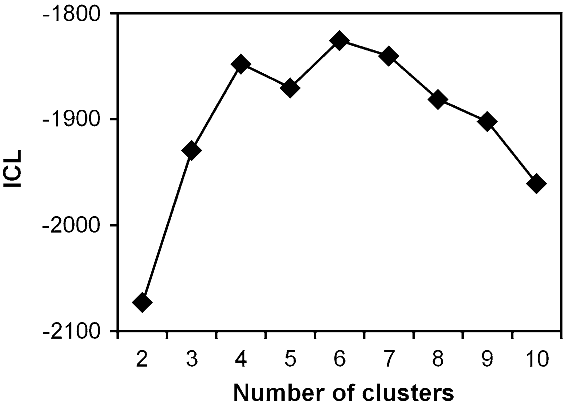

Fig. 2 Variation of the integrated completed likelihood (ICL) criterion with the number of network clusters. The maximum value of ICL indicates the optimal number of clusters

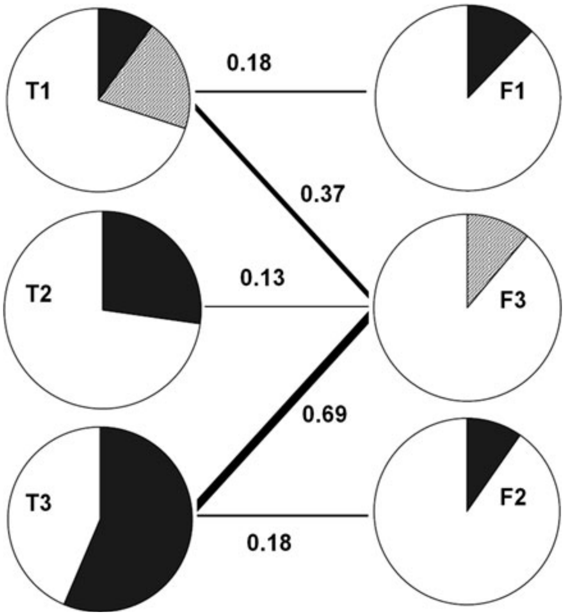

Fig. 3 Schematic representation of the network architecture. *Circles* correspond to groups of tree taxa or parasitic fungal species sharing similar interactions (i.e. clusters). Clusters of tree taxa are denoted by "T" whereas clusters of fungal species are denoted by "F". Within each circle, the *white area* represents the proportion of native species, the *black area* represents the proportion of alien species and the *hatched area* represents the proportion of species of unknown introduction status. The *lines joining the clusters* indicate the probabilities of connections between the clusters. Only probabilities greater than 0.10 are shown

history strategies. Root decay fungi were the least frequently represented in F1 and F2, accounting for only about 5% of species. By contrast, F3 contained only nine fungal species, five of which (i.e. 55%) were root decay fungi.

Discussion

This study is the first to explore the integration of alien species into a host-parasite (and host-pathogen) network. Indeed, despite their importance in nature (Dobson et al. 2008), parasitic and pathogenic interactions have rarely been considered from an ecological network perspective (Ings et al. 2009). By contrast, mutualistic networks (particularly plant-pollinator networks) have been extensively investigated, and several studies have already assessed the extent of alien species integration (Aizen et al. 2008; Bartomeus et al. 2008; Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002; Morales and Aizen 2006; Olesen et al. 2002). The successful integration of alien species into plant-pollinator networks is expected, because pollination interactions are rather unspecific and diversified. Alien mutualists therefore have a reasonable chance of interacting with native generalists (Aizen et al. 2008). About half the studies on this topic (Memmott and Waser 2002; Morales and Aizen 2006; Olesen et al. 2002) have concluded that alien species are well integrated into mutualistic webs. However, the remaining studies (Aizen et al. 2008; Bartomeus et al. 2008; Lopezaraiza-Mikel et al. 2007) concluded that the integration of alien species affected the interactions of native species. The integration of alien species has also been assessed for a network of

Table 4 Composition of the three clusters of fungal species

Cluster	F1	F2	F3
Total number of species	90	52	9
Percentage of alien species	12	10	0
Percentage of species belonging to Basidiomycota	30	29	55
Percentage of strict foliar necrotrophic parasites	22	36	0
Percentage of canker agents	28	19	11
Percentage of stem decay fungi	23	10	0
Percentage of obligate biotrophic parasites	12	15	0
Percentage of root decay fungi	4	6	55

Table 3 Composition of the three clusters of tree species

Cluster	T1	T2	T3
Total number of species	10	22	16
Percentage of alien species	10	27	56
Percentage of species belonging to the Magnoliophyta	100	63	0
Mean area per species in thousands of hectares (± SE)	649 ± 275	78 ± 42	311 ± 106
Mean sampling intensity per species in number of records (±SE)	1001 ± 258	58 ± 16	1248 ± 427

tree species and saprophytic insects from the Cerambycidae family (Sugiura et al. 2008). Alien species seemed to be well integrated because alien trees were used by native insects and native tree species were used by alien insects. Moreover, the results suggested that the integration of alien species did not disrupt the original, nested architecture of the network.

We hypothesized that alien species would be less well assimilated in plant-pathogen networks, because selection is continually at work, enabling plants to develop new defenses against pathogens, thereby making the emergence of new interactions less likely (Thompson 2006). As a result of prior selection of plant defenses, all plants are resistant to the majority of potentially pathogenic species (Heath 2000). This non specific resistance, called non host resistance, is based on an arsenal of constitutively produced defense compounds and inducible defense responses triggered by non specific plant products (Heath 2000). The establishment of a new interaction between a plant species and a pathogen species requires the pathogen to circumvent this non specific resistance and any specific resistance based on host-pathogen recognition selected in infected plant populations. When a pathogen moves to a new environment, its ability to form new interactions also depends on the environment being suitable for the completion of its life cycle. Thus, most new combinations of plant and pathogen species are highly unlikely to result in a compatible, disease-causing interaction (Parker and Gilbert 2004). In addition, the alien tree species widely planted nowadays in French forests have been selected for resistance to their new environment (including pathogens). Most were first planted in botanic gardens (Petit et al. 2004), and only those that grew well, with high survival rates, were subsequently planted in forests. We therefore expected alien tree species and alien pathogenic fungal species to display fewer interactions than their native counterparts.

Against these expectations, the absence of significant interactions between introduction status of tree species and phylum, abundance or sampling intensity indicated that alien tree species and native tree species with a similar phylogenetic history, abundance and sampling intensity were involved in similar numbers of interactions (with parasitic fungal species). This result is particularly interesting because weaker control by enemies has been identified as a possible reason for the rapid establishment and proliferation of invasive alien species. This hypothesis, the enemy release hypothesis (ERH; Keane and Crawley 2002; Mitchell and Power 2003), has been interpreted in two different ways within the scientific community. One group of authors compared the number of natural enemies in native and introduced host populations of the same species. Most [92% according to the review by (Colautti et al. 2004)] obtained evidence supporting the ERH. A second group of authors compared native and alien species (often congeners) in the introduced range, as in this study. Most of the investigations carried out (69% according to the review by Colautti et al. (2004)), including this study, obtained no evidence supporting the ERH, and some even came to conclusions diametrically opposed.

In the case of fungal species, significant interactions between introduction status and phylum on the one hand, and between introduction status and life-history strategy on the other, suggested that alien and native fungal species with close phylogenetic histories and similar life-history strategies had different numbers of interactions (with host tree species). However, only two alien fungal species (*Cronartium ribicola* and *Microsphaera alphitoides*) seemed to be responsible for these significant interactions, so we considered that these interactions were not meaningful. The difficulties involved in interpreting some results arose from our statistical approach. In this study, we assumed that the probability of recording an interaction between a tree species and a parasitic fungal species would depend not only on introduction status, but also on the ecological features and the evolutionary history of the species involved. This approach was designed to limit the possibility of identifying significant differences between aliens and natives due to confounding factors. For tree species, for example, if we had not taken phylogeny into account, a significant difference in the number of interactions of alien and native species might have reflected an effect of introduction status or an effect of phylogeny, because 87% of the alien species belonged to the Conipherophyta, versus only 33% of native species. By taking into account the phylogeny of tree species, together with area and sampling intensity, we aimed to detect differences truly due to introduction status. The downside of this approach is that a few combinations of descriptors were rarely represented in the database. *Cronartium* *ribicola* was, for example, the only alien species from Basidiomycota.

In addition to differences in the numbers of interactions established by alien and native species, we expected to find qualitative differences. We thought that alien tree species would interact preferentially with the fungal pathogenic species with the highest likelihood of host shifts, such as facultative saprobes (Parker and Gilbert 2004). We also expected alien tree species and alien fungal species to associate preferentially with each other to some extent, because many fungal pathogens are introduced with their host plant (Desprez-Loustau et al. 2007). Unexpectedly again, our results indicated that the introduction status of a species had very little effect on the species with which it interacted. Logistic regression analyses (Table 2) revealed no significant interaction between the introduction status of tree species and the various descriptors of fungal species (phylum, life-history strategy), or between the introduction status of fungal species and the various descriptors of tree species (except sampling intensity). Interestingly, the interaction between the introduction status of tree species and the introduction status of fungal species was not significant, suggesting an absence of preferential associations between alien species. Moreover, the composition of network clusters indicated that even if there was some similarity in the interactions established by alien species, this similarity was too weak for clusters comprising only alien species to emerge. Instead, we found that the clustered architecture of the network resulted mostly from the phylogenetic history of plant species and the life-history strategy of fungal species. This finding is consistent with logistic regression analyses (Table 2), which highlighted a very significant interaction between the two variables, and with the results of a previous study (Vacher et al. 2008a). Finally, tree sampling intensity also affected the clustered architecture, raising questions about the impact of sampling on the topology of ecological networks (Bluthgen et al. 2008; Nielsen and Bascompte 2007).

In conclusion, we found that alien species were well integrated into the tree-fungus network, consistent with previous findings for several plant-pollinator networks (Memmott and Waser 2002; Morales and Aizen 2006; Olesen et al. 2002) and a tree-saprophytic insect network (Sugiura et al. 2008). Both alien tree species and alien parasitic fungal species had similar types and numbers of interactions to the native species they resembled. These results are of interest because the topological features of interaction networks (i.e. the number of interactions per species and with whom the species interact) have been shown to underlie the robustness of networks to disturbances (Bascompte and Jordano 2007). Conservation of the topology of interactions, in addition to the conservation of species, is therefore important for the maintenance of ecosystem services, such as pollination (Memmott et al. 2007) or parasitism (Montoya et al. 2003). In the case of this qualitative network of tree-fungus interactions, the newly introduced species did not significantly modify the topology of the network. The architecture of the network including the alien species continued to reflect the long-term evolutionary history of the species within it (Vacher et al. 2008a), as reported for other contemporary networks (Ives and Godfray 2006; Rezende et al. 2007). However, it was recently shown that perturbation of the structure and function of ecological networks might be overlooked if species interactions are not quantified (Tylianakis et al. 2007). We might therefore end up with different results by using quantitative data. In the case of the tree-parasitic fungus network, the intensity of an interaction can be defined as the number of times the fungal species was reported on the tree species and involved in the emergence of disease symptoms. Quantitative data might therefore reveal that tree-fungus interactions involving alien fungal species have a higher intensity than tree-fungus interactions involving native fungal species, since alien fungal species are often responsible for devastating epidemics, sometimes even threatening the survival of the host tree species (see Desprez-Loustau et al. 2007 for precise examples). Alternatively, incomplete adaptation of an introduced pathogen to new host species might result in only a few fortuitous infections (Antia et al. 2003; Parker and Gilbert 2004; Bertheau et al. 2010). Unfortunately, these predictions could not be tested here because quantitative data are not currently available for the tree-fungus network.

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References

Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. PLoS Biol 6:e31

Antia R, Regoes RR, Koella JC, Bergstrom CT (2003) The role of evolution in the emergence of infectious diseases. Nature 426:658–661

Bartomeus I, Vila M, Santamaria L (2008) Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155:761–770

Bascompte J, Jordano P (2007) Plant-animal mutualistic networks: the architecture of biodiversity. Annu Rev Ecol Evol Syst 38:567–593

Bertheau C, Brockerhoff EG, Roux-Morabito G, Lieutier F, Jactel H (2010). Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. Ecol Lett (in press)

Bluthgen N, Frund J, Vazquez DP et al (2008) What do interaction network metrics tell us about specialization and biological traits? Ecology 89:3387–3399

Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? Trends Ecol Evol 21:369–374

Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110

Colautti RI, Ricciardi A, Grigorovich IA et al (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Daudin JJ, Picard F, Robin S (2008) A mixture model for random graphs. Stat Comput 18:173–183

Desprez-Loustau ML (2009) The alien fungi of Europe. In: Nentwig W, Hulme P, Pysek P, Vila M (eds) Handbook of alien species in Europe. Springer, Berlin, p 400

Desprez-Loustau ML, Robin C, Buee M et al (2007) The fungal dimension of biological invasions. Trends Ecol Evol 22:472–480

Desprez-Loustau ML, Courtecuisse R, Robin C et al (2010) Species diversity and drivers of spread of alien fungi in Europe with a particular focus on France. Biol Invasions 12:157–172

Dobson A, Lafferty KD, Kuris AM et al (2008) Homage to Linnaeus: how many parasites? How many hosts? Proc Natl Acad Sci USA 105:11482–11489

Garcia-Guzman G, Morales E (2007) Life-history strategies of plant pathogens: distribution patterns and phylogenetic analysis. Ecology 88:589–596

Hawksworth DL, Rossman AY (1997) Where are all the undescribed fungi? Phytopathology 87:888–891

Heath MC (2000) Nonhost resistance and nonspecific plant defenses. Curr Opin Plant Biol 3:315–319

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. J Appl Ecol 43:835–847

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Hulme PE, Bacher S, Kenis M et al (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J Appl Ecol 45:403–414

Ings TC, Montoya JM, Bascompte J et al (2009) Ecological networks—beyond food webs. J Anim Ecol 78:253–269

Ives AR, Godfray HCJ (2006) Phylogenetic analysis of trophic associations. Am Nat 168:E1–E14

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Lopezaraiza-Mikel ME, Hayes RB, Whalley MR et al (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. Ecol Lett 10:539–550

Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. Proc R Soc Lond B Biol Sci 269:2395–2399

Memmott J, Craze PG, Waser NM et al (2007) Global warming and the disruption of plant-pollinator interactions. Ecol Lett 10:710–717

Mielke PW, Berry KJ (2001) Permutation methods: a distance function approach. Springer, New York

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Montoya JM, Rodriguez MA, Hawkins BA (2003) Food web complexity and higher-level ecosystem services. Ecol Lett 6:587–593

Morales CL, Aizen MA (2006) Invasive mutualisms and the structure of plant-pollinator interactions in the temperate forests of north-west Patagonia, Argentina. J Ecol 94:171–180

Nielsen A, Bascompte J (2007) Ecological networks, nestedness and sampling effort. J Ecol 95:1134–1141

Oksanen J, Kindt R, Legendre P et al (2006) Vegan: community ecology package version 1.8-3. R package URL http://www.R-project.org

Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Divers Distrib 8:181–192

Parker IM, Gilbert GS (2004) The evolutionary ecology of novel plant-pathogen interactions. Annu Rev Ecol Evol Syst 35:675–700

Petit RJ, Bialozyt R, Garnier-Gere P et al (2004) Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. For Ecol Manag 197:117–137

Picard F, Miele V, Daudin JJ, et al (2009) Deciphering the connectivity structure of biological networks using MixNet. BMC Bioinformatics

Pimentel D, Lach L, Zuniga R et al (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65

Prado PI, Lewinsohn TM (2004) Compartments in insect-plant associations and their consequences for community structure. J Anim Ecol 73:1168–1178

Rezende EL, Lavabre JE, Guimaraes PR et al (2007) Nonrandom coextinctions in phylogenetically structured mutualistic networks. Nature 448:925–928

SAS/STAT (2000) SAS Institute Inc., SAS OnlineDoc, version 8. SAS Institute Inc, Cary

Sugiura S, Yamaura Y, Makihara H (2008) Biological invasion into the nested assemblage of tree-beetle associations on the oceanic Ogasawara Islands. Biol Invasions 10:1061–1071

Thompson JN (2006) Mutualistic webs of species. Science 312:372–373

Thuiller W, Richardson DM, Pysek P et al (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biol 11:2234–2250

Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of host-parasitoid food webs. Nature 445:202–205

Vacher C, Piou D, Desprez-Loustau M-L (2008a) Architecture of an antagonistic tree/fungus network: the asymmetric influence of past evolutionary history. PLoS ONE 3:e1740

Vacher C, Vile D, Helion E et al (2008b) Distribution of parasitic fungal species richness: influence of climate versus host species diversity. Divers Distrib 14:786–798

Valéry L, Fritz H, Lefeuvre J-C et al (2008) In search of a real definition of the biological invasion phenomenon itself. Biol Invasions 10:1345–1351

Vermeij GJ (1996) An agenda for invasion biology. Biol Conserv 78:3–9

Vitousek PM, Dantonio CM, Loope LL et al (1996) Biological invasions as global environmental change. Am Sci 84:468–478

Wilson JB, Steel JB, Dodd ME et al (2000) A test of community reassembly using the exotic communities of New Zealand roadsides in comparison to British roadsides. J Ecol 88:757–764

Worner SP, Gevrey M (2006) Modelling global insect pest species assemblages to determine risk of invasion. J Appl Ecol 43:858–867